# Cooperative breeding in reindeer (*Rangifer tarandus*): testing the hypothesized causes of allosuckling and allonursing.

Sacha C. Engelhardt

A Thesis
In the Department
Of
Biology

Presented in Partial Fulfillment of the Requirements
For the Degree of
Doctor of Philosophy (Biology) at
Concordia University
Montreal, Quebec, Canada

March 2016

**CONCORDIA UNIVERSITY**

**School of Graduate Studies**

This is to certify that the thesis prepared

By: Sacha C. Engelhardt

Entitled: **Cooperative breeding in reindeer (*Rangifer tarandus*): testing the hypothesized causes of allosuckling and allonursing.**

and submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy (Biology)

complies with the regulations of the University and meets the accepted standards with respect to originality and quality.

Signed by the final examining committee

____________________________________________ Chair
Dr. J. Kornblatt

____________________________________________ External examiner
Dr. E. Vander Wal

____________________________________________ External to Program
Dr. J. Pfaus

____________________________________________ Examiner
Dr G. Brown

____________________________________________ Examiner
Dr J. Grant

____________________________________________ Thesis Supervisor
Dr R. Weladji

Approved by ____________________________________________
Dr. S. Dayanandan, Graduate Program Director

April 7th , 2016 ____________________________________________
Dr. A. Roy, Dean, Faculty of Arts and Science

# Abstract

**Cooperative breeding in reindeer (*Rangifer tarandus*): testing the hypothesized causes of allosuckling and allonursing.**

**Sacha C. Engelhardt, Ph.D.**

**Concordia, 2016**

Cooperative breeding is a social system in which members of the social group provide parental care to the offspring of other parents. The suckling by offspring from females other than their mother is referred to as allosuckling. The provision of milk to the offspring of other mothers is referred to as allonursing. Allonursing is often believed to have evolved by kin-selection, however, other causes have been hypothesized. My thesis examines the misdirected parental care, kin-selection, reciprocity, milk evacuation, improved nutrition, compensation hypotheses, and these hypotheses can co-occur and influence each other. Using reindeer (*Rangifer tarandus*) as a model species, behavioural observations were collected in the field in 2012 and 2013. Allosuckling and allonursing were common in reindeer, and most mothers allonursed and most calves allosuckled. Reindeer calves stole milk, and mothers discriminated their offspring from the offspring of others. Mothers exchanged allonursing at the group level and at the dyadic level, which supported the reciprocity hypothesis. Mothers did not allonurse while their offspring was still attempting to allosuckle, which did not support the milk evacuation hypothesis. Percentage of mass gain and mass at the end of the study increased as the number of allosuckling bouts increased, and allosuckling was not influenced by low birth mass or measures of insufficient maternal milk supply, which supported the improved nutrition hypothesis but not the compensation hypothesis. Mothers in the closely related group allonursed more often than mothers in the distantly related group, which supported the kin-selection hypothesis at the extremes of genetic relatedness. Given that we initially did not find an effect of genetic relatedness, we suggest that kin-selection alone is not sufficient to explain alloparental care. My thesis provides evidence that allonursing contributions detected can depend upon the research design, and we suggest that the indirect fitness benefits of alloparental care may have been overestimated. The evolution of allonursing in reindeer may have originated from inclusive fitness, but the results of my thesis demonstrate that the direct fitness benefits of milk-theft, reciprocal allonursing and improved nutrition and mass gain maintain allonursing in reindeer.

## Acknowledgements

I first want to thank my doctoral thesis supervisor, Dr. Robert Weladji. I am grateful for your supervision, support, time and patience you dedicated. You always welcomed me in your office. I wish to thank Dr. Øystein Holand, Dr. Knut Røed and Dr. Mauri Nieminen for their support, collaborations and discussions. To all four of you, I will happily remember the discussions we had and time spent together in Northern Finland. I learned a great deal about ecology from all of you.

I wish to thank my committee members, Dr. James Grant and Dr. Grant Brown, for your helpfulness and availability. I knocked on your doors and asked some questions, and you welcomed me in your office and discussed the matters at hand. I wish to thank the external committee members for reading and reviewing this thesis. Many thanks to all the reviewers of my articles. Your reviews improved my thesis.

This thesis required the logistical support of the Reindeer Research Station (Porontukimusasema) and the Kutuharju Field Reindeer Research Station. I wish to thank Heikki Törmänen, Jukka Siitari, Mika Tervonen, the late Veijo Tervonen, Sari Siitari, Ilmo Pehkonen and Erkki Paltto. I had good experiences with you and many laughs.

I wish to thank my field assistants: Covadonga M. de Rioja, Blanca González Herrero, Nina Marcin, Rosina K. Ehmann and Dr. Stefania Uccheddu. We worked long hours and collected much data, and we had some very good times together. It was a pleasure making camp fires for you and teaching you how to climb trees.

I wish to thank the Quebec Centre for Biodiversity Science for the awards granted to me. Additionally, it was a great pleasure to work with the QCBS student network and to be part of the QCBS' scientific and executive committees.

Great thanks must be given to the Fonds de Recherche du Québec – Nature et Technologies (FRQNT) for awarding me scholarships to conduct this thesis. Great thanks must be given to the The Natural Sciences and Engineering Research Council of Canada (NSERC) for granting Dr. Robert Weladji an NSERC Discovery Grant, without which this doctoral thesis would not be possible. I do want to extend my gratitude and thanks for the funding sources that granted me awards to conduct this thesis: Northern Scientific Training Program (NSTP), Ministère de l'Éducation, de l'Enseignement supérieur et de la Recherche (MEESR) and Concordia International.

I wish to thank the Concordia Biology Department, and its faculty and staff for the support you always so diligently and professionally provided. I wish to thank all the past and present members of Dr. Robert Weladji's lab and Concordia's Biology Department students for interesting discussions and for the many enjoyable experiences I shared with you.

I want to thank my mother, Diane Séguin, and my father, Dr. Christoph-Peter Engelhardt. You supported me throughout my academic studies. You were there when times were proven to be tough. Thank you for your love, parental care and freedom.

And most of all, I need to thank my girlfriend, Averil Parker, for her patience and help, and more so all my friends and extended family for your presence and kind support.

My respect goes out to all of you.

## Contributions of Authors

As first author, I was responsible for the conceptions, designs, set-ups, data collection, data analyses, the writing of manuscripts related to this thesis and the writing of this thesis. I wrote Chapters 1, 2 and 7, and these chapters were improved by the comments of my thesis supervisor and the examiners of my thesis defense. The manuscripts were all co-authored by Dr. Robert Weladji, Dr. Øystein Holand and Dr. Mauri Nieminen. Dr. Robert Weladji advised on experimental designs, reviewed and assisted with the statistical analyses and corrected the manuscripts. Dr. Øystein Holand advised on experimental designs, reviewed and corrected manuscripts. Dr. Mauri Nieminen advised on experimental designs, collected data and provided data. Dr. Knut Røed provided pairwise genetic relatedness data and reviewed and corrected manuscripts. Covadonga M. de Rioja and Rosina K. Ehmann collected data and entered data.

Chapter 3 was published in 2014 in Behavioural Processes, volume 107, pages 133-141, and authors were credited in the following order: Sacha C. Engelhart, Robert B. Weladji, Øystein Holand, Covadonga M. de Rioja, Rosina K. Ehmann and Mauri Nieminen.

Chapter 4 was published in 2015 in Ethology, volume 121, pages 245-259, and authors were credited in the following order: Sacha C. Engelhardt, Robert B. Weladji, Øystein Holand, Knut H. Røed and Mauri Nieminen.

Chapter 5 was published in 2016 in Mammalian Biology, volume 81, pages 146-152, and authors were credited in the following order: Sacha C. Engelhardt, Robert B. Weladji, Øystein Holand and Mauri Nieminen.

Chapter 6 was first published online on March 10th 2016 by Journal of Mammalogy (DOI: 10.1093/jmammal/gyw027), and authors were credited in the following order: Sacha C. Engelhardt, Robert B. Weladji, Øystein Holand, Knut H. Røed and Mauri Nieminen.

## Table of Contents

## List of Figures

## List of Tables

## List of Equations

# Chapter 1 General Introduction

## 1.1 Darwin, Parental Care and Altruism

The evolution of parental care was not considered in great detail by Darwin (1871). He inferred the evolution of parental care by natural selection and noted that the origins of parental care lied at the basis of social behaviour. At the time, little was known about the evolutionary history of care:

"With respect to the origin of the parental and filial affections, which apparently lie at the base of the social instincts, we know not the steps by which they have been gained; but we may infer that it has been to a large extent through Natural Selection." (Darwin, 1871, p. 105).

The evolution of altruism (i.e. behaviour that is costly to the actor and beneficial to the recipient; Hamilton, 1964) was one of Darwin's (1859) greatest challenge to his theory of natural selection, and this challenge has been generalized as the problem of altruism (Hamilton, 1964a, 1964b). Darwin (1859) recognized the evolution of eusocial insect colonies as a special difficulty that challenged his theory of natural selection:

"I will not here enter on these several cases, but will confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind. The subject well deserves to be discussed at great length, but I will here take only a single case, that of working or sterile ants. How the workers have been rendered sterile is a difficulty; but not much greater than that of any other striking modification of structure; for it can be shown that some insects and other articulate animals in a state of nature occasionally become sterile; and if such insects had been social, and it had been profitable to the community that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by Natural Selection." (Darwin, 1859, p. 170).

### 1.2 Inclusive Fitness and Kin-selection

Hamilton (1964a) recognized that the classical models of natural selection did not explain the evolution of altruistic behaviour and limited social behaviour to sexual selection and parental care.

Danchin, Cézilly, and Giraldeau (2008) provide an overview of inclusive fitness. Prior to the formalization of inclusive fitness theory, the evolution of altruistic behaviour was at odds with individual fitness (Hamilton, 1964a, 1964b):

"Inclusive fitness may be imagined as the personal fitness which an individual actually expresses in its production of adult offspring as it becomes after it has been first stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual's social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quantities of harm and benefit which the individual himself causes to the fitnesses of his neighbours. The fractions in question are simply the coefficients of relationship appropriate to the neighbours whom he affects."

Stripping all components due to an individual's social environment can lead to the inclusive fitness of breeders, specifically those that only reproduce with the assistance of helpers (e.g. eusocial insects), equalling zero (Creel, 1990). Therefore, Creel (1990) proposed an improved definition of inclusive fitness by replacing "… all components which can be … as due to the individual's social environment" for the per capita average effect (i.e. number of additional direct offspring produced with the help of neighbours divided by the total number of individuals minus the number of direct offspring lost due to neighbours divided by the total number of individuals) of one individual on another individual's production of adult offspring is removed.

Kin-selection can be defined as natural selection maintaining altruistic traits directed towards genetically related kin (Danchin, Cézilly, et al., 2008). Hamilton (1964a, 1964b) explained the evolution of altruistic traits. Hamilton's rule explains how altruistic genes responsible for a social behaviour can be selected for and spread within populations or can be selected against, and that this depends on the effects the social behaviour has on recipient kin (Hamilton, 1964a). Specifically, altruistic traits can spread within populations if the product of the degree of genetic similarity multiplied by the benefit to the recipient is greater than the costs to the bearer of the altruistic genes (Hamilton, 1964a).

### 1.3 Parental Care

There is a large diversity of parental care patterns within taxa and across taxa (Clutton-Brock, 1991; Davies, Krebs, & West, 2012; Smiseth, Kölliker, & Royle, 2012). These patterns can be explained by animals having different physiological and life-history constraints which may predispose one sex to care more, and ecological conditions and mating opportunities influence the costs and benefits of care for each sex (Davies et al., 2012). Therefore, the study of the evolution of parental care improves our understanding of life-history, sex allocation, sociality, cooperation and conflicts within families, the genetic and epigenetic inheritance of traits, and its co-evolution with sexual selection and mating systems (Smiseth et al., 2012).

Parental care is a trait, which is defined as any form of parental behaviour that appears likely to increase the fitness of a parent's offspring (Clutton-Brock, 1991). Parental care is a consequence of selection pressures for individual fitness, and parental care is directed to close kin (Dawkins, 1979). Parental expenditure is the expenditure of parental resources on parental care of one or more offspring (Clutton-Brock, 1991). Trivers (1972) defined parental investment as any investment by the parent in an individual offspring that increases the offspring's chance of surviving, and hence reproductive success, at the cost of the parent's ability to invest in other offspring. The current definition of parental investment is any characteristics or actions of parents that increase the fitness of their offspring at a cost to any component of the parent's fitness (e.g. reduced fecundity, survival, mating success and reproductive success) (Davies et al., 2012). Parental effort is the combined fitness costs that the parent incurs due to the production and care of all offspring in a given biologically relevant period (Smiseth et al., 2012).

There are three main types of conflicts that are interrelated: 1) parent-offspring conflicts over the supply and demand of care, 2) sexual conflicts between male and female parents over who should care and how much care each sex should provide, and 3) conflicts between siblings over how much care each should demand (Davies et al., 2012). Parent-offspring conflicts arise from, and are not restricted to, the optimal parental investment from the point of view of the offspring and the parent, sex ratio conflicts between workers and their queen in social

Hymenoptera, resolution of evolutionary conflict and brood parasitism (Davies et al., 2012). Sibling conflicts include intra- and inter-brood conflicts and siblicide (Davies et al., 2012).

### 1.4 Cooperative Breeding Social Systems

Cooperative breeding is a social system in which members of the social group provide parental care to the offspring of other parents (Cant, 2012; Solomon & French, 1997). Based on this definition, researchers have reported cooperative breeding social systems in shrimp species of the genus *Synalpheus* (Duffy & Macdonald, 2010), hundreds of insects species (Wilson, 1971), 25 arachnid species (Bilde & Lubin, 2011; Salomon & Lubin, 2007), 20-38 (< 0.5 %) fish species (Taborsky, 1984, 2009; Wisenden, 1999), 852 (9%) avian species (Cockburn, 2006) and approximately 2% of mammalian species (Lukas & Clutton-Brock, 2012; Riedman, 1982). Riedman (1982) reported that over 120 mammalian species were cooperative breeders. Lukas and Clutton-Brock (2012) classified 34 and 23 mammalian species as cooperative breeders and communal breeders, respectively, and they sum the number of cooperative breeding mammalian species to 57. Lukas and Clutton-Brock (2012) defined cooperative breeding as breeding females assisted in protecting and feeding their offspring by non-breeding helpers, and they defined communal breeding as breeding females that pool their young and share care and provisioning. The explanation for cooperative breeding being more common in birds than in mammals may be explained by monogamy, territoriality, defense of resources and the methods used to estimate the number of cooperative breeding bird species. There are more monogamous bird species than mammalian bird species, and monogamy is one of the major routes to cooperative breeding in birds (Cornwallis, West, Davis, & Griffin, 2010), mammals (Lukas & Clutton-Brock, 2012) and insects (Boomsma, 2009; Hughes, Oldroyd, Beekman, & Francis, 2008). Most avian (Cornwallis, West, Davis, & Griffin, 2010) and mammalian (Lukas & Clutton-Brock, 2012) cooperative breeders had monogamous ancestors. Territoriality and defence of non-mate resources are more common in birds than in mammals (Greenwood 1980). Brown (1987) estimated at least 222 of 9 016 (~ 2.5%) bird species were cooperative breeders. Cockburn (2006) determined that there were 462 conventional species that were cooperative breeders, 148 that were strongly suspected, and 2 in captivity for a total of 612 species, and then he added 240 unknown species to that total based on the likelihood of natural history habitats.

Thus, the range of cooperative breeders in birds ranges anywhere from 4.9% to 9% (Brown 1987; Cockburn 2006).

Researchers have often used communal and cooperative breeding synonymously (Brown, 1987; Lewis & Pusey, 1997; Solomon & French, 1997), and there is much confusion concerning the terminology in the cooperative breeding literature (Brown, 1987; Solomon & French, 1997). Solomon and French (1997) provide a full discussion of the problems, inconsistencies and confusions with the terminology in the cooperative breeding literature. Brown (1987) used communal breeding instead of cooperative breeding, since cooperation implies accrued fitness benefits. However, researchers have used communal breeding to refer to systems with shared parentage, which would exclude monogamous systems with non-breeding alloparents (Solomon & French, 1997). In addition, communal breeding implies the use of a communal nest or den (Solomon & French, 1997). Solomon and French's (1997) definition of cooperative breeding is not meant to imply a priori fitness benefits.

The individuals that provide alloparental care are referred to as helpers, auxiliaries, alloparents or care-giving individuals (Brown, 1987; Cant, 2012; Solomon & French, 1997). The term helper stems from Skutch's (1935) term helper-at-the-nest, which did not imply fitness benefits for recipient parents or offspring (Brown, 1987; Solomon & French, 1997). Some researchers believe that the terms helper and helping suggest altruistic behaviour (Gilchrist, 2007). However, there are requirements for help to be considered true help as opposed to apparent help (Gilchrist, 2007). Apparent helpers may have gained personal reproductive success, but they provide care for the young of other parents because of an inability to distinguish their own offspring from those of other parents (Gilchrist, 2007). True help (i.e. altruism) is costly to individuals directing help to the offspring of other parents, and it is beneficial to recipients (Gilchrist, 2007). The term auxiliaries is Latin for helpful, which does not distinguish auxiliary from helper (Solomon & French, 1997). I use alloparent, which is defined as an individual engaging in parentlike care of young that have been produced by parents other than the caregiver (Solomon & French, 1997; Wilson, 1975), to avoid fitness implications (Brown, 1987; Gilchrist, 2007; Solomon & French, 1997).

Cooperative breeding is characterized by three distinctive attributes of alloparents: 1) delayed dispersal from the natal group, 2) reproductive suppression (i.e. to keep back, restrain, check without implying which individual controls reproduction by alloparents) (Solomon &

French, 1997), and 3) alloparental care (Solomon & French, 1997). As such, the main questions in cooperative breeding are: Why delay dispersal? Why delay breeding? Why help? (Brown, 1987; Solomon & French, 1997). Alloparents retain the potential to reproduce in the present and in the future (Bourke & Franks, 1995; Cant, 2012), except for some eusocial insect castes that are truly non-reproductive (i.e. no potential to reproduce) (Bourke & Franks, 1995; Wilson, 1971). Alloparents may be non-breeding adults or subadults, or reproductive adults that provide alloparental care (Solomon & French, 1997). In non-breeding adults and subadults, all three attributes of alloparents may be expressed in cooperative breeding social systems (Solomon & French, 1997). Whereas in reproductive adults, only the expression of alloparental behaviour is typically required to consider social groups as cooperative breeders (Solomon & French, 1997). Alloparental care, delayed dispersal and delayed breeding are associated in many species, while in other species, these decisions are independent behavioural decisions (Doerr, Doerr, & Safran, 2007; Ekman, Dickinson, Hatchwell, & Griesser, 2004; Pruett-Jones, 2004). Some alloparents delay dispersal, while others provide alloparental care after dispersing (Pruett-Jones, 2004).

Cooperative breeding social systems can be dichotomized as singular and plural breeding social systems. In singular breeding social systems, a single pair is responsible for all reproduction and subordinate group members do not produce young, whereas in plural breeding social systems, most or all adults within a group produce young of their own (Brown, 1987; Creel & Waser, 1997). The majority of cooperative breeding social systems can be classified as singular breeders in most taxa, as exemplified by most eusocial cooperative breeding isopterans and formicans, most cooperative breeding carnivorans and 89% of cooperative breeding birds (Brown, 1987; Creel & Waser, 1997; Wilson, 1971). However, this dichotomization is an oversimplification. Singular and plural breeding systems are better conceptualized as extremes of a continuum of reproductive suppression (Mumme, 1997). Species of cooperative breeding social systems occupy positions on this continuum of reproductive suppression (Mumme, 1997). Complete reproductive suppression, along with a high skew in reproductive success and singular breeding, is at one extreme of the continuum, whereas no reproductive suppression, along with a low skew in reproductive success and plural breeding, is at the other extreme (Mumme, 1997). However, the positioning of species along this continuum of reproductive suppression does not take into account intraspecific variation in reproductive suppression (Mumme, 1997).

Truly obligate cooperative breeding bird and mammalian species are rare, and one example is the white-winged chough, *Corcorax melanorhamphos* (Pruett-Jones, 2004). White-winged chough breeders must have at least two non-breeding alloparents to breed successfully (Heinsohn & Legge, 1999). The diet (soil invertebrates) and habitat (hard pan soil) are selective pressures for obligate cooperative breeding (Pruett-Jones, 2004), since offspring have limited foraging skills and have a learning to forage period that lasts 4 years (Heinsohn, Cockburn, & Cunningham, 1988). In nearly all species, breeding pairs, capable of successfully raising offspring without alloparents, occur at varying frequencies within populations (Pruett-Jones, 2004).

See Chapter 2 for a literature review of cooperative breeding social systems. I review evolutionary conflicts, routes to cooperative breeding, delayed dispersal, delayed breeding and alloparental care. I added a literature review of cooperative social systems, because it is important to consider allosuckling and allonursing in the context of alloparental care and cooperative breeding social systems.

## 1.5 Allosuckling and Allonursing

Lactating females providing milk to the offspring of other mothers is referred to as allonursing, and the suckling by offspring from females other than their own mother is referred to as allosuckling. Allonursing and allosuckling are types of alloparental care in cooperative breeding social systems (Roulin, 2002). To understand allosuckling and allonursing, I first have to introduce lactation.

### *1.5.1 Lactation*

Vaughan, Ryan and Czaplewski (2011) define lactation as the synthesis and secretion of milk to nourish the young. Lactation is a defining characteristic of mammals (Vaughan et al., 2011). Milk is produced by the mammae, which are specialized skin glands (Feldhamer, Drickamer, Vessey, Merritt, & Krajewski, 2007). The physiology and biochemistry of lactation are complex (Freeman, Kanyicska, Lerant, & Nagy, 2000), and I will provide a brief description of such. Lactation is regulated by hormones and the neuroendocrine system. During gestation, estradiol, progesterone and prolactin effect mammogenesis (i.e. the growth and development of the mammary glands) (Feldhamer et al., 2007; Freeman et al., 2000). Progesterone and stimulatory neurotransmitters indirectly inhibit the secretion of prolactin, and progesterone has an antagonistic effect on estrogen (Freeman et al., 2000). Estrogen indirectly stimulates the secretion of prolactin during gestation (Freeman et al., 2000). However, high concentrations of estrogen inhibit lactogenesis (i.e. the synthesis of milk) (Freeman et al., 2000). After parturition, and after the placenta is ejected, progesterone and estradiol concentrations decrease (Freeman et al., 2000). The decrease in estradiol concentrations signals the anterior pituitary gland to secrete prolactin (Feldhamer et al., 2007).

Suckling stimulates the secretion of prolactin and oxytocin by way of a neuroendocrine reflex (Freeman et al., 2000). Dopamine concentrations decrease as a result of suckling (Freeman et al., 2000). Suckling stimulates the nerve receptors of the teat (Feldhamer et al., 2007; Freeman et al., 2000). The stimulus information is transmitted to the hypothalamus and the posterior pituitary gland, and the pituitary gland secretes oxytocin (Feldhamer et al., 2007). Oxytocin stimulates myofibrils surrounding the mammae's alveoli to release the milk they contain (Feldhamer et al., 2007). The suckling stimulus is required for the maintenance of lactogenesis and milk secretion (Freeman et al., 2000). Prolactin also affects lactogenesis and galactopoiesis (i.e. the maintenance of milk secretion) (Freeman et al., 2000). Following peak milk production, milk production declines throughout lactation, even though suckling continues and milk is secreted (Luick, White, Gau, & Jenness, 1974).

Lactation is the most energetically expensive aspect of mammalian reproduction and increases the energetic costs, metabolic demands, and weight loss of lactating females (Gittleman & Thompson, 1988; König, Riester, & Markl, 1988). Lactating females lose energy and resources during nursing (i.e. lactation is a depreciable form of investment) (Clutton-Brock, 1991). Mothers transfer immunological compounds to their offspring during lactation (e.g. colostrum) (Becker, De Ioannes, León, & Ebensperger, 2007; Newman, 1995). In the first few days or weeks after parturition, milk is the exclusive source of nutrients for new-born mammals (Clutton-Brock, 1991). Lactation can have important implications for the survival and subsequent reproductive success of mothers and their offspring, with greater risks of mortality (Clutton-Brock, Albon, & Guinness, 1989) and lower future fecundity (Clutton-Brock et al., 1989; Huber, Millesi, Walzl, Dittami, & Arnold, 1999) in lactating than non-lactating females. Therefore, lactation is a constraint. Trade-offs have been demonstrated between calf growth and milk production and composition (Gjøstein, Holand, & Weladji, 2004; Landete-Castillejos, García, Molina, et al., 2000; Landete-Castillejos, García, Gomez, Berruga, & Gallego, 2005;

Luick et al., 1974; Oftedal, 1985; White & Luick, 1984), and between survival and reproductive success (Clutton-Brock et al., 1989; Huber et al., 1999). Females may compensate for the loss of energy and resources by increasing their fat stores pre-partum (Dufour & Sauther, 2002), energy intake (e.g. increased food intake) (Bowen, Iverson, Boness, & Oftedal, 2001; Dufour & Sauther, 2002; Oswald & Mcclure, 1990), inter-litter intervals (Clutton-Brock et al., 1989; Oswald & Mcclure, 1990), by decreasing the size of litters (Oswald & Mcclure, 1990), and by decreasing their activity to reduce caloric costs (Dufour & Sauther, 2002; Tardif, 1997).

### *1.5.2 Allonursing Costs*

Allonursing is an additional lactation cost for several species (Roulin, 2002). Females that allonurse can incur costs to their survival, current and future reproductive success, and allonursing may decrease their indirect fitness benefits. Allonursing increases energy expenditure and loss of resources. Allonursing may also increase nursing loads, and females with heavier nursing loads may incur greater risks of mortality and lower future fecundity than those with lighter nursing loads (Clutton-Brock et al., 1989). If allonursing loads are not reciprocated or do not tend towards strong reciprocity, the risks of mortality and future fecundity should increase with heavier allonursing loads than those with lighter allonursing loads. The inclusive fitness of allonursing females can decrease, if genetically unrelated offspring opportunistically steal milk or mothers misdirect their nursing to genetically unrelated offspring (Hayes, 2000; Packer, Lewis, & Pusey, 1992; Roulin, 2002). Allonursing may increase the risk of pathogen transmission between foster and genetic mothers, which implies costs to all allosuckling offspring and allonursing females (Roulin & Heeb, 1999). Pathogen transmission during allonursing could cause haemolitic diseases and infections (Roulin & Heeb, 1999; Roulin, 2002). The transfer of antibodies during allonursing could retard the maturation of offspring (Carlier & Truyens, 1995). Allonursing may decrease amounts of nutrients available to an allonursing female’s own offspring. When the parturition interval between mothers is large, the current reproductive success of allonursing females can decrease because of inter-litter competition for access to milk, and offspring may grow less (König, 1993; Mennella, Blumberg, McClintock, & Moltz, 1990; Sayler & Salmon, 1969; Werboff, Steg, & Barnes, 1970). Infanticide decreases the direct fitness of mothers. Infanticide is common in communally nesting and nursing rodents, and pregnant mothers generally kill one or more of their nesting partner's pups shortly before giving birth (Gerlach & Bartmann, 2002; König, 1994b).

### *1.5.3 Occurrence of Allonursing*

Even though lactation is the most energetically expensive aspect of mammalian reproduction, researchers have reported that allonursing occurs in over 68 mammalian species and across most mammalian families (Hayes, 2000; Packer et al., 1992; Roulin, 2002). Researchers have reported allonursing in communally nesting rodents (Hayes, 2000; Solomon & Getz, 1997), carnivorans, primates and ungulates (Lewis & Pusey, 1997; Packer et al., 1992; Roulin, 2002), cetaceans (see Leung, Vergara, & Barrett-Lennard, 2010) and species that share roosts such as bats (Kerth, 2008; McCracken & Gustin, 1991; Wilkinson, 1992). Researchers have reported spontaneous lactation (i.e. induced allonursing without pregnancy) in many species with or without previous maternal experience in, for example, dwarf mongooses, *Helogale parvula* (Creel et al., 1991), beluga, *Delphinapterus leucas* (Leung et al., 2010), bottlenose dolphins, *Tursiops truncates* (Ridgway, Kamolnick, Reddy, Curry, & Tarpley, 1995), humans, *Homo sapiens* (Richardson, 1975; Ryba & Ryba, 1984). Spontaneous lactation is often directed towards offspring of close kin (Creel et al., 1991; Leung et al., 2010; Richardson, 1975). Animals in captivity allonurse more often than animals in natural populations (Packer et al., 1992; Zapata, Gaete, Correa, González, & Ebensperger, 2009; Zapata, González, & Ebensperger, 2009). Animals with larger litter sizes allonurse more often than animals that produce smaller litters (Packer et al., 1992). Allonursing is more common in polytocous (i.e. giving birth to more than one offspring per parturition) than monotocous species (MacLeod & Lukas, 2014; Packer et al., 1992). Monotocous species tend to allonurse more often when group size is large, while polytocous species tend to allonurse more often when group size is small (Packer et al., 1992). The occurrence of allonursing varies between taxa (Packer et al., 1992). In ungulates, the percentage of nursing bouts that are allonursing bouts ranges from 0.8% in Grevy's zebra, *Equus greyvi* (Olléová, Pluháček, & King, 2012) to 50% in river buffalo, *Bubalus Bubalis* (Murphey, Paranhos da Costa, Da Silva, & de Souza, 1995) (see Gloneková, Brandlová, & Pluháček, 2016). The incidence of allonursing is not greater in singular cooperative breeders, which have greater mean within-group relatedness, than in non-singular cooperative breeders, and the incidence of allonursing is not associated with relatedness in these groups (MacLeod & Lukas, 2014).

### *1.5.4 Allosuckling and Allonursing Hypotheses*

To explain allosuckling and allonursing, researchers have proposed a number hypotheses that can co-occur and influence each other (i.e. non-mutually exclusive hypotheses) (e.g. Packer et al., 1992; Roulin, 2002, 2003; Víchová & Bartoš, 2005).

Alloparental care is often believed to have evolved from inclusive fitness benefits (i.e. kin-selection) (see Table 1.1; Brown, 1987; Emlen, 1997). The 7 studies that supported kin-selection allonursing reported that females associate with and allonurse close kin (e.g. Eberle & Kappeler, 2006; Ekvall, 1998; MacLeod, Nielsen, & Clutton-Brock, 2013), and only 3 of the 7 studies reported that allonursing contributions varied with relatedness (Creel et al., 1991; MacLeod et al., 2013; Pusey & Packer, 1994). In contrast, of the 10 studies that did not supported kin-selection, 9 studies have reported that females that allonurse do not associate more strongly with close kin than with unrelated females and do not preferentially allonurse offspring of close kin (e.g. Gerlach & Bartmann, 2002; Lunn et al., 2000; Wilkinson, 1992). A meta-analysis of the incidence of allonursing in singular cooperative breeders, which have greater mean within-group relatedness than non-singular cooperative breeders, revealed that the incidence of allonursing was not associated with relatedness in these groups (MacLeod & Lukas, 2014). Kin-selection alone may not be sufficient to explain allonursing in cooperative breeding social systems (Clutton-Brock, 2002; Cockburn, 1998). Scientists have proposed alternative explanations for the expression of allonursing (Hayes, 2000; Roulin & Heeb, 1999; Roulin, 2002, 2003; Víchová & Bartoš, 2005).

Allonursing is often believed to have evolved from reciprocity among distantly related individuals (see reciprocity in Table 1.1), since reciprocal allonursing among distantly related females, based on genetic relatedness, increases the direct fitness of the females (Roulin, 2002). Reciprocal altruism is defined as cooperation among non-relatives, and reciprocal altruism is selected for if the recipient returns the exchange (e.g. allonursing) and both individuals accumulate a net benefit (Trivers, 1971). By interacting repeatedly, reciprocal altruism can occur by use of conditional strategies (e.g. tit-for-tat or win-stay, lose-shift) whereby giving an allonursing bout depends on the probability of another interaction being sufficiently high and the outcome of previous solicitations for allonursing by a female's own calf (Rand & Nowak, 2013). Alternatively, reciprocal allonursing may occur among closely related kin, which provides an opportunity for each mother to spread the genes she shares by common descent in the population and to increase her inclusive fitness (Roulin, 2002). If a member of a reciprocal relationship cheats and provides less milk than the other member, reciprocal allonursing may be selected against. Due to the ease of cheating in reciprocal relationships, the benefits of reciprocating should outweigh the costs of cheating for reciprocity to be selected (Axelrod & Hamilton, 1981; Roulin, 2002).

Nearly all allonursing studies have reported no evidence to support reciprocal allonursing (Pusey & Packer, 1994; Roulin, 2002). In addition, there is yet no evidence to support that two females achieve a higher fitness when allonursing reciprocally than when they do not. Some studies, however, have found support for the reciprocity hypothesis. In wild fallow deer, *Dama dama*, the duration of allonursing was exchanged in 4 pairs (possibly mother-daughter pairs, based on observations) of females composed of the 2 oldest females in each of four groups (Ekvall, 1998). These 4 pairs of fallow deer reciprocally allonursed each other's fawn (Ekvall, 1998). In giraffes, *Giraffa camelopardalis*, milk-theft may be tolerated when reciprocal (Gloneková et al., 2016). In communally nesting and nursing Norway rats, *Rattus norvegicus* (Mennella et al., 1990), house mice, *Mus musculus* (Ferrari, Lindholm, & König, 2015; König, 2006) and prairie voles, *Microtus ochrogaster* (Hayes & Solomon, 2004) allonursing tends to be reciprocal when the interval between the first mother's parturition and the second mother's parturition was less than 15 days. However, nursing loads are not equally shared (Hayes & Solomon, 2004; Mennella et al., 1990). When food was limited in a laboratory study of communally nesting and nursing prairie vole sisters, second mothers to produce a litter allonursed more pups per day than the first mother to produce a litter (i.e. the proportion of non-descendant pups nursed per day was greater for the second mother than the first mother) (Hayes & Solomon, 2004). Communally nesting and nursing house mice that form egalitarian reproductive relationships with a familiar female allonurse reciprocally, and tend to wean more pups than solitary breeders (König, 2006). House mice may not share nursing loads equally, even though they reciprocally allonurse (Ferrari et al., 2015).

The misdirected parental care hypothesis postulates that mothers inadvertently transfer milk to offspring that opportunistically steal milk (see misdirected parental care due to milk-theft in Table 1.1), or mothers lack efficient kin-recognition mechanisms (see misdirected parental care due to mismothering in Table 1.1) (Packer et al., 1992; Roulin, 2002). Milk-theft and mismothering are often considered separately (e.g. Brandlová, Bartoš, & Haberová, 2013; Gloneková et al., 2016; Zapata, González, et al., 2009). Of all the allosuckling and allonursing hypotheses, milk-theft and mismothering are the only mutually exclusive hypotheses and researchers assess them as such (e.g. Gloneková et al., 2016; Zapata et al., 2009). The offspring parasitism strategy of milk-theft is adaptive from the point of view of offspring stealing milk (Brandlová et al., 2013; Landete-Castillejos, García, Garde, & Gallego, 2000; Zapata, González, et al., 2009). If offspring steal milk, lactating females should become aggressive towards milk-thieves (Reiter, Stinson, & Le Boeuf, 1978; Zapata, González, et al., 2009). Offspring, therefore, should approach in a way to avoid being detected (Murphey et al., 1995; Zapata, González, et al., 2009) by attempting to steal milk while lactating females are nursing their own offspring (Brandlová et al., 2013). Researchers have proposed that the misdirected parental care hypothesis is maladaptive from the point of view of lactating females, because of a potential reduction in fitness, when mothers transfer milk to unrelated offspring during milk-theft or mismothering (Packer et al., 1992). If lactating females lack efficient kin-recognition mechanisms, lactating females should not reject offspring of other mothers more often than their own offspring, and offspring should approach lactating females without having to avoid detection (Bartoš, Vaňková, Šiler, & Illmann, 2001; McCulloch, Pomeroy, & Slater, 1999). Packer et al. (1992) suggested that in monotocous species, allosuckling was explained by milk-theft because: 1) mothers invest more per offspring in monotocous than polytocous species, and 2) in monotocous species, investing in additional offspring should significantly increase the lactation costs (Packer et al., 1992). Crowding and disturbance are thought to increase the chances of misdirected parental care, which may explain why allonursing is more common in captive than in natural populations (Packer et al., 1992; Roulin, 2002).

Allonursing is often assumed to increase the nutrition, and hence mass gain, of allosuckling offspring (see improved nutrition in Table 1.1), but researchers have only found support for the improved nutrition hypothesis in laboratory rodents (e.g. Hayes & Solomon, 2004; König, 1993; Mennella et al., 1990) and domesticated red deer, *Cervus elaphus* (Landete-Castillejos et al., 2005), which were provided with unlimited access to food. Offspring may, however, allosuckle to compensate for deficiencies (see compensation in Table 1.1). Researchers found support for the compensatory function of allosuckling in 9 studies (8 of domesticated animals and 1 of wild animals) consisting of 6 ungulate species (see Table 5.1of

Chapter 5). Alternatively, allonursing benefits may be neutral (MacLeod, McGhee, & Clutton-Brock, 2015; Pusey & Packer, 1994). Lion, *Panthera leo*, offspring that allosuckled did not gain nutritional benefits (Pusey & Packer, 1994). Meerkat, *Suricata suricatta*, mothers that allonursed did not have litters with greater average emergence mass than mothers that nursed alone, and offspring that received allonursing did not have a greater mass at emergence and survival rate than offspring that did not receive allonursing (MacLeod et al., 2015). When allonursing females associate with close kin or vary their allonursing contributions with genetic relatedness, kin-selection may play a role in the behaviour of offspring that allosuckle to compensate for deficiencies or improve their nutrition and mass gain (Bartoš, Vaňková, Hyánek, & Šiler, 2001). Thus, there may be adaptive benefits of allonursing relative to kin-selection.

As a consequence of an increase in nutrition for all allosuckling offspring, the number of offspring weaned may increase (Solomon & Hayes, 2012). Under laboratory conditions, house mice that form egalitarian reproductive relationships with a familiar female allonurse reciprocally and improve the number of pups weaned compared to solitary breeders and mothers that communally nest and nurse in non-egalitarian reproductive relationships (König, 2006). However, communally nesting and nursing mothers in non-egalitarian reproductive relationships produce fewer offspring than solitary breeders, and reproductive competition reduces the survival of offspring (König, 2006). Under laboratory conditions, wood mice, *Apodemus sylvaticus*, wean more offspring by breeding solitarily than by communally nesting and nursing, and offspring survival is lower in communal nests (Gerlach & Bartmann, 2002). Solitary breeding and communally nesting and nursing mothers did not differ in the number of offspring weaned in feral fat dormice, *Glis glis* (Pilastro, 1992), deer mice, *Peromyscus maniculalus*, and white-footed mice, *Peromyscus leucop* (Wolff, 1994).

Females are thought to allonurse to evacuate surplus milk that their own offspring did not consume (see milk evacuation in Table 1.1). The milk evacuation hypothesis does not apply when a female’s offspring is hungry and attempting to suckle or allosuckle (Roulin, 2002). Allonursing females may evacuate milk to reduce their body mass before foraging, to avoid teat infection and mastitis, and to induce their neuroendocrine system to adjust prolactin concentrations and increase milk production (Wilkinson, 1992). However, there appears to be no data that supports this hypothesis (Solomon & Hayes, 2012).

Females may allonurse to improve their maternal skills (see learning to parent in Table 1.1). According to this hypothesis, inexperienced females should allonurse more than experienced mothers. Females that allonurse to learn to parent may increase their current and/or future direct fitness (Roulin, 2002). Inexperienced spontaneous lactators (Creel et al., 1991) may benefit by learning to parent without the costs of reproduction, but there is no evidence that spontaneous lactators improve their maternal abilities or current and/or future fitness (Roulin, 2002). In callitrichid monkeys, experience with offspring prior to first parturition is important for offspring survival, since offspring of primiparous mothers with experience have higher survival than offspring of primiparous mothers without experience (Tardif, 1997). However, the incidence of allonursing in callitrichid monkeys appears to be low (Smith, Herrera, Buchanan-Smith, & Heymann, 2001). In wild and captive populations of red deer, older mothers allonursed more than younger mothers (Birgersson, Ekvall, & Temrin, 1991; Ekvall, 1998).

Offspring that allosuckle may obtain a greater diversity of antibodies and improve resistance against pathogens (see immunological function of allosuckling in Table 1.1). Immunodeficient laboratory house mice survived and grew in nonsterile conditions only when immunocompetent females allonursed them (Gustafsson, Mattsson, Holmdahl, & Mattsson, 1994). When researchers transferred B-cell deficient offspring to B-cell normal mothers for 16 hours, mothers allonursed the B-cell deficient offspring, which gave a chance to the transferred offspring of ingesting IgG-containing milk (Arvola, Gustafsson, & Mattsson, 2001). Once offspring were adults, spleens were transplanted, and individuals that allosuckled had higher concentrations of serum IgG and splenic B cells and a higher number of Ig-secreting cells in the spleen and bone marrow than individuals who did not allosuckle (Arvola et al., 2001). Antibody concentrations did not differ in offspring that allonursed from mothers with the same or different major histocompatibility complex (MHC) (König, 2006). House mice that allosuckled from mothers with different MHC had intermediate levels of B-cells and T-cells compared to higher concentrations of either B-cells or T-cells in offspring that allosuckled mothers with the same MHC (König, 2006). Therefore, house mice that allosuckle may gain a more variable immunocompetence (König, 2006). Further, the growth of house mice that allosuckled from mothers with different MHC did not differ from those allosuckling from mothers with the same MHC (König, 2006). The transmission of pathogens during allosuckling could reduce the net immunological benefits (Roulin & Heeb, 1999).

The maintenance of lactation depends upon various hormones and continued milk removal (Feldhamer et al., 2007; Freeman et al., 2000). The most important hormone for the synthesis of milk and the maintenance of milk secretion is prolactin (Freeman et al., 2000). As previously mentioned, the suckling of a teat stimulates the nervous system, which stimulates prolactin secretion from the posterior pituitary gland (i.e. a neuroendocrine reflex) (Freeman et al., 2000). When milk stops being removed, temporarily or completely, mammary tissues undergo involution (i.e. mammary tissues change and return to a pre-pregnant state) (Radisky & Hartmann, 2009). Therefore, frequent suckling is required for the maintenance of milk production and secretion (Freeman et al., 2000). If a mother's own offspring does not sufficiently suckle, the mother may allonurse to induce the neuroendocrine system (see neuroendocrine function of allosuckling in Table 1.1). Prolactin also stimulates immunological reactions, improves maternal immunocompetence, and increases the concentration of antibodies in milk (Roulin, 2003). Therefore, supposing that lactating females do not allonurse to induce the neuroendocrine system to adjust and/or maintain prolactin concentrations, allonursing provides benefits. In addition, prolactin is involved in the proximate causation of parental and alloparental care (Angelier & Chastel, 2009; Schoech, Reynolds, & Boughton, 2004; see Chapter 2, section 2.6 Proximate Causation of Alloparental Care ).

Allonursing may be a by-product of group living, when the benefits of living in groups are greater than the costs of allonursing (see by-product of group living in Table 1.1). Several communally nesting rodents also communally nurse, which are separate behaviours under different selection pressures (Hayes, 2000). If allonursing is a by-product of group living: 1) mothers should lack efficient kin discrimination mechanisms and be unable to reject offspring of other mothers sharing a communal nest (Hayes, 2000), and 2) the costs of allonursing should be greater than the costs of solitary nursing (Hayes, 2000). Habitat saturation and clumping of food and nesting resources were proposed as selection pressures on communal nesting in rodents (Hayes, 2000). Enhanced thermoregulation (Hayes, 2000; Sayler & Salmon, 1969), reduced infanticide (König, 2006; Manning, Dewsbury, Wakeland, & Potts, 1995) and defence against predators (Hayes, 2000; Pilastro, 1992) were proposed as selection pressures for philopatry and communal nesting.

**Table 1.1** List of allosuckling and allonursing hypotheses. Predictions for each hypothesis studied are in Chapters 3 to 6.

| Names of hypotheses | Hypotheses |
|---|---|
| Kin-selection | Lactating females preferentially allonurse offspring with whom they share genes by common descent, allowing lactating females to spread their genes in the population and increase their inclusive fitness (Roulin, 2002). |
| Reciprocity | Reciprocal allonursing is hypothesized to occur when two females achieve a higher fitness when nursing each other's offspring to a similar extent than when they do not share milk (Roulin, 2002). |
| Misdirected parental care due to milk-theft | Lactating females inadvertently transfer milk to offspring that opportunistically steal milk (Packer et al., 1992; Roulin, 2002). |
| Misdirected parental care due to mismothering | Lactating females inadvertently transfer milk to offspring, because lactating females lack efficient kin-recognition mechanisms (Packer et al., 1992; Roulin, 2002). |
| Compensation | Offspring may allosuckle to compensate for low birth mass, insufficient maternal milk supply (e.g. high maternal rejection rates, low mass of mother and a large number of allonursing bouts performed by a calf's mother) or inadequate growth (Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005) |
| Improved nutrition | Allosuckling functions to improve offspring |

| | |
|---|---|
| | nutrition, and hence mass gain, by ingestion of non-maternal milk in addition to maternal milk (Packer et al., 1992; Riedman, 1982). |
| Milk evacuation | Mothers allonurse to evacuate surplus milk that their own offspring did not consume (Roulin, 2002; Wilkinson, 1992). |
| Learning to parent | Females allonurse to improve their maternal skills (Roulin, 2002). |
| Immunological function of allosuckling | Allosuckling improves the immunocompetence of offspring by transferring specific immune compounds not possessed by its mother (Roulin & Heeb, 1999). |
| Neuroendocrine function of allosuckling | Mothers allonurse to induce their neuroendocrine system to adjust and/or maintain prolactin concentrations at optimal levels by teat stimulation, if own offspring do not sufficiently stimulate the teats (Roulin, 2003). |
| By-product of group living | Allonursing is an unavoidable consequence of the selection pressures for group living (Hayes, 2000; Pusey & Packer, 1994). |

Allonursing may be better explained by cost constraints (i.e. occurring when the costs are likely the lowest) rather than explained by the likely benefits (MacLeod & Lukas, 2014). Allonursing may have evolved when the costs to females of allonursing additional offspring are low (MacLeod & Lukas, 2014). The incidence of allonursing may be higher in polytocous compared to monotonous species because the costs of transferring milk to an additional offspring are lower in polytocous species, which are adapted to providing milk for multiple offspring (Packer et al., 1992). When lactating females allonurse to evacuate milk, the costs of allonursing are low (Pusey & Packer, 1994; Wilkinson, 1992). Allonursing may be more common in captivity because of easy access to forage, which lowers the costs of allonursing (Packer et al., 1992). When the risk of allonursing a distantly related offspring is low and alloparental care is indiscriminate (i.e. unconditional altruism) (Hamilton, 1964b), the cost of allonursing may be low compared to the indirect fitness benefits. A lack of efficient kin recognition mechanisms implies that the costs of being vigilant to recognize and reject non-descendant kin and distantly related kin may be greater than the loss of milk and potential transmission of pathogens (Roulin, 2002).

The best studied model species for allonursing is the house mouse, and researchers have investigated allonursing under laboratory conditions and in barns. House mice pups did not steal milk (König, 2006). During communal nursing, mothers do not discriminate between their own pup and the pups of others (Ferrari et al., 2015; König, 2006; Manning et al., 1995; but see Penn, 2002 for MHC-dependent mating preferences), which supports the misdirected parental care hypothesis because of a lack of efficient kin recognition mechanisms (Roulin, 2002). House mice can breed solitarily or communally, and solitary breeding can occur even when females reproduce within the same territory, which suggests that mothers do not indiscriminately allonurse (König, 2006). When an egalitarian reproductive relationship is established, house mice communally nest and nurse, and mothers gain direct, mutualistic benefits (i.e. they wean more offspring than non-egalitarian relationships) and allonurse offspring reciprocally (König, 2006). House mice preferentially nest with a familiar relative, but the effect of familiarity overrides the effect of relatedness (König, 2006). In free-ranging house mice, the genetic relatedness of communally nesting females is low (mean ± *SE* = 0.16 ± 0.03; range = 0 to 0.54) (Auclair, König, Ferrari, Perony, & Lindholm, 2014). Allonursing in house mice may have evolved from inclusive fitness benefits, but the direct fitness benefits from egalitarian reproductive relationships among familiar mothers and reciprocal allonursing maintain allonursing (König, 2006). Communal nursing loads are not shared equally, since mothers invest according to the total number of pups in the communal nest (Ferrari et al., 2015). The benefits of reciprocal allonursing may decrease because of exploitation from mothers with larger litters, since mothers with larger litters invest less per weaned offspring than mothers with smaller litters (Ferrari et al., 2015). Communal nursing may be an unavoidable consequence of the selection pressures for communal nesting (i.e. a by-product of group living) (Hayes, 2000). Weidt, Lindholm and König (2014) argued that communal nursing was not a by-product of group living, because females nursed communally in 33% of cases with overlapping nest box use with another female, while in 66% of cases mothers nursed solitarily (Weidt et al., 2014). During the non-reproductive period, high spatial associations predicted which communally nursing partner was chosen (Weidt et al., 2014).

### 1.6 Model Species

Reindeer and caribou, *Rangifer tarandus*, are considered the same species (Røed, 2005). Reindeer refers to wild and domestic animals in Eurasia and to North American reindeer of Eurasian origin, while caribou refers to wild animals in North America (Røed, 2005). According to conventional taxonomic classification of the species, there are eight subspecies (Røed, 2005). Researchers refer to forms based on the ecological adaptations of reindeer/caribou: arctic, tundra, barren-ground, woodland or forest (Røed, 2005). Therefore, I have studied the Eurasian tundra subspecies, *Rangifer tarandus tarandus*. Reindeer are distributed throughout the northern Holartic, and reindeer and muskoxen, *Ovibos moschatus*, are the only two ungulate species that are permanently found in the arctic.

Reindeer belong to the Cervidae family. The reindeer represents the only species of cervids in which both sexes are antlered (Geist, 1999; Melnycky, Weladji, Holand, & Nieminen, 2013). Among ungulate species, sexual size dimorphism is greatest in reindeer, in which the mass of males can attain twice that of females (Geist & Bayer, 1988). The reindeer's social mating system is polygynous. Male reproductive success is highly skewed (Røed et al., 2002; Skogland, 1989) and correlated with body mass, age and dominance status (Røed et al., 2002; Røed, Holand, Gjøstein, & Hansen, 2005). Reproductive skew in females is low. Reindeer mothers and yearling daughters tend to associate throughout the year, except during calving when their associations do not differ from a control sample of unrelated females (Hirotani, 1990). Female reindeer preference for kin, male-male competition and male age influence female association during rut (Djaković et al., 2012). There is no evidence that females avoid inbreeding (Holand et al., 2007) or discriminate between males based on MHC dissimilarities (Djaković, 2012). In addition, there is little evidence to strongly support female mate choice or leaving groups to sample potential mates (Body, 2014).

The mean gestation length of reindeer is 221 days (Mysterud, Røed, Holand, Yoccoz, & Nieminen, 2009). Females are monotocous and give birth in May-June. Parental care is provided by females alone. The sexes segregate by sex during the non-rutting period (Hirotani, 1990). Calves are precocial and follow their mother shortly after birth (Espmark, 1971c). Mothers spend little time grooming their offspring, with the exception of licking the offspring's ano-genital region during nursing (Espmark, 1971c).

Calves are dependent on maternal milk supply until the rumen is developed to digest other sources of food (Luick et al., 1974). Mothers nurse their offspring for up to 26 weeks, and lactation is usually terminated during rut in October (Gjøstein, Holand, & Weladji, 2004; Lavigueur & Barrette, 1992). Calves must grow quickly and have fat deposits to survive winter, and mothers have to transmit a great deal of energy and protein before rut. Researchers have reported that mothers produce on average 99.5 Kg (Gjøstein, Holand, & Weladji, 2004), 57 Kg (Oftedal, 1985) or 118 Kg (Oftedal, 1985) of milk over the entire nursing period. The volume of milk produced peaks within 3-4 weeks postpartum (Gjøstein, Holand, & Weladji, 2004; White & Luick, 1984) and decreases linearly thereafter (Gjøstein, Holand, & Weladji, 2004; White & Luick, 1984). Peak daily energy output is 7006 ± 820 kJ/d, which decreases after the volume of milk production peaks (Gjøstein, Holand, & Weladji, 2004; White & Luick, 1984). This is comparable to other monotocous ungulates (Oftedal, 1984, 1985). Daily energy output declines at a slower rate than the daily volume of milk produced from mid-lactation to the end of lactation (Gjøstein, Holand, & Weladji, 2004; Parker, White, Gillingham, & Holleman, 1990). The energy content per gram increases throughout lactation (51%, Gjøstein, Holand, & Weladji, 2004; 67% Luick et al., 1974). The composition of reindeer milk changes greatly during lactation (Gjøstein, Holand, & Weladji, 2004; Luick et al., 1974). The concentrations of fat and protein increase throughout lactation, while lactose decreases (Gjøstein, Holand, & Weladji, 2004; Luick et al., 1974), and the protein to fat ratio decreases throughout lactation (Gjøstein, Holand, & Weladji, 2004; Luick et al., 1974).

Researchers reported that calves suckled 3 times/hr (Espmark, 1971c) or 1.7 times/hr (Lavigueur & Barrette, 1992) during the first week, and the frequency of suckling decreased throughout the lactation period. The duration of suckling bouts also decreases over time from a mean of 49.3 s (range = 28.5-66.9 s) during the first 20 days to 19.4 s (range = 16.0-24.0 s) between 141-145 days of age (Lavigueur & Barrette, 1992). Reindeer were classified as non-cooperative breeders (Lukas & Clutton-Brock, 2012). Based on Lukas and Clutton-Brock's (2012) definitions of cooperative and communal breeding, reindeer were not cooperative breeders or communal breeders (Lukas & Clutton-Brock, 2012). The definition of communal breeding included plural breeders (Lukas & Clutton-Brock, 2012). However, researchers have reported allosuckling and allonursing in reindeer (Espmark, 1971c; Lavigueur & Barrette, 1992; Marken, 2003), and reindeer mothers are plural breeders. Espmark (1971c) recorded 85 allonursing bouts, where 14 of the 15 mothers allonursed and all calves solicited allosuckling bouts. In another study, 6 of 6 mothers allonursed and each of their calf allosuckled, and there were 290 allonursing bouts (Marken, 2003). And in yet another study, 2 mothers allonursed once and 1 calf allosuckled twice (Lavigueur & Barrette, 1992). Though the occurrence of allosuckling and allonursing have been documented, the hypothesized causes of allosuckling and allonursing were not tested in these studies.

### 1.7 Objectives

The purpose of my thesis is to study allosuckling and allonursing and test hypothesized causes of these behaviours using reindeer as a model species. To achieve these goals, I studied a semi-domesticated population of reindeer, and I tested the misdirected parental care, kin-selection, reciprocity, milk evacuation, compensation and improved nutrition hypotheses. Few studies to date have the necessary behavioural, age, sex, genetic relatedness and mass data to assess multiple hypothesized causes of allosuckling and allonursing. In addition, few studies have assessed more than 2 hypotheses of allosuckling and allonursing. Importantly, even fewer studies of allosuckling and allonursing in large mammals have tested whether research designs influence the detected results. Researchers have often attributed the evolution of cooperative breeding primarily to kin-selection (Brown, 1987; Emlen, 1997), but researchers have also questioned whether the indirect fitness benefits of alloparental care may be overestimated (Clutton-Brock, 2002; Cockburn, 1998). Allonursing may have additional causes than kin-selection (Hayes, 2000; Roulin & Heeb, 1999; Roulin, 2002, 2003; Víchová & Bartoš, 2005). Additionally, few research projects have demonstrated support for the reciprocal allonursing hypothesis (Roulin, 2002). Chapter 3 tests the misdirected parental care and kin-selection hypotheses. Chapter 4 tests the reciprocity hypothesis and interprets the results taking into account the milk evacuation hypothesis. Chapter 5 tests the compensation and improved nutrition hypotheses. Chapter 6 tests kin-selection hypothesis by selecting two experimental groups at two extremes of genetic relatedness.

# Chapter 2 Literature Review of Cooperative Breeding Social Systems

## 2.1 Evolutionary Conflicts

This section is based on a review by Cant (2012). Cooperative breeding social systems are often studied to investigate evolutionary conflict (i.e. conflict that occurs when all interacting individuals cannot simultaneously achieve optimal fitness), resolutions of these conflicts and their effects on group dynamics and behaviour (Cant, 2012). Direct fitness and inclusive fitness of breeders are generally greater than that of non-breeding alloparents (Creel & Creel, 2002; Reyer, 1984). Evolutionary conflict occurs over indirect fitness benefits, reproductive potential, skew and roles and the extent of alloparental contributions (Cant, 2012; Ratnieks, Foster, & Wenseleers, 2006). Dominant breeders may coerce other members to provide alloparental care by harassment, eviction or threat of punishment (Clutton-Brock, 2002). In small groups of cooperative breeding cichlids, *Neolamprologus pulcher*, breeders punished or evicted idle (i.e. experimentally removed) alloparents (Fischer, Zöttl, Groenewoud, & Taborsky, 2014).

Conflicts over reproductive skew in banded mongoose, *Mungos mungo*, become apparent near parturition (Gilchrist, 2006a; Hodge, Bell, & Cant, 2011). Dominant banded mongoose breeders cause abortion by evicting pregnant subordinates (Gilchrist, 2006b). Banded mongoose mothers express extreme birth synchrony (i.e. within 24 hours), and asynchronous litters born first are killed by other mothers (Hodge et al., 2011). However, the survival of litters born after mass birth synchrony is lower than that of litters born during mass synchrony, and researchers suggest that older pups outcompete younger pups of asynchronous litters (Hodge et al., 2011).

Evolutionary conflicts are resolved during the transition from simple (i.e. few or no morphological differences between breeders and workers, no caste polymorphisms among workers, and relatively simple nests and communication systems) to complex (i.e. eusocial) insect social systems (Bourke, 1999). The explanation for the transition from simple to complex social systems in insects may be colony size (Bourke, 1999). In a small colony, the probability that a worker replaces a queen is high, and the reproductive potential of workers is high (Bourke, 1999). As the size of a simple social insect colony increases, the reproductive potential of a worker decreases, and the morphological skews between breeders and workers and among worker casts increase (Bourke, 1999). In social insects, kinship, coercion and constraints are generally combined to limit the effects of evolutionary conflicts and can lead to complete resolution (Ratnieks et al., 2006).

### 2.2 Routes to Cooperative Breeding

The evolutionary transition from solitary breeding to cooperative breeding is generally associated with monogamous ancestors in birds (Cornwallis, West, Davis, & Griffin, 2010), mammals (Lukas & Clutton-Brock, 2012) and insects (Boomsma, 2009; Hughes, Oldroyd, Beekman, & Francis, 2008). Monogamy promotes high relatedness within family groups, which favours the evolutionary transition from solitary breeding to cooperative breeding (i.e. the monogamy hypothesis) (Boomsma, 2009; Cornwallis et al., 2010). Progressive provisioning (i.e. the gradual feeding of developing offspring) and extended parental care are precursors of cooperative breeding in insects, since adult mortality is high and prolonged offspring dependency may lead surviving adults to rear the remaining offspring (e.g. an insurance when a mother dies) (Field, Shreeves, Sumner, & Casiraghi, 2000; Lucas & Field, 2011; Shreeves, Cant, Bolton, & Field, 2003). For example, Lucas and Field (2011) reported that apoid wasp, *Microstigmus nigrophthalmus*, mothers provisioned orphans for at least 2 weeks. A phylogenetic analysis of shrimp species of the genus *Synalpheus* revealed that eusociality arose only in shrimp species that produce non-dispersing larvae, which promotes the aggregation of close relatives (Duffy & Macdonald, 2010). Therefore, kin-structure is important for the evolutionary transition from solitary breeding to cooperative breeding (Cant, 2012). Routes to cooperative breeding are further discussed in sections 2.3 to 2.7.

### 2.3 Why Delay Dispersal?

The evolutionary causes of dispersal are variation in the social environment, variation in the non-social environment and variation in the genetic environment (i.e. inbreeding avoidance and co-adapted genes prompt the avoidance of dispersal over large distances) (Clobert, de Fraipont, & Danchin, 2008). Dispersal can be caused by variation in the social environment, which is due to variation in inter- and intra-sexual and inter-age competition between individuals and variation in competition among close kin (Clobert et al., 2008). Variation in the quality of habitat (e.g. breeding sites, food and predation) varies in space and time and causes dispersal (Clobert et al., 2008). Sex-biased dispersal is common in animals (Brown, 1987; Clobert et al., 2008; Lawson Handley & Perrin, 2007). Dispersal is male-biased in mammals (Greenwood, 1980) and in social Hymenoptera (Johnstone, Cant, & Field, 2012), and dispersal is female-biased in birds (Greenwood, 1980).

The constraints on group living influence delayed dispersal, since delayed dispersal cannot arise without group living (Russell, 2004). For herbivorous ungulates and primates, group living is constrained by foraging competition when individuals selectively forage on dispersed food and by crypsis (Russell, 2004). Ecological conditions constrain dispersal and solitary breeding and promote the formation of groups (i.e. ecological constraints hypothesis) (Selander, 1964). Alternatively, the evolution of cooperative breeding may arise from indirect fitness benefits to offspring that delay dispersal and provide alloparental care (Hamilton, 1964a, 1964b). As group size increases, the fitness of individuals in the group increase because of improved abilities to forage, produce and defend food (Creel & Creel, 2002; Wilson, 1971), to produce mature offspring, and detect or defend against predators (Clutton-Brock, 2002). Selection pressures for delayed dispersal lead to kin structure, which can promote the evolution of cooperative breeding social systems (Hatchwell, 2010).

In insects, other than eusocial insects, the high probability of parent mortality because of predators and parasitoids (Field & Brace, 2004; Strassmann, 1981), and altitude, latitude and length of summer (Field, Paxton, Soro, & Bridge, 2010) are ecological constraints of dispersal and promote phylopatry. In cooperative breeding spiders, juveniles generally delay dispersal before reproduction, and genetic relatedness estimates are high (Johannesen, Lubin, Smith, Bilde, & Schneider, 2007; Jones & Parker, 2002). In cooperative breeding social spiders of the genus, *Stegodyphus*, higher vegetation productivity was positively associated with insect prey biomass, which facilitates delayed dispersal (Majer, Svenning, & Bilde, 2013). In the cooperative spider, *Anelosimus studiosus*, delayed dispersal increased the number and size of captured prey, reduced variation in captured prey, and improved the direct and indirect benefits of both juveniles (e.g. increased survival and faster development) and mothers (e.g. increased survival and shorter inter-brood duration) (Jones & Parker, 2002). Researchers reported that the saturation of breeding substrate (Bergmüller, Heg, & Taborsky, 2005) and predation risk (Heg, Bachar, Brouwer, & Taborsky, 2004) constrained dispersal and promoted cooperative breeding in African cichlids, *Neolamprologus pulcher*.

In birds, habitat saturation (e.g. shortage of suitable breeding habitats) (Koenig, Hooge, Stanback, & Haydock, 2000; Komdeur, 1992), shortage of mates (Pruett-Jones & Lewis, 1990), inadequate foraging skills because of diet and hard soil (Heinsohn & Legge, 1999), predation (Griesser & Ekman, 2004; Griesser, 2003), and higher quality of the natal territory relative to the quality of available territories (Komdeur et al., 1995) constrain dispersal from the natal habitat. Habitat saturation is a selective pressure in cooperative breeding birds, and experimental tests have revealed that lack of vacancies of suitable habitats generally lead to delayed dispersal (Ekman et al., 2004). In birds, delayed dispersal is associated with the future inheritance or budding off of a breeding territory, and it is associated with access to food and mates (Ekman et al., 2004). A phylogenetic analysis revealed that semiarid savanna habitats and temporal variability in rainfall were selective pressures for cooperative breeding in African starlings (Rubenstein & Lovette, 2007).

This paragraph is based on Russell (2004). In mammals, there is some evidence that habitat saturation constrains dispersal (Creel & Macdonald, 1995; Doncaster & Woodroffe, 1993; Lucia et al., 2008), but dispersal decisions can be independent of habitat saturation (Cheeseman, Mallinson, Ryan, & Wilesmith, 1993; Clutton-Brock, 2006; Creel & Creel, 2002). For herbivorous mammals, predation and the distribution of food (e.g. clumped distribution) are selective pressures constraining dispersal, and the costs of dispersal are high because of these two selective pressures (Russell, 2004). In xeric environments, rainfall, distribution of food, and predation are selective pressures constraining dispersal in cooperative breeding mole-rats (Faulkes, Bennett, Bruford, O'Brien, Aguilar, & Jarvis, 1997; Spinks, Jarvis, & Bennett, 2000). For carnivoran mammals, the nature of prey species and the method of obtaining prey are selective pressures that constrain dispersal (Russell, 2004). Carnivoran species that feed on prey species with high reproductive rates and high densities (e.g. insects or rodents) may delay dispersal, and carnivorans species that hunt for large prey tend to delay dispersal (Russell, 2004).

### 2.4 Why Delay Breeding?

Competition for resources that limit breeding, the monopolization of these resources, and a positive relationship between monopolization of these resources and reproductive success are selection pressures for reproductive suppression (Emlen, 1991; Russell, 2004). If dominant individuals suppressing the reproduction of subordinates incur low costs and increases the dominant's direct fitness benefits, selection should favour dominant individuals suppressing the reproduction of unrelated subordinates, unless indirect fitness costs outweigh direct fitness benefits (Creel and Waser, 1997). Therefore, reproductive skew will be high in a system with a dominant individual that can outcompete subordinates and monopolize limited resources that are positively associated with the dominant individual's reproductive success. Reproductive suppression is rare in carnivorans with no dominance hierarchy, while reproductive skew favours dominant breeders with a clear dominance hierarchy (Creel & Waser, 1997). Reproductive skew tends to be low where resources cannot be monopolized and where the association between reproductive skew and monopolization is low (Russell, 2004). Female ungulates generally have low reproductive skew, because: 1) the distribution of food is clumped, 2) access to unrelated male mates is not limited, and 3) female fecundity is low, since most species give birth to one offspring per year (i.e. monotocous) (Russell, 2004). In contrast, reproductive skew is high for male ungulates. Male ungulates can compete and monopolize females, and monopolization of females is strongly associated with reproductive success (e.g. reindeer, see Røed et al., 2002, 2005; Skogland, 1989).

In many species of mammals, fertility is constrained by many variables. Individuals are constrained by being below a mass or age threshold (Albon, Mitchell, & Staines, 1983; Clutton-Brock, 2006; Creel & Creel, 2002). Many avian and mammalian species avoid incest (Koenig & Haydock, 2004). Low concentrations of reproductive hormones in the absence of genetically, unrelated breeders of the opposite sex constrains female fertility in birds (Mumme, 1997; Schoech, Mumme, & Wingfield, 1996) and mammals (Mumme, 1997; Russell, 2004). Dominant individuals may cause stress and induce high glucocorticoid concentrations in subordinate individuals, which is believed to constrain fertility (Russell, 2004). Elevated glucocorticoid concentrations can constrain reproduction (Pottinger, 1999). However, dominant mammalian individuals often have greater glucocorticoid concentrations than subordinates (Carlson et al., 2004; Creel & Creel, 2002; Creel, 2001; Russell 2004), and glucocorticoid concentrations did not differ in dominant and subordinate birds (Schoech et al., 1996).

The presence of dominant individuals constrains breeding (Dengler-Crish & Catania, 2007; Keller & Ross, 1998; Wilson, 1971). In termites, *Cryptotermes secundus*, gene expression of Neofem2 by queens is much greater than by kings and workers, and Neofem2 may be necessary for queens to suppress the reproduction of workers (Korb, Weil, Hoffmann, Foster, &

Rehli, 2009). Inhibition of Neofem2 in queens increased aggression in workers. Aggression is associated with worker reproduction in termites (Korb et al. 2009), and social bees, ants and wasps (Bourke & Franks, 1995). In social insects, queens commonly use pheromones to suppress worker reproduction (Wyatt, 2014).

Reproductive skew may occur by behavioural and/or physiological means (French, 1997; Schoech et al., 2004; van Zweden, 2010). The proximate mechanisms of reproductive suppression of subordinates vary along temporal (i.e. preconception and postconception) and mechanistic (i.e. physiological and behavioural) dimensions (Faulkes & Abbott, 1997; French, 1997; van Zweden, 2010). Intrasexual aggression and harassment of mating are preconception, behavioural mechanisms, and infanticide and poor provisioning are postconception, behavioural mechanisms (Faulkes & Abbott, 1997; French, 1997). Suppression of ovulation and delayed puberty are preconception, physiological mechanisms, and induced abortion and impaired lactation are postconception, physiological mechanisms (Faulkes & Abbott, 1997; French, 1997).

Researchers have used transaction (i.e. reproduction is offered as a reward for alloparental care) and compromise models (i.e. reproductive skew is determined by competitive abilities) to study reproductive skew (Magrath, Heinsohn, & Johnstone, 2004). Concession (Vehrencamp, 1983) and restrain models are transaction models, and they allow for group stability (Magrath et al., 2004). Concession models assume that the dominant breeder has complete control over subordinate reproduction, and the dominant breeder achieves an optimal skew and gains fitness benefits by allowing subordinate reproduction as a compensatory incentive to stay in the group (Magrath et al., 2004). The concession model predicts that the dominant breeder is less likely to allow subordinate reproduction when they are closely related, the ecological constrains on subordinate dispersal are greatest (e.g. the likelihood of subordinate reproduction is low because the costs of dispersal are high), and the subordinate increases the dominant's reproductive success (Magrath et al., 2004). The restraint model uses the same framework as the concession model, but assumes that the dominant can only evict a subordinate instead of having complete control over subordinate reproduction (Magrath et al., 2004). The predictions of the restraint model are opposite to the concession model (i.e. as genetic relatedness, dispersal costs and the effect of the subordinate on the dominant's reproductive success increase, reproductive skew decreases) (Magrath et al., 2004).

The tug-of-war model is a compromise model (Reeve, Emlen, & Keller, 1998), and individuals compete for direct reproduction without regard for group stability and the fitness of group members (Magrath et al., 2004). The tug-of-war model predicts that reproductive skew is mainly determined by the competitive ability of the subordinate (e.g. more competitive subordinates achieve a higher reproductive success) (Magrath et al., 2004). In the tug-of-war model, as genetic relatedness increases, reproductive skew either does not change or decreases slightly because of inclusive fitness benefits, while reproductive skew decreases as genetic relatedness decreases because of increased competition for reproductive success (Magrath et al., 2004). Researchers have used many other models to study reproductive skew, and I will not review them (Magrath et al., 2004).

No model has received unequivocal support, and there are several confounding variables (Magrath et al., 2004). The assumptions of reproductive skew models do not apply to all animals (Clutton-Brock, 1998; Russell, 2004). Older dwarf mongoose are generally less related to the dominant breeders, more likely to disperse and more likely to breed in their natal group, which supports the concession model (Creel & Waser, 1991). However, interpretations of results vary. Individuals that do not breed may lack the presence of unrelated individuals and avoid incest (Clutton-Brock, 2006; Magrath et al., 2004; Russell, 2004), or individuals that breed may be the most difficult for dominant breeders to control because of competition and evolutionary conflict (Cant, 2012; Clutton-Brock, 2006; Magrath et al., 2004). Reproductive skew decreases as genetic relatedness decreases between the beta male and the dominant male and female breeders in white-browed scrubwrens, *Sericornis frontalis* (Magrath et al., 2004). Of the subordinates, only the beta male can gain reproductive success (Magrath et al., 2004). The reproductive skew in white-browed scrubwrens is consistent with the concession and tug-of-war models and incest avoidance (Magrath et al., 2004).

### 2.5 Why Provide Alloparental Care?

Although I use a definition of alloparent that avoids fitness implications (Solomon & French, 1997), alloparental care researchers assess the expression of alloparental care, its costs and benefits and the present and future direct and indirect fitness of the alloparent and the recipient parents and offspring (Mumme, 1997; Russell, 2004; Solomon & Hayes, 2012). Alloparental care can be altruistic, if the behaviour is costly to the alloparent and beneficial to the recipient. Alloparental care is generally thought of as being cooperative (i.e. joint behaviour that is mutually beneficial in terms of fitness for all participants) (Connor, 1995; Le Galliard & Ferrière, 2008). West, Griffin, and Gardner (2007) differ slightly in their definition of cooperation, which they define as a behaviour that provides a benefit to a recipient, and the evolution of the behaviour is dependent on its beneficial effect for the recipient. If the benefits of alloparental care are direct, cooperation can be non-enforced or enforced (Gardner & Foster, 2008; West et al., 2007). Alloparental care may be reciprocal if the altruistic actions are exchanged among individuals, and reciprocity can be direct or indirect (i.e. reputation-based) (West et al. 2007). Unrelated reciprocal alloparents can gain direct fitness benefits (Trivers, 1971). Alloparents may cheat and cooperate less or not at all, while potentially gaining benefits from the cooperation of others (West et al. 2007). Cheaters may be coerced to cooperate, such that cooperation can be enforced (West et al. 2007). The expression of alloparental care may be coerced from alloparents by harassment, sanctions, policing, eviction or threat of punishment (Clutton-Brock, 2002). If the benefits of alloparental care are indirect, cooperation can evolve from unconditional altruism with limited dispersal or conditional altruism with kin discrimination (Hamilton, 1964a, 1964b; Le Galliard & Ferrière, 2008; West et al., 2007).

Both parents and offspring can be recipients of alloparental care. Recipients of alloparental care can benefit from alloparental care (for several examples, see Chapter 2, section 2.7.2.2 Adaptive Hypotheses of Alloparental Care Based on Future Indirect Fitness). Optimal parental investment can be influenced by alloparental care (Hatchwell, 1999). Breeders may reduce their parental investment in the presence of alloparents, while total care does not decrease (Hatchwell, 1999; Russell, 2004; Scantlebury, Russell, McIlrath, Speakman, & Clutton-Brock, 2002). If breeders do not reduce their parental investment, alloparental care is additive (Hatchwell, 1999). The presence or number of alloparents is generally positively correlated with reproductive success (Creel & Creel, 2002; Russell, Brotherton, McIlrath, Sharpe, & Clutton-Brock, 2003; Stacey & Koenig, 1990; Wilson, 1971).

Alloparental care may not benefit the offspring or the parents (Brown, 1987). Alloparents may be selfish if the alloparental care is beneficial for the alloparents and costly for the recipient (Brown, 1987; Clutton-Brock 2002). Some studies have reported negative effects of alloparental care on the fitness of parents (Dugdale, Ellwood, & Macdonald, 2010; Legge, 2000; Woodroffe & Macdonald, 2000). In the laughing kookaburra, *Dacelo novaeguineae*, female alloparents reduced fledgling success, which may be due to both poor alloparental contributions by females and an overvaluation of female alloparental contributions by other group members (Legge, 2000). The effects of the number of non-breeding alloparents on the number of yearlings raised and the number of cubs weaned were negative in the European badger, *Meles meles*, and the body condition (i.e. an index of length and mass) of mothers with alloparents present was significantly poorer than that of mothers without alloparents (Woodroffe & Macdonald, 2000). The number of non-breeding alloparental badgers was negatively related with the probability of cub breeding and with the lifetime reproductive success of cubs (Dugdale et al., 2010). The negative effects of alloparents in the European badger were suggested to be related to intense competition for resources among females (Woodroffe & Macdonald, 2000). Therefore, alloparental care in cooperative breeding social systems may include mutual benefits, reciprocity, coercion, parasitism, kin-selection, selfishness, by-product mutualism and competition (Clutton-Brock, 2002).

Prior to the formalization of inclusive fitness theory (Hamilton, 1964a, 1964b), alloparental behaviour conflicted with delayed breeding and maximizing fitness (Fisher, 1930; Solomon & French, 1997). Following the formalization of inclusive fitness theory (Hamilton, 1964a, 1964b), the study of alloparental behaviour was focused on the adaptive significance of alloparental behaviour in light of inclusive fitness theory (Solomon & French, 1997). The adaptive significance of alloparental care was historically interested in whether: 1) alloparental care was costly to the alloparent, and 2) whether alloparental care was beneficial to the recipient (Brown, 1987; Gilchrist 2007). The determination of the adaptiveness of alloparental care was based on whether the inclusive fitness benefits of the alloparent were greater than the alloparenting costs (Brown, 1987; Gilchrist 2007). Inclusive fitness benefits are accumulated by alloparents along two axes: direct-indirect and present-future (Brown, 1987). Several adaptive and nonadpative hypotheses were later formulated for the study of alloparental behaviour (e.g. Brown, 1987; Emlen, Reeve, Sherman, & Wrege, 1991; Jamieson & Craig, 1987; Jamieson, 1989; Jennions & Macdonald, 1994; Mumme, 1997; Solomon & Hayes, 2012). The alloparental behaviour literature contains proximate and ultimate explanations of why individuals provide alloparental care (Mumme, 1997; Solomon & Hayes, 2012). Studies investigating the proximate causation of alloparental care have focused on the relationships between hormonal changes and alloparental care. Ultimate causations can be categorized based on adaptive and nonadaptive hypotheses (Brown, 1987; Mumme, 1997). Adaptive hypotheses postulate that alloparents gain direct and/or indirect fitness benefits and are favoured by natural selection (Mumme 1997).

To clarify proximate and ultimate causations of behaviour or trait, Tinbergen (1963) introduced four ways of answering questions about behaviour: 1) causation (i.e. mechanisms of a behaviour or trait such as physiological mechanisms, which include hormonal mechanisms and mechanisms of sensory and nervous systems). 2) development (i.e. genetic and developmental mechanisms), 3) adaptive advantage or function (i.e. the direct and indirect fitness consequences of a behaviour or trait and why the causal, genetic and developmental mechanisms have been favoured by natural selection); and 4) evolutionary history or phylogeny (e.g. the evolutionary origin of a behaviour or trait by descent with modification from ancestral species) (Davies et al., 2012). Proximate causation is composed of Tinbergen's (1963) causation and development questions and is concerned with the immediate causes of a behaviour or trait (e.g. how it works, how an individual comes to behave in a particular way during its lifetime, and physiological, neurological and motivational mechanisms) (Danchin, Cézilly, et al., 2008; Scott-Phillips, Dickins, & West, 2011). Ultimate causation is composed of Tinbergen's (1963) adaptive advantage or function and evolutionary history or phylogeny questions and is concerned with the adaptive or evolutionary explanation of a behaviour or trait (e.g. a behaviour or trait’s direct and indirect fitness consequences, and why and how a behaviour or trait evolved) (Danchin, Cézilly, et al., 2008; Davies et al., 2012; Scott-Phillips et al., 2011).

## 2.6 Proximate Causation of Alloparental Care

### *2.6.1 Hormones*

The proximate physiological mechanisms of the expression of alloparental care have been associated with endocrinological changes in alloparents. Studies investigating the endocrinological mechanisms of alloparental care have focused on pituitary hormones (e.g. prolactin and luteinizing hormone), hypothalamic (e.g. oxytocin and vasopressin) and steroid hormones (e.g. corticosterone, testosterone, cortisol, estrogen and progesterone) steroid, and hypothalamic and pituitary hormones (Bales, Pfeifer, & Carter, 2004; Carlson, Russell, et al., 2006; Khan, McNabb, Walters, & Sharp, 2001; Moltz, Lubin, Leon, & Numan, 1970; Solomon & Hayes, 2012). Different hormones may be associated with different types of alloparental care within species (Carlson, Manser, et al., 2006; Carlson, Russell, et al., 2006) and between species. The expression of a type of alloparental care may be associated with endocrinological changes immediately preceding its expression (Carlson, Russell, et al., 2006) or with endocrinological changes over a longer time period (Kreeger, Seal, Cohen, Plotka, & Asa, 1991; Schoech et al., 1996). Alloparental male meerkats that babysat for the day had higher levels of prolactin and lower levels of cortisol before babysitting than at the end of the day, after they babysat (Carlson, Russell, et al., 2006). Therefore, there were changes in the prolactin and cortisol levels during the day, and babysitting was associated with reductions in prolactin levels and with increases in cortisol levels (Carlson, Russell, et al., 2006). Testosterone levels in male meerkats were not associated with the expression of babysitting immediately before or during the day, and prolactin, cortisol and testosterone levels were not associated with the cumulative individual expression of babysitting over approximately one month (Carlson, Russell, et al., 2006). However, the rate of pup feeding by alloparental male meerkats was positively associated with cortisol levels but not prolactin or testosterone levels (Carlson, Manser, et al., 2006).

In dwarf mongoose, the estrogen conjugate levels of pregnant dominant, pregnant subordinate and spontaneously lactating females increased from the first to the second half of the dominant female' gestation period (Creel, Monfort, Wildt, & Waser, 1991). The estrogen conjugate levels did not differ between pregnant dominant and subordinates females, but the estrogen conjugate levels of spontaneously lactating females were lower than those of the pregnant females (Creel et al., 1991). Pregnant subordinates and spontaneously lactating females preferentially allonursed the offspring of the dominant female, with whom they were closely, genetically related (Creel et al., 1991).

Alloparental care may be facilitated by hormones, such as hormonal effects prior to or shortly after parturition. Prenatal developmental endocrine events can influence the expression of alloparental care (Carter & Roberts, 1997). Pregnant prairie voles treated prenatally with exogenous corticosterone had juvenile females and males that tended to express prolonged durations in contact with infants, while male and female newborn infants treated postnatally with exogenous corticosterone expressed significantly shorter durations in contact with infants (Carter & Roberts, 1997). A control group of juvenile females with endogenous corticosterone expressed the same durations in contact with infants as the juvenile females from the prenatal treatment of corticosterone (Carter & Roberts, 1997).

Non-breeding adult and subadult rats and house mice are generally not cooperative breeders (Carter & Roberts, 1997). However, virgin female and male rats and mice can be induced to express alloparental care (e.g. building a nest, licking and retrieving in rats; Rosenblatt, 1967) by continuously exposing them to neonates for 10 to 15 days (i.e. concaveation; see Chapter 2, section 2.7.3 Nonadaptive Hypotheses of Alloparental Care) (Mumme, 1997). The injection of estrogen, progesterone and prolactin reduced the time it took for virgin females to express alloparental care to 35-40 hours (Moltz et al., 1970). The same protocol of hormone injection used for virgin female rats (Moltz et al., 1970) did not decrease the time it took castrated males to express alloparental care, but doubling the dosage of estrogen and/or progesterone did significantly decrease the time it took for the males to express alloparental care (Lubin, Leon, Moltz, & Numan, 1972). Therefore, there are sex-based differences in the hormonal induction of alloparental care in rats (Lubin et al., 1972; Moltz et al., 1970).

Prairie voles spontaneously express alloparental care in response to exposure to infants (Carter & Roberts, 1997). Males injected with both an oxytocin antagonist and an arginine vasopressin antagonist reduced alloparental care and attacked the infants more often, but treatment with either of the antagonists did not interfere with the expression of alloparental care (Bales et al., 2004). Therefore, access to the oxytocin or vasopressin receptors may regulate the expression of alloparental care in prairie voles (Bales et al., 2004).

Increases in prolactin levels have been associated with the expression of alloparental care in cooperative breeding social systems in some species of birds (Angelier, Barbraud, Lormée, Prud'homme, & Chastel, 2006; Brown & Vleck, 1998; Schoech et al., 1996; Vleck & Goldsmith, 1991) and mammals (Asa, 1997; Carlson, Manser, et al., 2006), but not in fish (Bender, Taborsky, & Power, 2008). Over three breeding seasons, the prolactin levels of Florida scrub jay, *Aphelocoma coerulescens*, female and male breeders and non-breeders changed from low levels of prolactin during the pre-nesting phase, steadily increased from the pre-nesting phase to the nest building or laying phases, and reached a maximum during the incubation and nestling phases (Schoech et al., 1996). The prolactin levels of Florida scrub jay females were higher than those of males, and breeders had higher prolactin concentrations than non-breeders (Schoech et al., 1996). The prolactin levels of non-breeders that expressed alloparental e (i.e. provisioning of nestlings) were higher than those of non-breeders that did not express alloparental care (i.e.

non-provisioning of nestling) (Schoech et al., 1996). Prolactin levels of male and female breeders and male alloparents in red-cockaded woodpecker, *Picoides borealis*, did not differ and increased from the pre-breeding phase to a reach a maximum during the egg-laying/incubation phase (Khan et al., 2001). The prolactin levels of the female breeders were higher than those of the male breeders and alloparents during the nestling provisioning phase (Khan et al., 2001). In the arctic fox, *Vulpes lagopus*, prolactin levels of pregnant, non-pregnant and ovariectomized females increased during gestation and reached a peak that coincided with parturition (Mondain-Monval, Møller, Smith, McNeilly, & Scholler, 1985). Prolactin levels of pregnant females were greater than in non-pregnant and ovariectomized females during the late stage of gestation and during lactation (Mondain-Monval et al., 1985). In the grey wolf, *Canis lupus*, prolactin levels of mated, non-mated and neutered individuals increased prior to parturition and reached a peak that coincided with parturition (Kreeger et al., 1991). Mated female grey wolves had higher prolactin levels than all other individuals; non-mated females had higher prolactin levels than mated and non-mated males; mated and non-mated males had similar prolactin levels; and neutered females and males had similar prolactin levels that were lower than all other individuals (Kreeger et al., 1991).

Prolactin levels of alloparental Florida scrub jays (Schoech et al., 1996), red-cockaded woodpecker (Khan et al., 2001), Mexican jays, *Aphelocoma ultramarina* (Brown & Vleck, 1998), grey wolves (Kreeger et al., 1991), arctic foxes (Mondain-Monval et al., 1985) and red foxes, *Vulpes vulpes* (Maurel, Lacroix, & Boissin, 1984) increased prior to parturition and the patterns of prolactin levels of breeders and non-breeding alloparents were similar, which suggest that the increase in prolactin levels was not a simple response to the stimulus of being exposed to offspring (Brown & Vleck, 1998; Mumme, 1997). Alternatively, if increasing prolactin levels were a simple response to the stimulus of being exposed to offspring, the increase in prolactin levels should follow the stimulus, not precede it (Brown & Vleck, 1998) (see Chapter 2, section 2.7.3 Nonadaptive Hypotheses of Alloparental Care).

In common marmosets, *Callithrix jacchus,* prolactin levels did not increase prior to parturition and carrying offspring was not associated with increased cortisol levels (da Silva Mota, Franci, & de Sousa, 2006). Increasing prolactin levels were associated with carrying infants (da Silva Mota & de Sousa, 2000; da Silva Mota et al., 2006; Dixson & George, 1982). A causal connection between prolactin levels and alloparental care has been demonstrated in the common marmoset (Roberts, Jenkins, Lawler, Wegner, & Newman, 2001) and in the Emperor Penguin, *Aptenodytes forsteri* (Angelier et al., 2006). Kidnapping is a type of alloparental behaviour in Emperor Penguin, and the probability of kidnapping is positively associated with prolactin levels (Angelier et al., 2006). The injection of bromocriptine, a dopamine agonist that inhibits prolactin in birds and mammals, eliminated the retrieval of infants or increased the latency to retrieve infants and decreased carrying durations in common marmosets (Roberts et al., 2001) and decreased the occurrence of kidnapping in Emperor Penguins (Angelier et al., 2006). In contrast, in the cooperative breeding cichlid *Neolamprologus pulcher*, prolactin levels were not associated with brood caring by breeders and non-breeding alloparents, and experimental injections of prolactin did not influence brood care propensity of breeders and non-breeding alloparents (Bender et al., 2008).

## 2.7 Ultimate Causation of Alloparental Care

The adaptive hypotheses for alloparental care can be classified based on the alloparent's component of inclusive fitness that is increased: direct fitness, present indirect fitness and future indirect fitness (Brown, 1987). I will provide a brief description of each. Direct fitness (inclusive fitness minus the indirect fitness component) is also known as individual fitness or classical fitness and is composed of a personal component and a kinship component (Brown, 1987). Indirect fitness is the component of inclusive fitness due to effects on nondescendent kin (Brown, 1987; Creel, 1990).

### *2.7.1 Adaptive Hypotheses of Alloparental Care Based on Direct Fitness Benefits*

If providing parentlike care increases an alloparent's probability of future survival and reproductive success, an alloparent may gain direct fitness benefits by recruiting future alloparents (Emlen et al., 1991; Mumme, 1997; Solomon & Hayes, 2012), learning to parent (Emlen et al., 1991; Salo & French, 1989; Solomon & Hayes, 2012), gaining access to group resources (Gaston, 1978; Taborsky, 1985), increasing the group size effects (Emlen et al., 1991), gaining access to mating opportunities (Cockburn, 1998) and gaining social prestige (Zahavi, 1990). The sub-sections on direct fitness benefits are partially based on the reviews by Cockburn (1998), Emlen et al. (1991), Mumme (1997) and Solomon and Hayes (2012).

#### *2.7.1.1 Recruitment of Future Helpers*

It has been proposed that by providing alloparental care, irrespective of genetic relatedness, alloparents can recruit, in the future, the help of offspring they helped (i.e. recruiting future alloparents in the form of delayed reciprocation) (Clarke, 1989; Ligon & Ligon, 1978, 1983). However, the delayed reciprocation of alloparental care hypothesis has not received much support (Curry & Grant, 1990; Solomon & Hayes, 2012), except for a study of green wood hoopoes, *Phoeniculus purpureus* (Ligon & Ligon, 1983). Irrespective of genetic relatedness, alloparental green woodhoopoes recruited the future help of recipient offspring, who helped alloparents acquire a territory and breeding status and subsequently provide alloparental care (Ligon & Ligon, 1983).

#### *2.7.1.2 Acquisition of Skills*

Alloparents may acquire skills that improve their reproductive skills by practicing or copying others or by acquiring skills through prolonged alloparental care (Brown, 1987; Cockburn, 1998). Brown (1987) proposed that alloparents may acquire foraging, territorial, agonistic, predator avoidance, learning to parent and nest building skills. There is little evidence to associate direct fitness benefits for alloparents and their acquisition of foraging, territorial, agonistic, predator avoidance and nest building skills (Cockburn, 1998), and there is little evidence to support that alloparents fail to breed and/or disperse due to a lack of those skills (Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992).

Alloparents may learn to parent, gaining parentlike experience, which may promote successful rearing and increase their own future reproductive success when they are parents (Mumme, 1997). According to the learning to parent hypothesis, alloparental care should be provided by young, inexperienced individuals (Roulin, 2002; Solomon & Hayes, 2012). There is evidence of an association between alloparental care and increased future direct fitness (Salo & French, 1989). Reproductive performance (i.e. time to produce the first litter), pup growth and development (i.e. age of eye opening) were enhanced by alloparental experience in Mongolian gerbil, *Meriones unguiculatus*, pairs (Salo & French, 1989). There is also evidence suggesting that alloparental primates can learn parentlike care (Hrdy, 1976; Lancaster, 1971), and previous allomaternal experience in callitrichid monkeys was associated with increased survival of own offspring (Tardif, 1997). Seychelles warblers, *Acrocephalus sechellensis*, with alloparental experience had greater reproductive success (e.g. higher hatching success, shorter time period to produce first fledgling) than same-aged breeders without alloparental experience prior to breeding (Komdeur, 1996).

#### *2.7.1.3 Access to Group Resources*

Alloparental care may be a payment provided to breeders for access to group resources (Cockburn, 1998; Emlen et al., 1991; Mumme 1997). This is known as the payment of rent hypothesis (Cockburn, 1998). The alloparents benefit by having access to the physical and social (e.g. improved efficiency of foraging and coordinated vigilance) resources of the group (Cockburn, 1998; Emlen et al., 1991). Close, genetic relatedness between alloparents and group members is not required for this hypothesis to be supported. Dominant individuals may harass, punish or evict alloparents to induce alloparenting (Clutton-Brock, 2002). Dominant breeders were more aggressive towards experimentally removed alloparents in superb fairy-wrens, *Malurus cyaneus* (Mulder & Langmore, 1993), and in cichlids, *Neolamprologus pulcher* (Fischer et al., 2014). Cichlid breeders evicted some alloparents (Fischer et al., 2014). Superb fairy wren males are more aggressive towards alloparental males that leave the group for 24 hours during the breeding season than during the non-breeding season, and they coerce alloparents to remain in the territory and provide alloparental care (Mulder & Langmore, 1993).

#### *2.7.1.4 Group Size Effects/Group Augmentation*

Group augmentation benefits can be gained by an alloparent, irrespective of its genetic relatedness with members of the group, if it increases the reproductive success of breeders, thereby increasing group size (Emlen et al., 1991). Living in groups provides fitness benefits, such as improved foraging, communal defence of territory and resources and decreased risk of predation (e.g. vigilance and dilution) (Krause & Ruxton, 2002). Thus, living in groups may increase the group size and enhance the survival and reproductive success of alloparents (Clutton-Brock, 2002; Emlen et al., 1991). However, non-cooperative breeding social groups also benefit from these group fitness effects (Jennions & Macdonald, 1994). Disentangling group fitness effects from fitness benefits due to alloparental care can be difficult, since some of the group fitness benefits are due to increased group size (Jennions & Macdonald, 1994; Krause

& Ruxton, 2002). If alloparents delay breeding due to a shortage of suitable breeding territories, providing alloparental care may increase group size and subsequently territory size, which may increase the probability of an alloparent acquiring (e.g. budding-off) a portion of the territory as its breeding territory (Emlen et al., 1991). In the paper wasp, *Polistes dominulus*, 15-35% of subordinate co-foundresses are unrelated to the dominant co-foundress, who monopolizes most of the reproduction (Leadbeater, Carruthers, Green, Rosser, & Field, 2011; Queller et al., 2000). However, unrelated subordinate paper wasps can inherit the nest and monopolize reproduction (Leadbeater et al., 2011). Lifetime direct offspring production of subordinate paper wasps was greater than that of solitary breeders, generally after inheriting the dominant position in the nest (Leadbeater et al., 2011). Alternatively, delayed breeding due to a shortage of suitable breeding territories may lead to the formation of social coalitions with other group members, with whom the alloparent can disperse and outcompete other breeders for a breeding territory, which may increase the alloparent's probability of breeding (Emlen et al., 1991).

#### *2.7.1.5 Access to Mating Opportunities*

In many cooperative breeding social systems, alloparents may share reproduction within the group (see Table 3 in Cockburn, 1998), gain access to reproduction outside the group (for examples of extra-pair copulations see Table 3 in Cockburn, 1998) or gain access to future mates (Cockburn, 1998; Emlen et al., 1991). Through fertilizations within the group and/or outside the group, there is a lower skew in reproductive success (see Table 3 in Cockburn, 1998). In plural breeding social systems, alloparents are often breeders themselves, and there is a low reproductive skew (Mumme, 1997). Alloparental care by male tessellated darters, *Etheostoma olmstedi*, may have evolved due to female mating preferences for males with nests with young eggs (Stiver & Alonzo, 2010). Male tessellated darters that provide alloparental care for the eggs of unrelated larger males and for their own eggs increase their mating success (Stiver & Alonzo, 2010). Alloparental male tessellated darters prefer nests with eggs over nests without eggs (Farmer & Alonzo, 2008). Alloparental males are smaller than deserting (i.e. non-alloparental) males that spawn at a series of nests, and alloparental and deserting males do not compete for spawning territories (Farmer & Alonzo, 2008).

If alloparents delay breeding due to a shortage of suitable mates, providing alloparental care may promote the acquisition of future mates (Clarke, 1989; Reyer, 1984; Sherley, 1990).

The breeding-aged male bell miners, *Manorina melanophrys*, that provided the most alloparental care in previous broods (and who were unmated and unrelated to a widowed, breeding female) had a higher probability of breeding with the widowed female (Clarke, 1989). Six male riflemen, *Acanthisitta chloris*, that provided alloparental care bred with recipient offspring, and one male rifleman bred with the breeding female after the previous male breeder died (Sherley, 1990). By providing alloparental care, the alloparent demonstrates its parentlike behaviour and promotes its chances of being chosen as a suitable mate in the future (Emlen et al., 1991).

#### *2.7.1.6 Social Prestige*

If male alloparents gain social prestige, irrespective of their genetic relatedness with members of the group, they may influence mate choice and increase their mating opportunities, assuming alloparental care is a handicap and costly (Zahavi, 1990). Under this assumption, only high-quality, healthy males should be alloparents, and alloparents may form alliances (Zahavi, 1990). Alloparents should provide more alloparental care in the presence of an audience, and providing high amounts of alloparental care should increase social status or mating success (Cant, 2012; McDonald, te Marvelde, Kazem, & Wright, 2008). There is no strong evidence to support this hypothesis (Baker, Dietz, & Kleiman, 1993; McDonald et al., 2008; Solomon & Hayes, 2012). Support for this hypothesis is suggestive and based on two results: 1) Arabian babblers, *Turdoides squamiceps* competed to provide alloparental care (Carlisle & Zahavi, 1986), and 2) alloparental male cotton-top tamarins, *Saguinus oedipus*, that carried offspring increased their mating opportunities (Price, 1990). However, in another study, Arabian babblers did not compete to provide alloparental care (Wright, 1999). Infant carrying may be a type of courtship signalling that male carriers may provide competent parental care (Price, 1990).

### *2.7.2 Adaptive Hypotheses of Alloparental Care Based on Indirect Fitness*

Genes for alloparental care may be selected for if alloparents discriminately or indiscriminately direct alloparental care to close kin (Hamilton, 1964b). Alloparents may recognize and preferentially direct alloparental care to close kin (Hamilton, 1964b). The evolution of kin recognition mechanisms (e.g. recognition alleles, phenotype matching, spatial cues, prior association) (Blaustein, 1983; Le Galliard & Ferrière, 2008) could promote the evolution of alloparental care, if kin discrimination functioned to preferentially direct alloparental care towards closely related recipients (Hamilton, 1964b).

Red fire ants, *Solenopsis invicta*, form polygene (i.e. multiple queens) colonies, and only queens that are heterozygous at the locus Gp-9 lay eggs (Keller & Ross, 1998). Workers with at least one copy of the recessive allele for the locus Gp-9 execute queens that are homozygous dominant (Keller & Ross, 1998). All individuals that are homozygous recessive die prematurely (Keller & Ross, 1998). Evidence for recognition alleles is rare (Keller & Ross, 1998; Komdeur, Richardson, & Hatchwell, 2008).

Researchers have reported evidence of differential provisioning of alloparental care to recipients according to their genetic relatedness in several avian species (see Koenig & Haydock, 2004; Komdeur et al., 2008). Kin recognition mechanisms in birds are generally based on vocal cues and templates that are learned by associative learning (Komdeur et al., 2008). In birds and mammals, relatedness between alloparents and recipients explains 10% of the variance in probability of expressing alloparenting, but genetic relatedness and amount of help are generally not related (Cornwallis, West, & Griffin, 2009; Griffin & West, 2003).

Kin discrimination can result from nestmate recognition, but a distinction has to be made between kin recognition and nestmate recognition (D'Ettorre & Lenoir, 2009; van Zweden & D'Ettorre, 2010). Kin recognition is differential behaviour towards conspecifics based on the degree of relatedness, while nestmate recognition is a binary recognition of group membership (van Zweden & D'Ettorre, 2010). Social ants, wasps and termites use cuticular hydrocarbons as nestmate recognition cues, and other nestmate recognition cues (e.g. cuticular fatty acids and esters, and steroids) are used by ants and honeybees (D'Ettorre & Lenoir, 2009; van Zweden & D'Ettorre, 2010).

Alternatively, selection pressures that constrain dispersal can favour genes for alloparental care when alloparents indiscriminately direct alloparental care to recipients that are on average more closely related to the alloparent than the population outside the natal group (Hamilton, 1964b). Sex-biased dispersal can select for indiscriminate alloparenting among the philopatric sex (Cant, 2012). In social Hymenoptera, male-biased dispersal and haplodiploidy select for the expression of alloparental care in females (Johnstone et al., 2012). In birds and mammals, the alloparent tends to be the philopatric sex (Brown, 1987; Cockburn, 1998; Russell, 2004). The sub-sections on indirect fitness benefits are partially based on the reviews by Cockburn (1998), Emlen et al. (1991), Mumme (1997) and Solomon and Hayes (2012).

#### *2.7.2.1 Adaptive Hypotheses of Alloparental Care Based on Present Indirect Fitness*

Alloparental care directed to closely, genetically related breeders may increase the reproductive success of breeders and increase the present indirect fitness of alloparents (Brown, 1987). To support this hypothesis, alloparental care should be directed to close kin, and alloparental care should enhance the production and survival of recipient breeders' offspring (Cockburn, 1998). The evolution of eusocial cooperative breeding in insects was driven by kin-selection among ancestral, monogamous species (Hughes et al., 2008), in which the coefficient of relatedness between alloparents and offspring is approximately 0.5 (Boomsma, 2007). Kin-selection is an important driver of cooperative breeding in socially monogamous mammals (Lukas & Clutton-Brock, 2012) and birds (Cornwallis et al., 2010). Five percent of mammals are socially monogamous (Kleiman, 1977), and coefficients of relatedness within and between litters are high (Lukas & Clutton-Brock, 2012). Of the hypotheses investigating the drivers of cooperative breeding social systems, kin-selection has received the most support and is the most researched (McDonald, 2014).

Of the 9% of avian species categorized as cooperative breeders (Cockburn, 2006), 91% of those species are kin-based, with alloparental care occurring within nuclear families or within kin neighbourhoods (Dickinson & Hatchwell, 2004; Hatchwell, 1999). Alloparental care is directed towards close kin in Florida scrub jays (Mumme, 1992), grey-crowned babblers, *Pomatostomus temporalis* (Blackmore, Peakall, & Heinsohn, 2011), and in moorhens, *Gallinula chloropus* (Leonard, Horn, & Eden, 1989), and experimental removal of alloparents reduced the reproductive success of breeders in Florida scrub jays (Mumme, 1992) and grey-crowned babblers (Brown, Brown, Brown, & Dow, 1982) but not in moorhens (Leonard et al., 1989). Cooperative breeding shrimp and spider species aggregate and interact with close kin (Duffy, 2003; Johannesen et al., 2007). Cooperative breeding spiders generally do not disperse before breeding, which leads high levels of inbreeding and high relatedness estimates (Johannesen et al., 2007; Jones & Parker, 2002). Alloparental care is preferentially directed towards close kin in brown hyenas (e.g. male provisioning of food to offspring, Owens & Owens, 1984) and in golden lion tamarins, *Leontopithecus rosalia* (e.g. infant carrying by males, Tardif, 1997). The number of alloparents is positively correlated with the number of surviving offspring in African wild dogs, *Lycaon pictus* (Courchamp & Macdonald, 2001; Creel & Creel, 2002), and meerkats (Russell, Brotherton, et al., 2003). African wild dogs in packs with ten or more adults raised an average of 10.4 offspring, while packs with nine or less adults raised an average of 3.4 offspring (Creel & Creel, 2002).

#### *2.7.2.2 Adaptive Hypotheses of Alloparental Care Based on Future Indirect Fitness*

By investigating the effect of alloparental care directed to closely, genetically related breeders on the survival and reproductive success of breeders, the future indirect fitness of alloparents can be assessed (Brown, 1987; Mumme, 1997). If alloparental care increases the survival of breeders, the probability that the breeder will reproduce successfully in the future may increase (Khan & Walters, 2002; Lucas, Creel, & Waser, 1997; Ross & MacLarnon, 2000). Alloparental care may lighten the workload of closely, genetically related breeders, and therefore improve the condition of breeders (Mumme, 1997; Solomon & Hayes, 2012), which could increase the survival of breeders (Khan & Walters, 2002; Meade, Nam, Beckerman, & Hatchwell, 2010), decrease parental investment (e.g. reduce energetic demands, Scantlebury et al., 2002; increase foraging Tardif, 1997), decrease mass loss (Achenbach & Snowdon, 2002; Sánchez, Peláez, Gil-Bürmann, & Kaumanns, 1999), increase a breeder's reproductive rate (e.g. decrease inter-birth intervals Mitani & Watts, 1997; Ross & MacLarnon, 2000; Russell, Brotherton, et al., 2003) and increase the length of time a breeder maintains its breeding status (Bales, Dietz, Baker, Miller, & Tardif, 2000).

This paragraph is closely based on work of Solomon and Hayes (2012), who provided a review of the influence of alloparental care on the mass gain of recipient offspring and future indirect fitness of alloparents. Early postnatal growth and mass gain from parturition to weaning/fledgling of offspring is an important predictor of future fitness for avian and mammalian offspring (Lindström, 1999). There is an association between alloparental care and mass gain of recipient offspring in laboratory studies (Solomon, 1991), and field studies (Hodge, 2005; Russell, Young, Spong, Jordan, & Clutton-Brock, 2007) and meta-analyses (Mitani & Watts, 1997; Ross & MacLarnon, 2000). This relationship may increase the future indirect fitness of closely, genetically related alloparents. Offspring provided with both parental and alloparental care in laboratory conditions gained more mass than offspring only provided with parental care in prairie voles (Solomon, 1991). The survival to reproductive maturity was higher for heavier than lighter prairie vole offspring at weaning (Solomon, 1991). Alloparental care increased the growth of recipient meerkat pups, which increased the probability of lifetime reproductive success of recipient offspring (Russell et al., 2007) by increasing the probability of becoming the dominant breeder (Clutton-Brock et al., 2002; Russell et al., 2007) and by decreasing the age of first reproduction by subordinate meerkats (Russell et al., 2007). Two meta-analyses investigating the effects of different amounts of alloparental care provided to recipient primate offspring (Mitani & Watts, 1997; Ross & MacLarnon, 2000). Among primates, offspring of alloparental species grew faster than non-alloparental species (Mitani & Watts, 1997), and offspring of species with higher levels of alloparental care had an earlier age at weaning and grew faster prenatally and postnatally than species with lower levels of alloparental care (Ross & MacLarnon, 2000).

### *2.7.3 Nonadaptive Hypotheses of Alloparental Care*

An epigenetic hypothesis for the evolutionary origins of alloparental care in insects was postulated (West-Eberhard, 1987). The expression of worker or breeder phenotypes in insects was facultative, based on a single genotype, and originated from developmental/ontogenic and/or behavioural circumstances (e.g. broodcare in the presence of larvae by broodless females lacking a mature ovarian egg, and oosorption when oviposition is blocked, West-Eberhard, 1987). In carpenter ants, *Camponotus floridanus*, behavioural castes are regulated and can be reprogrammed by inhibitors of histone acetyltransferases and histone deacetylases in the central brain (Simola et al., 2016). Minor and major carpenter ant workers are morphologically distinct and express distinct foraging and scouting behaviours, with minor workers performing most of the foraging and scouting behaviours (Simola et al., 2016). Inhibition of histone deacetylases increased foraging and scouting behaviours, which were subsequently decreased via inhibition of histone acetyltransferases (Simola et al., 2016). Injection of histone deacetylase inhibitors in the brain of young majors induced minor-like foraging and scouting behaviours for up to 50 days (Simola et al., 2016).

Another epigenetic hypothesis postulated that alloparental care was an expression of a heterochronic change in ontogeny brought about as an unselected consequence of group living, due to a shift in life-history pattern (e.g. delayed dispersal), and the neuroendocrine mechanisms and development responsible for the expression of parental care (Jamieson & Craig, 1987; Jamieson, 1989). In itself, alloparental care is not a trait, but an expression of parental care, which is a more general trait, in a nonparental context (i.e. parentlike behaviour expressed in an alloparental context) (Jamieson & Craig, 1987). These critiques of a priori assumptions that natural selection has influenced alloparental care have pointed out that: 1) all members of a group respond to the begging of offspring by feeding them, 2) alloparents feed related and unrelated offspring, and 3) there is a lack of strong evidence that expressing alloparental care is costly (Jamieson & Craig, 1987; Jamieson, 1989). This hypothesis is supported by induction of parentlike behaviour in virgin rats (Lubin et al., 1972; Moltz et al., 1970; Rosenblatt, 1967) and mice (Carter & Roberts, 1997) when exposed to neonates (i.e. concaveation). Generally, non-breeding rats and mice are not alloparents (Mumme, 1997).

### 2.8 Costs of Alloparental Care

There are short-term costs and long-term costs to alloparenting (Russell, Sharpe, Brotherton, & Clutton-Brock, 2003; Tardif, 1997). Increased energy expenditure, reduced body mass or growth, and decreased foraging efficiency are short-terms costs (Russell, Sharpe, et al., 2003; Tardif, 1997). Fitness costs (e.g. survival and present and future reproductive success) are long-term costs (Russell, Sharpe, et al., 2003; Tardif, 1997). This section is partially based on the reviews by Cockburn (1998), Heinsohn and Legge (1999), Mumme (1997), Sefc (2011), Solomon and Hayes (2012) and Wiesenden (1999).

The short-term energetic costs of alloparenting have been investigated in a few species. Alloparenting may be energetically costly and reduce body mass or growth (Heinsohn & Legge, 1999). Reductions in body mass or growth of alloparents have been reported in the cichlid fish, *Lamprologus brichardi* (Taborsky, 1984), white-winged coughs (Heinsohn & Cockburn, 1994), marmots, *Marmota marmota* (Arnold, 1990), cotton-top tamarins (Achenbach & Snowdon, 2002; Sánchez et al., 1999), and meerkats (Clutton-Brock et al., 1998; Russell, Sharpe, et al., 2003). *Lamprologus brichardi* alloparents invest in broodcare and territorial maintenance and defence, and the growth of alloparents is slower than that of nonterritorial fish (Taborsky, 1984).

Young (i.e. one-year old or less) alloparental white-winged choughs lose body mass in proportion to their contribution to incubation, while older alloparents do not generally lose mass due to incubation (Heinsohn & Cockburn, 1994). Marmots hibernate socially (Arnold, 1990). Subordinates that hibernated without offspring present lost less mass than subordinates that assisted in the thermoregulation of offspring (Arnold, 1990). As group size increased, subordinates without offspring present in the hibernaculum lost less mass compared to subordinates with offspring present in the hibernaculum, who lost increasingly more mass (Arnold, 1990).

In contrast, mean maximum mass loss of captive, adult, male cotton-top tamarins, carrying infants was 5.7% of body mass, and maximum mass loss was not associated with maximum percentage of time spent carrying infants (Achenbach & Snowdon, 2002). In another study, infant carrying led to 7.0% and 2.5% losses of body mass for captive fathers and alloparental male cotton-top tamarins, respectively (Sánchez et al., 1999). The food intake of cotton-top tamarins decreased while carrying infants, but mass loss of males was not correlated with feeding or energetic intake during feeding (Sánchez et al., 1999).

Alloparental meerkats babysit young pups for 24 hours at the natal borrow and forego foraging (Clutton-Brock et al., 1998). During a day of babysitting, a babysitter lost an average of 1.3% of their body mass, while alloparents that did not babysit gained an average of 1.9% of their body mass (Clutton-Brock et al., 1998). During a breeding attempt, alloparents that invested heavily in babysitting and alloparents that invested less heavily lost 3.8% and 0.73% of their body mass, respectively (Clutton-Brock et al., 1998). The probability of breeding during the next breeding event for subordinate meerkat females that invested heavily in alloparental care was lower than for subordinate females that invested less heavily (Russell, Sharpe, et al., 2003).

In contrast to the alloparental costs in meerkats, an alloparental meerkat's contribution to babysitting and pup feeding during a breeding event did not influence its probability of survival or dispersing before the next breeding event (Russell, Sharpe, et al., 2003). Alloparental meerkats use behavioural modifications to minimize the long-term costs of alloparental care (Russell, Sharpe, et al., 2003). Meerkats that invested heavily in alloparental care show greater foraging rates and have greater daily mass gain and growth during the non-breeding period compared to alloparents that invested less heavily (Russell, Sharpe, et al., 2003).

Assessing the effects of alloparental care on fitness requires an investigation of the costs and benefits of alloparental care (Tardif, 1997). However, the fitness costs of alloparental care are less studied than the proximate causes and adaptive and nonadaptive hypotheses of alloparental care. Male tessellated darters provide alloparental care for the eggs of unrelated males and will later breed at the nest (Stiver & Alonzo, 2010). The future potential reproductive success of alloparental tessellated darters may decrease, because the amount of eggs that alloparents can deposit decreases as the amount of eggs deposited by other males increases (Stiver & Alonzo, 2010). Alloparental investment by related, non-breeding pied kingfisher, *Ceryle rudis*, is similar to parental investment in relation to energy expenditure for nest guarding and feeding, while unrelated, non-breeding alloparents invest less energy (Reyer, 1984). Related, non-breeding alloparents have lower chances of surviving and mating the following year than unrelated, non-breeding alloparents (Reyer, 1984). Taking into account the fitness costs and benefits of alloparental care, a comparison of inclusive fitness values in pied kingfishers reported that individuals that delayed breeding had lower inclusive fitness values than first-year breeders (Reyer, 1984). The inclusive fitness of related and unrelated alloparents were similar after 2 years, since related alloparents gained significant indirect fitness benefits, if they survived to the second year, and unrelated alloparents gained direct fitness benefits by becoming breeders in the second year (Reyer, 1984). Despite these gains, alloparental care provided by unrelated pied kingfisher was costly for breeders because of competition for access to mates (Reyer, 1984).

Alloparental care may influence the survival of alloparents. Energetic variation in alloparental investment was associated with survival of alloparents in the stripe-backed wrens, *Campylorhynchus nuchalis* (Rabenold, 1990). When one breeder died, alloparents that invested more energy (i.e. contributed more to the feeding of nestlings) had a 47% chance of surviving to the next breeding season compared to an 83% chance of survival for alloparents that invested less energy (Rabenold, 1990). In contrast, the fitness costs of alloparenting were small in Galápagos mockingbirds, *Mimus parvulus* (Curry & Grant, 1990), and Florida scrub jays (Mumme, 1992). The survival of Galápagos mockingbirds, *Mimus parvulus*, who expressed alloparental care (i.e. feeding nestlings) did not differ from those that did not express alloparental care (Curry & Grant, 1990). The apparent mortality (i.e. disappearance) of non-breeding alloparents that provisioned nestlings and non-breeding individuals that did not provision nestlings did not differ in Florida scrub jays (Mumme, 1992).

Brood parasitism has been reported in fish, bird and insect species, and brood parasites trick others into providing all the parental care (Davies et al., 2012). Alloparental care may be maladaptive due to misdirected parental care when conspecifics or heterospecifics parasitize broods (Wisenden, 1999). Brood parasites may lay fertilized or unfertilized eggs in the nests of others, steal fertilizations (e.g. sneaking), dump their young in another brood (Wisenden, 1999) or be carried into the nest (Thomas & Settele, 2004). The individual fitness of foster parents, recipients of brood parasitism, is often reduced (Tallamy, 2005). Catfish, *Synodontis multipunctatus*, parasitize the broods of mouthbrooding cichlids by releasing zygotes onto the cichlids' spawning surface (Sato, 1986). The catfish hatch first and eat the cichlid young while in the mouth of the female cichlid (Wisenden, 1999). The dumping of free-swimming young in the broods of conspecifics and heterospecifics has been recorded in the mouthbrooding cichlid, *Perissodus microlepis* (Ochi & Yanagisawa, 2005; Sefc, 2011; Yanagisawa, 1985). When one member of a breeding pair of the mouthbrooding cichlid, *Perissodus microlepis*, was experimentally removed, some of the remaining parents dumped their free-swimming young in other broods, leaving the other parents to guard additional free-swimming young (Yanagisawa, 1985). Under natural conditions, only *Perissodus microlepis* males dumped their young in the broods of others, presumably to evade parental roles and remate (Ochi & Yanagisawa, 2005). The costs of alloparenting due to the dumping of young by *Perissodus microlepis* have not been studied, but the costs of mouthbrooding include reduced growth, delayed gonadal recovery and an increase in inter-spawning intervals (Sefc, 2011). Forty percent of cuckoo species are brood parasites and lay their fertilized eggs in the nests of other species (Davies et al., 2012), and the reproductive success of the foster parents is lost when the cuckoo nestling evicts the foster parents' own eggs or nestlings (Sorenson & Payne, 2005). Nest takeovers by large peacock wrasse, *Symphodus tinca*, pirates (i.e. an alternative reproductive tactic) occurs during the last third of the nest's spawning period (van den Berghe, 1988). Pirates parasitize the reproductive success of nesting males in the peacock wrasse (van den Berghe, 1988) and in the sheel-brooding cichlid, *Telmatochromis vittatus* (Ota & Kohda, 2005). Caterpillars of the genus *Maculinea* are brood parasites that secrete cuticular hydrocarbons that mimic those of the ants of the genus *Myrmica*, and they are carried into the ant nest (Thomas & Settele, 2004). The predatory caterpillars feed on grubs (Thomas & Settele, 2004). The cuckoo-like caterpillars are integrated in the ant society, and the nurse ants feed the caterpillars and neglect the broods, which may be fed to the caterpillars (Thomas & Settele, 2004).

The costs of alloparental care are low in several studies. In most fish species, the costs of alloparental care are low relative to endotherm, because of low post-zygotic investment to nourish offspring, low predation risk during brood defence and low incremental cost of defending additional offspring due to high fecundity in fish (Wisenden, 1999). The fecundity of insects is much greater than that of mammals and birds, and the incremental costs of defending additional offspring are low (Wisenden, 1999). The costs to insect recipients of egg dumping are predicted to be low for insects that only guard eggs or whose hatched offspring need little more than defence against predators (Tallamy, 2005). Alloparental costs were low in Galápagos mockingbirds (Curry & Grant, 1990) and Florida scrub jays (Mumme, 1992).

### 2.9 Types of Alloparental Care

There is a wide diversity of types of alloparental care. The types of alloparental care may include the formation of groups for the benefit of the dilution of predation risk, the formation of groups for the benefit of thermoregulation, communal defence of offspring against predators and infanticidal conspecifics, brood care, hygienic behaviours, consumption of alloparents, nest defence, sentineling, babysitting, adoption, food provisioning, carrying, helper-assisted birth and allonursing (Bilde & Lubin, 2011; Lewis & Pusey, 1997; Riedman, 1982; Russell, 2004; Wilson, 1971). The consumption of alloparents is a type of alloparental care exclusive to insects (Wilson, 1971) and social spiders (Grinsted, Breuker, & Bilde, 2014; Jain & Sharma, 2015; Salomon & Lubin, 2007). Helper-assisted birth and allonursing are types of alloparental care exclusively expressed by mammals (Lewis & Pusey, 1997).

Patterns of alloparental care can be classified as depreciable (i.e. vary based on the number of offspring that are cared for) and nondepreciable (i.e. do not vary based on the number of offspring that are cared for) (Clutton-Brock, 1991; Solomon & French, 1997). For example, food provisioning is depreciable, and burrow defence is nondepreciable (Clutton-Brock, 1991).

Alloparental care may be direct or indirect. Direct types of alloparental care are provided directly to the eggs or to offspring following parturition. Fishes provide alloparental care for eggs (e.g. sperm, egg and zygote dumping, zygote stealing and nest take-overs) and for free-swimming offspring (e.g. kidnapping for group augmentation benefits, dumping of young, brood amalgamation, adoption) (Wisenden, 1999). Other types of alloparental care are more indirect, such as nest and burrow building, mobbing of predators, sentineling and territory defence. Shrimp species of the genus *Synalpheus* are obligate inhabitants of tropical sponges (Tóth & Duffy, 2005) and feed from the sponge's feeding current and/or tissues (Duffy, 1996). Alloparents in eusocial shrimp species of the genus *Synalpheus* provide alloparental care in the form of territorial defence of the host sponge (Tóth & Duffy, 2005), and alloparents do not gather and process food for offspring or feed offspring (Duffy, 1996). Cooperative breeding spiders build communal nests and webs and express communal defence against predators (Bilde & Lubin, 2011). In the cooperative spider, *Anelosimus studiosus*, juvenile alloparents build webs and capture prey, and they do not rear offspring (Jones & Parker, 2002).

# Chapter 3 Allosuckling in Reindeer (*Rangifer tarandus*): Milk-theft, Mismothering or Kin-selection?

This chapter is based on the published manuscript: Sacha C. Engelhardt, Robert B. Weladji, Øystein Holand, Mauri Nieminen. 2014. Allosuckling in reindeer (*Rangifer tarandus*): milk-theft, mismothering or kin selection? Behavioural Processes 121: 133-141.

## 3.1 Abstract

Allosuckling, the suckling of offspring from females other than their own mother, has been reported in a number of mammalian species, including reindeer. The causes and function of this behaviour are still being investigated. We monitored 25 doe-calf pairs of semi-domestic reindeer over 10 weeks to test three allosuckling/allonursing hypotheses: (1) milk theft, calves opportunistically allosuckle; (2) mismothering, misdirected maternal care; and (3) kin-selected allonursing. A calf soliciting an allosuckling bout was categorized as non-filial (NF), and a calf soliciting a suckling bout from its mother was categorized as filial (F). We recorded 9757 solicitations, of which 5176 were successful F bouts and 1389 were successful NF bouts. The rejection rates were greater for NF than F calves. The proportions of antiparallel positions adopted were greater for F than NF calves. The odds of an allobout were lower for calves arriving 1st, 3rd, 4th, 5th or 6th than for those arriving 2nd, but the odds did not vary with position adopted and relatedness. Our results provided support to the milk-theft hypothesis, whereas limited support for the mismothering hypothesis was found. Our results did not support the hypothesized kin-selection function of allosuckling in reindeer.

Keywords: Allosuckling; Compensation; Cooperative breeding; Kin-selection; Milk-theft; Mismothering.

## 3.2 Introduction

The main characteristic of cooperative breeding is alloparental care, which is characterized by individuals contributing care to offspring that are not their own (Bergmüller, Johnstone, Russell, & Bshary, 2007). Alloparental care may be adaptive or nonadaptive (Emlen et al., 1991; Jamieson & Craig, 1987; Jamieson, 1989), and proximate and ultimate causes of alloparental care may be based on endocrinological levels of prolactin, future direct fitness, present and future indirect fitness, and social structures providing opportunities for the expression of parent like behaviour in an alloparental context (Mumme, 1997). However, future direct fitness and present and future indirect fitness of alloparents may not be maximized (Gilchrist, 2007; Mumme, 1997). Cooperatively breeding species can also be characterized by a continuum of reproductive skew from singular breeders to plural breeders with costs and benefits for alloparents associated to dispersal, delayed breeding, reproductive suppression, and the provision of care to the offspring of others that may be genetically related to the alloparent (Brown, 1987; Lewis & Pusey, 1997; Mumme, 1997). Additional costs for alloparents include increased energy expenditure, increased risk of predation, reduced foraging time, loss of body mass and reduced survival (Clutton-Brock et al., 1998; Mumme, 1997).

Lactation is the most energetically expensive aspect of mammalian reproduction since lactating females experience physiological stresses such as increases in energetic costs, metabolic demands, and weight loss (Gittleman & Thompson, 1988; König et al., 1988). Lactation can have important implications for the survival and subsequent reproductive success of mothers and their offspring (Clutton-Brock et al., 1989). In the first few days or weeks after parturition, milk is the exclusive source of nutrients for newborn mammals (Clutton-Brock, 1991). The lactation costs of many species also include allosuckling, the suckling of non-filial (NF) offspring from females other than their own mother (Packer et al., 1992). Allonursing, non-offspring nursing, may be a by-product of living in groups (Hayes, 2000; Lewis & Pusey, 1997; Packer et al., 1992). Allosuckling has been observed in the wild and in captivity in over 68 mammalian species that live in groups (Packer et al., 1992; Riedman, 1982), and it is common in plural breeders such as communally nesting rodents (Hayes, 2000; Solomon & Getz, 1997), carnivores, primates and ungulates (Lewis & Pusey, 1997; Packer et al., 1992; Roulin, 2002), and species that share roosts such as bats (Kerth, 2008; McCracken & Gustin, 1991; McCracken, 1984; Wilkinson, 1992).

A number of non-mutually exclusive hypotheses have been proposed to explain the causes and functions of allosuckling and allonursing, which are not well understood. The milk-theft and mismothering hypotheses are maladaptive hypotheses from the point of view of lactating females, while the calf parasitism strategy of milk-theft, the kin-selection, reciprocity, learning to parent, milk evacuation, compensation, neuroendocrine and improving immunocompetence hypotheses of allosuckling and allonursing are adaptive hypotheses (Bartoš, Vaňková, Hyánek, et al., 2001; Hayes, 2000; Landete-Castillejos, García, Garde, et al., 2000;

Packer et al., 1992; Roulin & Heeb, 1999; Roulin, 2002, 2003; Zapata, González, et al., 2009). As per our knowledge, rarely do journal articles include an investigation of more than 2-3 hypotheses, and for exceptions see Bartoš, Vaňková, Šiler, et al. (2001), Eberle and Kapperler (2006), and Ekvall (1998). Offspring have been hypothesized to opportunistically allosuckle, known as milk-theft (Packer et al., 1992). If allosuckling is driven by calves stealing milk, lactating females should reject NF offspring and may become aggressive towards NF offspring, and NF offspring should adopt the perpendicular or parallel positions to allosuckle, instead of the antiparallel position, to avoid being discriminated (Reiter et al., 1978; Zapata, González, et al., 2009). Evidence for the milk-theft hypothesis has been reported, among other studies, in red deer (*Cervus elaphus*) (Landete-Castillejos, García, Garde, et al., 2000), in river buffalo (*Bubalus bubalis*) (Murphey et al., 1995), guanacos (*Lama guanicoe*) (Zapata, González, et al., 2009), bactrian camels (*Camelus bactrianus*) (Brandlová et al., 2013), and multiparous Steller sea lions (*Eumetopias jubatus*) (Maniscalco, Harris, Atkinson, & Parker, 2007). Offspring have been hypothesized to allosuckle due to misdirected maternal care, known as mismothering, suggesting a lack of efficient kin recognition mechanisms by mothers and/or offspring. If allosuckling is caused by lactating females being unable to discriminate their own offspring, or offspring cannot discriminate their own mother, lactating females should not reject NF offspring, and NF offspring should equally adopt the antiparallel, parallel and perpendicular positions to allosuckle (Zapata, González, et al., 2009). Evidence for the mismothering hypothesis has been reported in domestic (*Ovis aries*) and wild (*O. canadiensis*) sheep (Hass, 1990; Welch & Kilgour, 1970), red deer (Bartoš, Vaňková, Šiler, et al., 2001), Hawaiian monk seals (*Monachus schauinslandi*) (Boness, 1990), primiparous Steller sea lions (Maniscalco et al., 2007), and Saharan arrui (*Ammotragus lervia*) (Cassinello, 1999). Allosuckling bouts reported in grey seals (*Halichoerus grypus*) can be accounted for by the lack of efficient kin recognition mechanisms (McCulloch et al., 1999).

Kin-selected allonursing is hypothesized to function by increasing indirect fitness benefits if a lactating female share genes by common descent, allowing her genes to spread in the population and increase her inclusive fitness (Pusey & Packer, 1994; Roulin, 2002). The kin-selection hypothesis received support from allonursing studies of lions (*Panthera leo*) (Pusey & Packer, 1994), dwarf mongooses (*Helogale parvula*) (Creel et al., 1991), fallow deer (*Dama dama*) (Ekvall, 1998), house mice (*Mus domesticus*) (König, 1994a; Wilkinson & Baker, 1988), and the grey mouse lemur (*Microcebus murinus*) (Eberle & Kappeler, 2006). Reciprocal allonursing is hypothesized to occur when two females achieve a higher fitness when nursing each other's offspring to a similar extent than when they do not share milk (Pusey & Packer, 1994; see review in Roulin, 2002).

Lactating females allonurse NF offspring to compensate for growth and/or nutritional deficiency by letting down milk surplus from non-maternal milk, such as in red deer (Bartoš, Vaňková, Hyánek, et al., 2001), cows (*Bos taurus*) (Víchová & Bartoš, 2005), river buffalo (Paranhos da Costa, Andriolo, Simplício de Oliveira, & Schmidek, 2000), and guanacos (Zapata et al., 2010). In contrast to the compensation hypothesis (Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005), allosuckling is hypothesized to increase offspring growth rates and mass at weaning due to improved nutrition by ingestion of milk surplus from non-maternal milk in addition to that which they receive from their own mother (Hayes, 2000; Packer et al., 1992). In studies of laboratory rodents provided with unlimited access to food, allosuckling offspring benefited in mass gain by ingesting milk surplus when compared to non-allosuckling offspring (Hayes, 2000; König, 1993; Werboff et al., 1970). Compared to early-born red deer calves in a control group of only early-born calves, early-born calves in a mixed group of early and late-born calves grew more than predicted by the milk production of their mother (Landete-Castillejos et al., 2005). The early-born red deer calves from a mixed group of calves had a greater possibility of allosuckling from hinds with late-born calves due to red deer mothers producing excess milk during the first 5 weeks of lactation to compensate for milk-theft and to ensure a surplus of milk for their own calves (Landete-Castillejos, García, Garde, et al., 2000; Landete-Castillejos et al., 2005), and red deer mothers appear less able to discriminate their own offspring during early stages of lactation (Vaňková, Bartos, Cízová-Schröffelová, Nespor, & Jandurová, 2001). The learning to parent, milk evacuation, neuroendocrine and improving immunocompetence hypotheses have received little empirical support (Roulin & Heeb, 1999; see review by Roulin, 2002, 2003).

Previous studies of allosuckling in reindeer (*Rangifer tarandus*) had a sample size of six calves (Marken, 2003) or only reported the behaviour (Espmark, 1971c), and neither study tested hypothesized causes or functions of allosuckling. The current study investigated three hypotheses, the milk-theft, mismothering and kin-selection hypotheses, using reindeer as a model species. According to the milk-theft hypothesis, we tested the following predictions. 1) Rejection rates are higher for NF calves than F calves. 2) NF calves arrive after the filial (F) calf (i.e. a calf suckling from its own mother), and as such the odds of a successful allobout are higher for NF calves arriving second than for NF calves arriving first, third, fourth, fifth or sixth. If does can discriminate NF calves and milk-theft is occurring, NF calves should arrive after the doe's own calf is suckling. Increasing numbers of thieves should increase the lactation costs of does thereby reducing the odds of successfully allosuckling, however, ending the F bout decrease the amount of nutrients transferred to a doe's own calf.  Therefore, there may be a trade-off between transferring maximal nutrients to the F calf and increasing allonursing costs, whereby lactating does trade-off maximal milk transfer for the transfer of milk to F calf at the cost of increased nursing loads and transferring milk to 1 NF calf. The odds of successfully allosuckling should be lower for NF calves arriving 1st, 3rd, 4th, 5th, and 6th compared to NF calves arriving 2nd, if milk-theft is occurring. 3) NF calves adopt the parallel and perpendicular positions instead of the antiparallel position. The parallel and perpendicular positions are thought to prevent lactating females from identifying calves by sniffing (i.e. olfaction) the ano-genital region (Bartoš, Vaňková, Šiler, et al., 2001). Therefore, the odds of a successful allobout are higher for calves adopting the parallel or perpendicular positions than for calves adopting the antiparallel position, and the proportions of antiparallel positions adopted are higher for F calves than for NF calves. According to the mismothering hypothesis, we made the following predictions. 4) Rejection rates do not differ between F and NF calves. 5) NF calves can successfully allosuckle by arriving before the F calf. If mismothering is occurring, NF calves should have higher odds of successfully allosuckling by arriving 1st than arriving 2nd, 3rd, 4th, 5th, or 6th since does cannot discriminate NF calves from their own calf. 6) NF calves can adopt any position, since does do not effectively distinguish and discriminate F and NF calves. Therefore, the odds of a successful allobout among calves do not differ based on the position adopted, and the proportions of positions adopted by F and NF calves do not differ. According to the kin-selection hypothesis, we made the following prediction. 7) Females preferentially allonursed calves of related females. Therefore the odds of a successful allobout among calves increase as genetic relatedness, hereafter relatedness, between allonursing females increases.

## 3.3 Materials and Methods

### *3.3.1 Study Species, Study Area, Study Population*

Reindeer/caribou (*Rangifer tarandus*) are ungulates that inhabit the northern part of Eurasia and North America, from the taiga to the high arctic islands (Staaland & Nieminen, 1993). Reindeer are polygynous, with high sexual dimorphism (Geist, 1999). Within the Cervidae family, reindeer are the only species in which females are antlered (Høymork & Reimers, 2002). Females are monotocous, giving birth to one offspring in May-June, and they are plural breeders. Previous studies of allosuckling in reindeer reported that most does and calves allonursed and allosuckled (Espmark, 1971c; Marken, 2003). Reindeer calves are gradually weaned, and lactation cycle usually ends in September to October during rut (Eloranta, Nieminen, & Soppela, 1990; White & Luick, 1984). Under normal range conditions and in the absence of severe food limitation, females reproduce annually during most of their adulthood life (Skogland, 1989). Depending on their body mass, female reindeer can breed in their first autumn (Reimers, 1983), however they most frequently breed at the age of one and a half year (Skogland, 1989; Staaland & Nieminen, 1993).

This study was conducted at the Kutuharju Field Reindeer Research Station near Kaamanen, Finland (69º N, 27º E). This project was in accordance with the Animal Ethics and Care Certificate provided by Concordia University (AREC-2010-WELA) and the Finnish National Advisory Board on Research Ethics. During calving all does of the experimental herd were confined to a small paddock (approximately 10 ha), where data on the birth date, calf sex, and mother-calf assignments were obtained. Date of calving for this study population began on May 4th, 2012, and the 25th parturition occurred on May 13th, 2012. The first 25 calves to be born and their mothers were selected for this study and separated from the herd for 10 weeks. Yearly, the semi-domesticated female reindeer are herded into open fenced paddocks prior to parturition and kept in the paddocks for 3-5 weeks. The study group was separated from the other does, without causing problems or the process being stressful, by opening and closing fence doors. The birth mass of the calves was recorded to the nearest 0.1 Kg. The entire study area was characterized by open birch (*Betula pendula*, *Betula pubescens*) and pine (*Pinus sylvestris*) forests with many bogs and lakes, and the actual paddocks where the doe-calf pairs were confined was characterized by generally flat and open area with birch and pine trees.

This population that has been monitored since 1969 (Eloranta & Nieminen, 1986). Does are slaughtered at the age of 10–12 yrs, which is when they start showing signs of reproductive senescence (Eloranta & Nieminen, 1986). The age of does in the population ranged from 2-13 yrs (mean ± SD = 7.32 ± 3.21 yrs), and the age of does in the study group ranged from 2-13 yrs (mean ± SD = 8.25 ± 2.96 yrs). Mother-calf pairs were assigned within 24 hours of parturition, with the exception of the assignment of 2 mother-calf pairs that were assigned within 48 hours. Collar tags of different colours and with numbers inscribed were fixed to individuals for identification. The study group had access to free running water, natural forage and supplemental feed (i.e. lichen, pellets, and leaves of young shoots of birch). The daily mass of Rasio Mullin-Herkku 2 pellets provided ranged from 80 Kg to 120 Kg, and the pellets were composed of 12.5% water, 3.5% crude fat, 13.3% crude protein, 11.5% crude fiber, 5.6% ash, 0.65% calcium, 0.5% phosphorus, 0.35% magnesium, and 0.35% sodium. To give the study group access to more natural forage, the study group was released in a large enclosure, after daily data collection from June 12th to July 20th. The study group was herded in the paddock the next morning at 6 am, and observations were recorded 60 to 90 minutes after the study group was herded in the paddock. At the end of the study, the study group was transferred back into their large fenced enclosure (approximately 15 $Km^2$) together with the rest of the animals.

Blood samples were obtained from all individuals and analysed by Dr. Knut Røed for 16 DNA microsatellite loci (Røed et al., 2002) to assess maternities and relatedness. Correct mother-calf assignments were analysed with the software CERVUS 3.0 (Kalinowski, Taper, & Marshall, 2007). Pairwise genetic relatedness (hereafter, relatedness) was estimated for all pairwise combinations of all females producing a calf by using the program GenAlEx v 6.4 (Peakall & Smouse, 2006) to generate estimates of methods-of-moments estimator of relatedness, QGM (Queller & Goodnight, 1989), and of methods-of-moments estimator of pairwise relatedness, LRM (Lynch & Ritland, 1999). Within our selected study group, the QGM estimates of relatedness ranged from -0.31-0.50, and the LRM estimates of relatedness ranged from -0.14-0.24. Jackknifing over all the loci generated standard errors for average relatedness values.

### *3.3.2 Behavioural Observations*

Behavioural observations were conducted between 7 am and 8:30 pm from May 4th to July 20th, 2012 over 65 days. All does were habituated to human presence. Observations were conducted by 3 trained observers, inside the paddock, at a distance ranging from 5 to 50 meters from animals. Binoculars were used to reliably record observations of solicitations, agonistic interactions, and identify individuals. Observations of suckling and allosuckling solicitations were collected on data collection sheets using behaviour sampling with continuous recording (Martin & Bateson, 2007). For each solicitation, the occurrence of suckling and allosuckling and the identity of the doe and calves were recorded. A solicitation was scored as an attempt when a calf brought its muzzle within a head from a doe's udder, and the doe did not allow the calf to suckle (e.g. walking away, kicking calf, head threat to calf, chasing calf). A solicitation was scored as a rejection when the calf suckled for less than 5 seconds (Víchová & Bartoš, 2005), and the termination was due to the doe not allowing the calf to suckle any longer. A solicitation was scored as successful (i.e. a bout) when a calf suckled for 5 seconds or more and ended when the calf no longer grasped the doe's udder. We selected a 5 seconds cut-off based on previous suckling and allosuckling research with reindeer (Lavigueur & Barrette, 1992; Marken, 2003). The smelling or licking of the ano-genital region of calves by does was scored as either yes or no. Information concerning which individual ended the solicitation was scored as calf or doe, and information as to how the solicitation ended was scored as walked away, jumped away, chased, kicked the calf or refused to nurse the calf. A rate of rejection for F calves was calculated as the number of unsuccessful F solicitations divided by the total number of F solicitations. A rate of rejection for NF calves was calculated as the number of unsuccessful NF solicitations divided by the total number of NF solicitations. The rejection rates were calculated as a measure of calf discrimination by the does (Zapata, González, et al., 2009).

The actual milk consumption was not measured. Based on behavioural sampling methods, suckling bout frequency and total time suckling were significantly and positively correlated with estimated milk intake, based on mass gain (Cameron, 1998). However, Cameron (1998) argued that assuming milk transfer based on behavioural sampling methods, such as time spent suckling, had inadequate empirical foundation due to these variables explaining less than 15% of the variation in estimated milk intake, having low predictive power, and there was significant heterogeneity between studies and between species. There is only one study in which allosuckling frequency was investigated in relation to actual milk production by mothers and milk intake by calves, and red deer mothers compensated for potential milk-theft by producing an excess of milk in the first 5 weeks after parturition, a period during which calves depend only on maternal milk production and calf mortality is highest, to ensure a surplus of milk for their own calves (Landete-Castillejos, García, Garde, et al., 2000). Milk was readily drawn by hand from each of the 4 udders of reindeer does within 1 minute prior to experimental treatments in a study of milk ejection both in the presence and absence of the doe's own calf and with and without the use of oxytocin (Gjøstein, Holand, Bolstad, Hove, & Weladji, 2004). Short calf stimulation (i.e. 2 seconds) of a doe's udder prior to machine milking significantly increased milk yield, and such short calf stimulation led to complete milk removal without the use of oxytocin (Gjøstein, Holand, Bolstad, et al., 2004). In reindeer, rapid milk ejection is required since calves suckle frequently and for short durations (White & Luick, 1984). Therefore, we assumed that milk transfer occurred, and a similar assumption was made in other studies (Drábková et al., 2008; Gauthier & Barrette, 1985; Paranhos da Costa et al., 2000; Pélabon, Yoccoz, Ropert-Coudert, Caron, & Peirera, 1998; Zapata, González, et al., 2009).

The position adopted during each solicitation was scored as antiparallel (A), parallel (P), or perpendicular (PER) (Bartoš, Vaňková, Šiler, et al., 2001; Zapata, González, et al., 2009). The antiparallel position was scored when the lactating doe had access, by moving her head, to the ano-genital region of a calf: the body and head of a calf were in the opposite direction of the body and head of the doe. The antiparallel position is thought to allow a lactating female to identify a calf by sniffing the calf's ano-genital region (Bartoš, Vaňková, Šiler, et al., 2001; Espmark, 1971c; Källquist & Mossing, 1982). The parallel and perpendicular positions are thought to prevent lactating females from identifying calves by sniffing the ano-genital region of calves (Bartoš, Vaňková, Šiler, et al., 2001). The parallel position was scored when the body and head of a calf were in the same direction as the body and head of the lactating female: the doe did not have access to the calf's ano-genital region. The perpendicular position was scored when the body of a calf was pointing to the side of the lactating doe, at least at a right angle from the doe's body axis: the doe did not have access to the calf's ano-genital region. For F and NF calves, we calculated two rates of antiparallel position adopted by dividing the number of antiparallel positions adopted by the total number of positions adopted.  The first rate was based solely on the number successful solicitations, and the second rate was based on the number of all solicitations.

### *3.3.3 Statistics*

A generalized linear mixed model (PROC GLIMMIX in SAS version 9.3, SAS Institute Inc. Carey, North Carolina, U.S.A.) (SAS, 2012) with a logit link function and binary distribution was conducted to assess the likelihood of a successful allosuckling bout, using the frequency of allosuckling solicitations data, with calf sex, order of arrival, relatedness, birth mass, the interaction of relatedness and birth mass, age of calf in days, age of does in years, and positions adopted as fixed effects. Age of does was added as a covariate since it has been shown in fallow deer and big horn sheep to be positively correlated with allosuckling (Ekvall, 1998; Hass, 1990). Because age of calf has been shown to increase the occurrence of allosuckling in calves of camels (Brandlová et al., 2013), fallow deer (Ekvall, 1998) and red deer (Landete-Castillejos, García, Garde, et al., 2000), we controlled for this effect by including age of calf (in days) as covariate in our model. Birth mass was added as a covariate since calves of cattle cows (Víchová & Bartoš, 2005) and red deer (Paranhos da Costa et al., 2000) with low birth mass performed more allosuckling. Sex of calf was added as a covariate since male river buffalo calves spent more time allosuckling than female calves (Paranhos da Costa et al., 2000), and female cattle calves had a higher incidence of allosuckling than male calves (Víchová & Bartoš, 2005). Mixed models control for repeated measures, and accordingly doe identify and calf identity were entered as random effects, since does allonursed several times a day and over the study period, and calves allosuckled repeatedly during the study period. Type 3 fixed effects were generated, and denominator degrees of freedom were computed separately for each *t* and *F* test by general Satterthwaite approximation, which is based on the adjustment of inflating the estimated variance-covariance matrix of the fixed and random effects (Littell, Miliken, Stroup, Wolfinger, & Schabenberger, 2006). Odds ratio (*OR*) is the ratio of the within group odds and assesses the odds of a particular outcome if a factor or characteristic is present (Szumilas, 2010). Odds ratios (*OR*) with 95% confidence intervals (*CI*) were generated for all fixed effects. Arrival orders 1st, 3rd and 4th for NF calves were compared to NF calves arriving 2nd, and we removed the 5th and 6th orders of arrival since all NF calves arriving 5th or 6th did not successfully allosuckle and represented less than 1% of the arrival orders data when combined. The parallel and perpendicular positions adopted were compared to the antiparallel position. An alpha of 0.05 was adopted.

A one-tailed paired Student's t-test was used to compare logarithm base 10 transformed rejection rates of F and NF calves, and data were transformed to satisfy the assumption of homogeneity of variance. We used a one-tailed Wilcoxon signed rank test to compare the proportions of antiparallel positions adopted by F and NF calves for all solicitations, and we used a one-tailed Mann Whitney U test to compare the proportions of antiparallel positions adopted by F and NF calves for successful solicitations only to compare our results with those of other ungulate species. The assumption of homogeneity of variance was not satisfied for both parametric tests of the proportions of positions adopted, and we used non-parametric tests. Throughout the paper, means are reported with their standard error, unless otherwise stated; and an alpha of 0.05 was adopted.

To describe the extent to which the observers obtained similar results when measuring the same observation simultaneously, we calculated the Pearson correlation coefficients between the 3 pairs of observers for the duration of allonursing, and we calculated the index of concordance between the 3 pairs of observers for the identities of the does and calves observed allonursing (Martin & Bateson, 2007).

### 3.4 Results

All mother-calf assignments from field observations were supported by the DNA analyses. The Pearson correlation coefficients for the duration of observations measured between the 3 pairs of observers were 0.997 (N = 418), 0.969 (N = 217), and 0.999 (N = 45). All identities of does and calves were reliably measured between the 3 pairs of observers (indexes of concordance = 1.0). There were a total of 9757 solicitations, of which 7327 (75.1%) were F and 2430 (24.9%) were NF (Table 3.1). We observed 1389 successful allosuckling bouts. The most frequent category of NF solicitation was composed of 1 F + 1 NF calves soliciting at the same time (54.59%), followed by the composition of 1 F + 2 NF calves soliciting at the same time (24.15%), 1 NF calf soliciting alone (13.52%) and 1 F calf with more than 2 NF calves soliciting at the same time (7.74%) (Table 3.2). Of the 234 NF solicitations where the NF calf arrived first and without other calves only 3 solicitations were successful. There were 3 occurrences with NF calves arriving first, successfully allosuckling and the F calf arriving second. NF calves solicited an allobout by arriving second, after the F calf, on 1482 occurrences, and of those 1142 (77.06%) were successful. Does ended: 96.7% of all F solicitations without NF calves soliciting, 99.7% of all F solicitations with NF calves soliciting, and 99.1% of all NF solicitations.

**Table 3.1** Observed number of solicitation by categories.

| Category | Number | % |
|---|---|---|
| Filial bout | 5176 | 53.05 |
| Allobout | 1389 | 14.24 |
| Filial rejection | 608 | 6.23 |
| Non-filial rejection | 379 | 3.88 |
| Filial attempt | 1543 | 15.81 |
| Non-filial attempt | 662 | 6.79 |

**Table 3.2** Observed number and percentages of filial (F) and non-filial (NF) solicitations of reindeer calves. 1 x F + 1 x NF means that 2 calves solicitated, where one calf was filial and the other calf was non-filial. 1 x F + 2 x NF means that 3 calves solicitated, where one calf was filial and the other two were non-filial.

| Suckling solicitations | Number | % |
|---|---|---|
| F alone | 5830 | 77.11 |
| NF alone | 234 | 3.09 |
| 1 x F + 1 x NF | 945 | 12.50 |
| 1 x F + 2 x NF | 418 | 5.53 |
| 1 x F + 3 x NF | 113 | 1.50 |
| 1 x F + 4 x NF | 17 | 0.22 |
| 1 x F + 5 x NF | 4 | 0.05 |

All does allonursed, and the frequency of nursing and allonursing ranged from 15 to 97 (55.56 ± 4.03) during the study period (Table 3.3). The frequency of calves allosuckling ranged from 0 to 229 (55.32 ± 11.22) (Table 3.4). The frequency of filial suckling bouts ranged from 155 to 292 (207.04 ± 7.95) (Table 3.3 and Table 3.4). Two calves did not successfully allosuckle, but one of the two calves attempted unsuccessfully on 3 occasions, and the other attempted and was rejected on 5 and 3 occurrences, respectively. The mean duration in seconds of F bouts was 2.71 times longer than that for NF bouts (F bouts: 40.23 ± 0.63; NF bouts: 14.82 ± 0.29). The F bouts function increased at an increasingly decelerating rate (Figure 3.1 top, Figure 3.2), and the NF bouts function was nearly constant until day 17, after which the function increased at a decelerating rate (Figure 3.1 top, Figure 3.3). NF unsuccessful solicitations started on Day 4. The F and NF unsuccessful solicitations functions were similar in the patterns of the rates of increase and deceleration from Day 14 onwards (Figure 3.1 bottom). None of the does or calves died, and there were no adoptions of calves.  Doe identity, age, filial (F) calf ID and observed number of solicitations by category. The acronyms F and NF refer to filial and non-filial calves, as defined in the text.

**Table 3.3** Doe identity, age, filial (F) calf ID and observed number of solicitations by category. The acronyms F and NF refer to filial and non-filial calves, as defined in the text.

| ID | Age | F Calf ID | F Nursings | F Rejections | F Attempts | NF Nursings | NF Rejections | NF Attempts |
|---|---|---|---|---|---|---|---|---|
| Neke28 | 2 | 1 | 161 | 29 | 36 | 15 | 10 | 23 |
| Vi16 | 3 | 6 | 190 | 48 | 63 | 51 | 16 | 25 |
| Ru10 | 5 | 65 | 163 | 15 | 55 | 51 | 15 | 23 |
| Ru12 | 5 | 119 | 166 | 12 | 37 | 66 | 10 | 21 |
| Ru11 | 5 | 84 | 170 | 13 | 62 | 24 | 10 | 21 |
| Ru8 | 6 | 8 | 206 | 15 | 33 | 59 | 19 | 25 |
| Ru5 | 6 | 150 | 210 | 20 | 76 | 62 | 16 | 27 |
| Ru6 | 6 | 132 | 261 | 58 | 64 | 68 | 18 | 43 |
| Va63 | 7 | 415 | 166 | 25 | 49 | 70 | 9 | 31 |
| Va50 | 8 | 163 | 263 | 41 | 76 | 66 | 26 | 31 |
| Pi5 | 10 | 5 | 213 | 18 | 79 | 53 | 14 | 32 |
| Pi2 | 10 | 2 | 155 | 26 | 80 | 33 | 14 | 26 |
| Pi3 | 10 | 76 | 292 | 39 | 79 | 97 | 16 | 34 |
| Pi1 | 10 | 160 | 160 | 9 | 70 | 26 | 16 | 20 |
| Pi15 | 10 | 3 | 242 | 26 | 42 | 63 | 22 | 33 |
| Pi14 | 10 | 13 | 284 | 54 | 100 | 24 | 20 | 32 |
| Pi4 | 10 | 157 | 231 | 28 | 114 | 65 | 8 | 26 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Li11 | 11 | 135 | 170 | 16 | 57 | 29 | 9 | 16 |
| Li22 | 11 | 355 | 211 | 29 | 53 | 72 | 25 | 25 |
| Li16 | 11 | 117 | 237 | 19 | 69 | 59 | 8 | 20 |
| Li6 | 11 | 58 | 210 | 24 | 56 | 64 | 15 | 29 |
| Li9 | 11 | 7 | 219 | 8 | 29 | 60 | 20 | 25 |
| Li19 | 11 | 112 | 198 | 20 | 69 | 57 | 9 | 23 |
| Li12 | 11 | 0 | 189 | 6 | 58 | 86 | 16 | 26 |
| M27 | 13 | 9 | 209 | 10 | 37 | 69 | 18 | 25 |
| Total | | | 5176 | 608 | 1543 | 1389 | 379 | 662 |

**Table 3.4** Calf identity, sex, date of birth, and frequency of solicitations. The acronyms F and NF refer to filial and non-filial calves, as defined in the text. There were 6 allobouts and 5 non-filial attempts for which the observers could not determine the identity of the calves.

| ID | Birth Date | Sex | F BOUTS | F REJECTIONS | F ATTEMPTS | ALLOBOUTS | NF REJECTIONS | NF ATTEMPTS |
|---|---|---|---|---|---|---|---|---|
| 117 | 04/05/2012 | M | 237 | 19 | 69 | 93 | 17 | 39 |
| 157 | 05/05/2012 | F | 231 | 28 | 114 | 176 | 26 | 59 |
| 58 | 05/05/2012 | F | 210 | 24 | 56 | 0 | 3 | 5 |
| 163 | 06/05/2012 | F | 263 | 41 | 76 | 113 | 29 | 44 |
| 84 | 07/05/2012 | M | 170 | 13 | 62 | 10 | 7 | 5 |
| 119 | 08/05/2012 | M | 166 | 12 | 37 | 61 | 23 | 25 |
| 132 | 08/05/2012 | F | 261 | 58 | 64 | 2 | 0 | 2 |
| 2 | 08/05/2012 | M | 155 | 26 | 80 | 50 | 20 | 26 |
| 76 | 08/05/2012 | M | 292 | 39 | 79 | 46 | 13 | 37 |
| 355 | 08/05/2012 | M | 211 | 29 | 53 | 2 | 2 | 2 |
| 7 | 08/05/2012 | M | 219 | 8 | 29 | 75 | 19 | 24 |
| 9 | 09/05/2012 | M | 209 | 10 | 37 | 37 | 17 | 28 |
| 65 | 09/05/2012 | M | 163 | 15 | 55 | 64 | 28 | 45 |
| 8 | 09/05/2012 | F | 206 | 15 | 33 | 60 | 7 | 17 |
| 112 | 09/05/2012 | M | 198 | 20 | 69 | 14 | 6 | 18 |
| 135 | 10/05/2012 | F | 170 | 16 | 57 | 76 | 16 | 16 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 415 | 10/05/2012 | F | 166 | 25 | 49 | 52 | 14 | 35 |
| 150 | 11/05/2012 | F | 210 | 20 | 76 | 12 | 6 | 11 |
| 6 | 11/05/2012 | F | 190 | 48 | 63 | 87 | 29 | 59 |
| 3 | 11/05/2012 | M | 242 | 26 | 42 | 3 | 0 | 4 |
| 5 | 11/05/2012 | F | 213 | 18 | 79 | 229 | 54 | 53 |
| 0 | 11/05/2012 | F | 189 | 6 | 58 | 83 | 33 | 62 |
| 160 | 12/05/2012 | M | 160 | 9 | 70 | 18 | 4 | 10 |
| 13 | 12/05/2012 | M | 284 | 54 | 100 | 0 | 0 | 3 |
| 1 | 13/05/2012 | M | 161 | 29 | 36 | 20 | 6 | 28 |
| Total | | | 5176 | 608 | 1543 | 1383 | 379 | 657 |

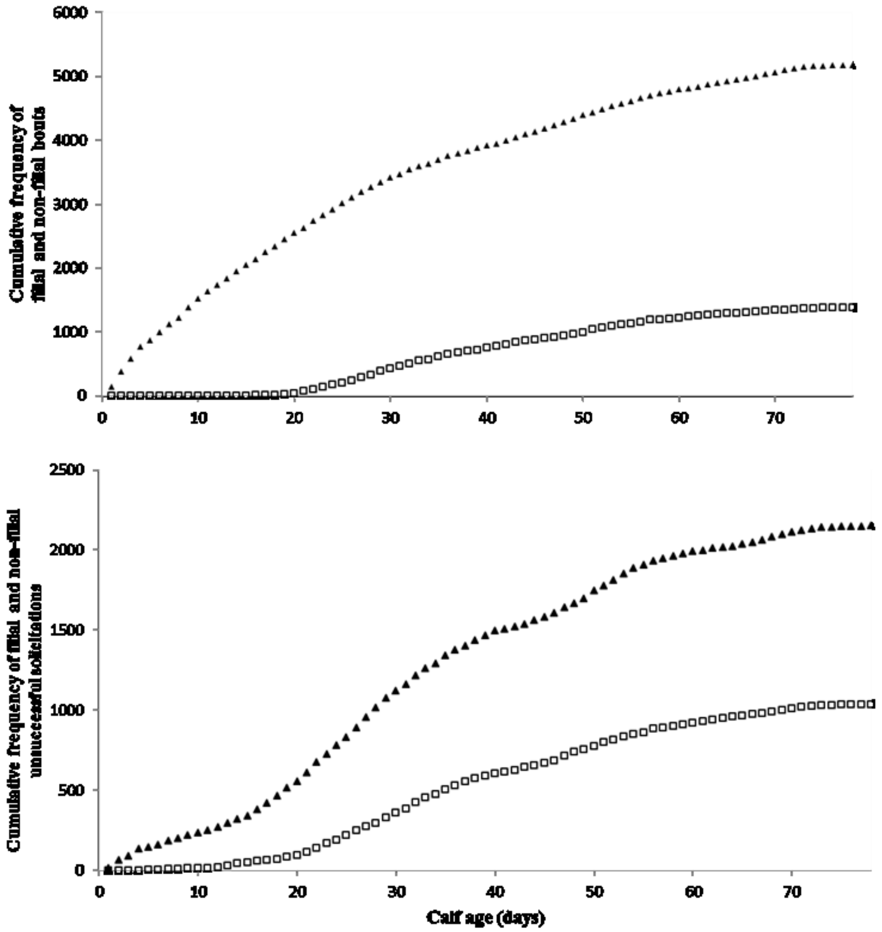

**Figure 3.1** Cumulative frequency of filial (▲) and non-filial (□) suckling of reindeer (*Rangifer tarandus*) calves during successful (top) and unsuccessful (bottom) solicitations.

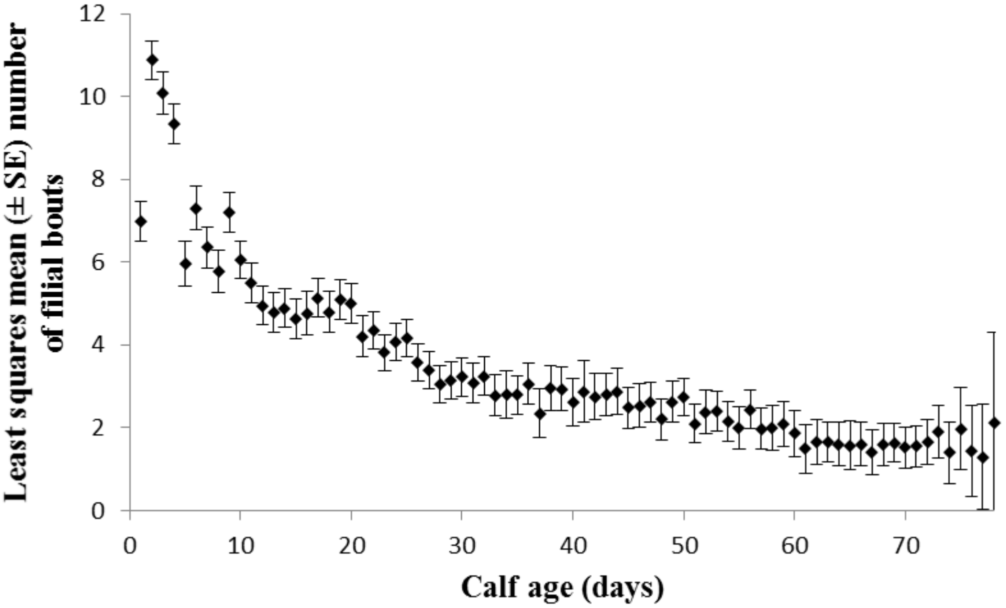

**Figure 3.2** Daily least squares mean (± 1 *SE*) number of filial bouts controlling for sex of calves.

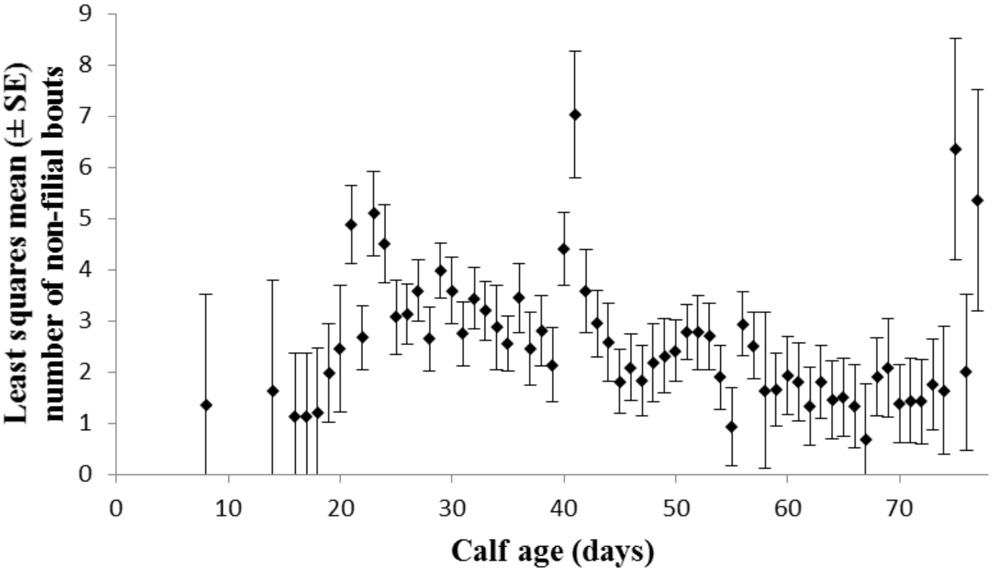

**Figure 3.3** Daily least squares mean (± 1 *SE*) number of non-filial bouts controlling for sex of calves. Day 8 and Day 14 had 2 and 1 allobouts, respectively.

The likelihood of a successful allobout occurring was marginally significant between sex of calves (PROC GLIMMIX: $F_{(1,18.45)} = 4.22$, $P = 0.0544$). The odds of a successful allobout seemed to be greater among female calves than among males, however the 95% *CI* did include the value 1.0. (Table 3.5). Order of arrival among NF calves also had a significant effect on the probability of a successful allobout occurring (PROC GLIMMIX: $F_{(3,\ 2334)} = 140.43$, $P < 0.001$; Figure 3.4). The odds ratios for NF calves arriving 1st, 3rd, and 4th indicated that the odds of a successful allobout were lower than those of the reference category of NF calves arriving 2nd, respectively (Figure 3.5), which support the milk-theft hypothesis but not the mismothering hypothesis. Calf age, doe age, birth mass, relatedness as well as the position adopted did not influence the likelihood of a successful allobout occurring (all $P > 0.05$; Table 3.5). The kin-selection hypothesis was not supported, since the odds of successfully allosuckling were not affected by relatedness. The position adopted by calves did not affect the odds of successfully allosuckling, which partially supported the mismothering hypothesis but not the milk-theft hypothesis. Does successfully attempted to sniff the ano-genital region of F and NF calves in 58.22% and 7.56% of solicitations, respectively. Does were recorded as unsuccessfully attempting to smell the ano-genital region in 1.934% of NF solicitations. For every 100 solicitations by both F and NF calves, there were 24.2 more rejections of NF calves than F calves, and the NF rate of rejections were significantly greater than the F rate of rejections (mean difference ± *SE*: 0.242 ± 0.032; Paired *t* test: $t_{(24)} = 7.644$, $P < 0.001$; Figure 3.5), which supported the milk-theft hypothesis but not the mismothering hypothesis.

**Table 3.5** Solutions for fixed effects for the likelihood of a successful allobout. Male sex, 2nd order of arrival, and the antiparallel position are the reference categories for the variables sex, order, and position, respectively. The 95%confdence intervals (*CI*) for the Odds ratio are also provided.

| Variables | *B* | *SE* | *t* | *df* | *P* | Odds ratio (95% *CI*) |
|---|---|---|---|---|---|---|
| Intercept | 0.284 | 0.975 | 0.29 | 22.93 | > 0.1 | 1.33 |
| Sex | 0.421 | 0.205 | 2.05 | 18.45 | 0.054 | 1.52 (0.99-2.34) |
| Order 1st | -5.06 | 0.426 | -11.88 | 2334 | < 0.001 | 0.00600 (0.00300-0.01500) |
| Order 3rd | -1.81 | 0.118 | -15.38 | 2334 | < 0.001 | 0.164 (0.130-0.207) |
| Order 4th | -3.27 | 0.270 | -12.09 | 2334 | < 0.001 | 0.0380 (0.022-0.0650) |
| Relatedness | -0.0513 | 0.989 | -0.05 | 2234 | > 0.1 | 0.950 (0.137-6.61) |
| Birth mass | 0.0673 | 0.145 | 0.46 | 13.65 | > 0.1 | 1.07 (0.783-1.46) |
| Calf age | -0.00324 | 0.00380 | -0.85 | 2334 | > 0.1 | 0.997 (0.989-1.00) |
| Doe age | 0.0472 | 0.0486 | 0.97 | 22.19 | > 0.1 | 1.045 (0.948-1.16) |
| Position P | -0.102 | 0.139 | -0.73 | 2334 | > 0.1 | 0.903 (0.689-1.19) |
| Position PER | -0.000880 | 0.130 | -0.01 | 2334 | > 0.1 | 0.999 (0.775-1.29) |

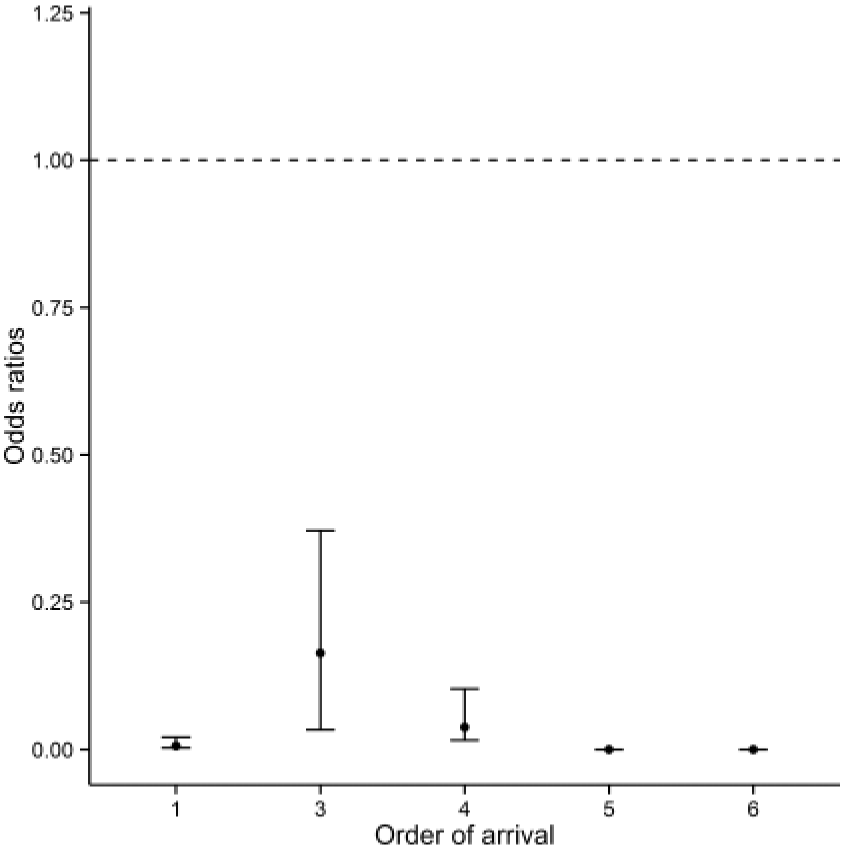

**Figure 3.4** The odds ratios, with 95% confidence intervals, of successfully allosuckling for non-filial calves arriving 1st, 3rd, 4th, 5th, and 6th in comparison to non-filial calves arriving 2nd.

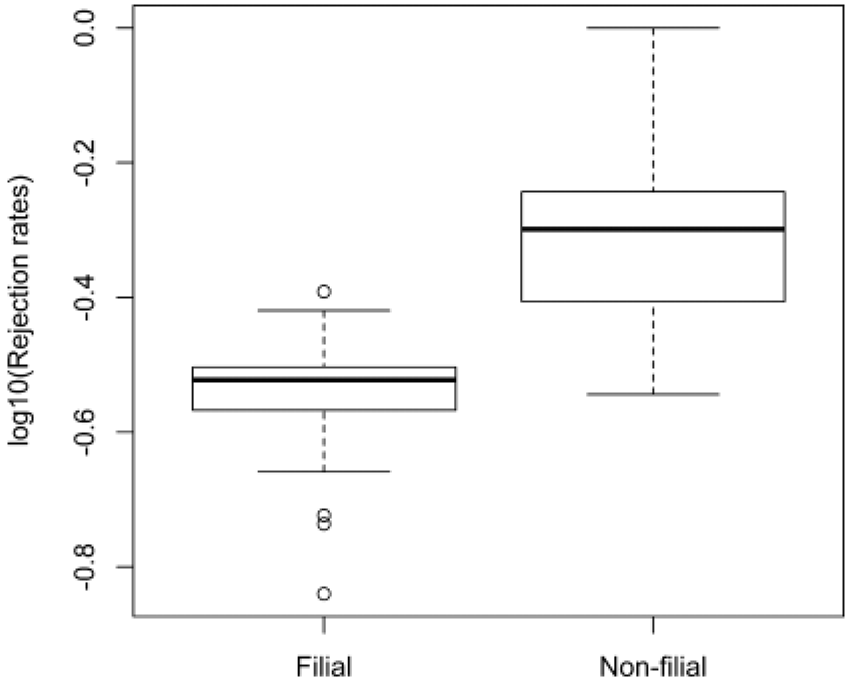

**Figure 3.5** Boxplot displaying rejection rates (Logarithm base 10 transformed) for filial and non-filial calves.

The proportions of antiparallel positions adopted by F calves during all types of solicitations were significantly greater than the proportions of antiparallel positions adopted by NF calves (Wilcoxon signed rank test: $T = 325$, $N = 25$, $P < 0.001$; Figure 3.6). For successful solicitations only, the proportions of antiparallel positions adopted by F calves were significantly greater than the proportions of antiparallel positions adopted by NF calves ((0.894 ± 0.013 vs. 0.585 ± 0.038); Mann-Whitney U test: $U = 542.000$, $N_1 = 25$, $N_2 = 23$, $P < 0.001$). These results supported the milk-theft hypothesis, but not the mismothering hypothesis.

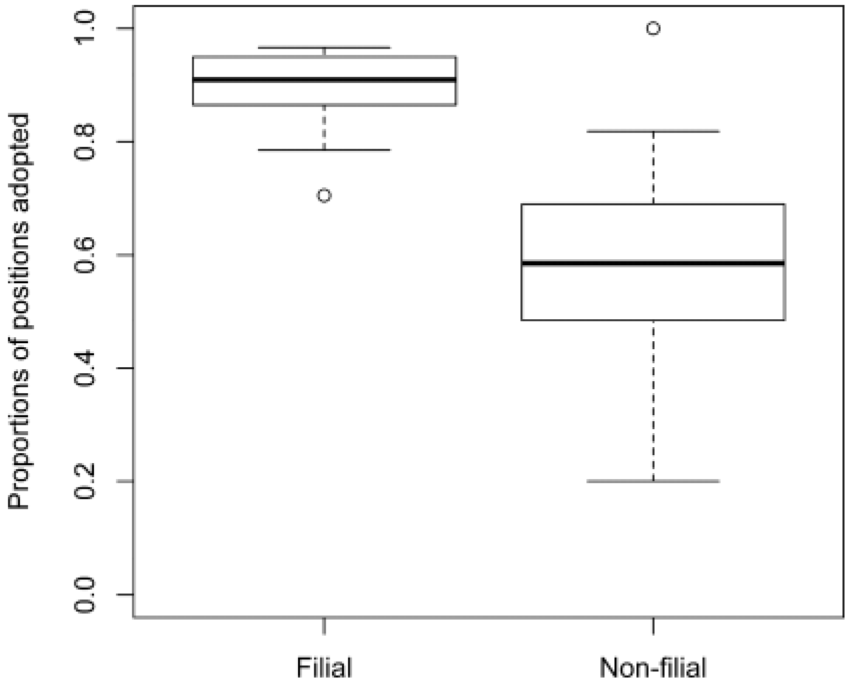

**Figure 3.6** Proportions of antiparallel positions adopted during all types of solicitations for filial and non-filial calves.

### 3.5 Discussion

With our sample size, our study is the first to test hypotheses of the causes and functional significance of the occurrence of allosuckling in reindeer. Our results strongly supported the milk-theft hypothesis. This suggests that the costs of being vigilant to detect and reject NF calves were greater than the loss of milk and potential transmission of pathogens (Roulin, 2002). Does had the opportunity and space to nurse and allonurse away from the herd but remained with the herd most of the time, which suggested that allosuckling may have been a by-product of living in groups (Hayes, 2000; Packer et al., 1992). There was limited support for the mismothering hypothesis. The maintenance of a high number of allosuckling bouts in this study was not accounted for by a lack of efficient kin discrimination and kin recognition mechanisms as reported in Hawaiian monk seals and grey seals (Boness, 1990; McCulloch et al., 1999). The association between reindeer mothers and daughters, other than calves, during the calving period was reported to not significantly different from a control sample of non-related females (Hirotani, 1989, 1990). Since association between females during calving was not influenced by relatedness, we could not argue that reindeer does would not have needed to evolve any specific mechanism to recognize relatives. The kin-selection hypothesis was not supported by our results.

The odds of successfully allosuckling for an NF calf arriving 2nd were greater than the odds for an NF calf arriving 1st, 3rd, 4th, 5th or 6th, and we argue that increasing numbers of thieves would have increased the lactation costs of does. These increases in lactation costs may have led to the rejection of additional NF calves and reduced the odds of successfully allosuckling. Consistent with our results of order of arrival, reindeer calves were reported to solicit an NF bout within a few seconds after an F calf was suckling, and 95.5% of successful NF solicitations were initiated after an F calf was suckling (Espmark, 1971c). Successful allosuckling bouts occurred after the F red deer calf was suckling (Pélabon et al., 1998). In this study, the rejection rates of NF reindeer calves were higher than those for F calves, which was evidence of discrimination against NF calves consistent with the milk-theft hypothesis. The rejection rates of NF attempts by guanaco calves were also significantly greater than the rejection rates of F attempts (Zapata, González, et al., 2009). Since we provided evidence that reindeer does could discriminate NF calves, and that the odds of a successful allobout were higher for NF reindeer calves arriving second than the odds for any other order of arrival, our results were consistent with the milk-theft hypothesis.

Contrary to our prediction for the milk-theft hypothesis, the likelihood of a successful allobout was not influenced by the position adopted, which was evidence in support of the mismothering hypothesis. This result could equally well have provided support for the compensation hypothesis (Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005), even if reindeer does discriminated F from NF calves. Reindeer does may have selectively allonursed particular NF calves, for compensation of growth and/or nutritional deficiency by letting down milk surplus, and allowed these particular NF calves to adopt any position while allosuckling. In our study, the tendency for F reindeer calves to adopt the antiparallel position during bouts (89.3%) was consistent with previous studies, while NF calves adopted the parallel and perpendicular positions in 41.5% of bouts, which was not consistent with previous studies. The antiparallel position was generally adopted by F offspring in camels (62.2%) (Brandlová et al., 2013), fallow deer (100%) (Ekvall, 1998; Pélabon et al., 1998), river buffalo (Murphey et al., 1995), guanacos (Zapata, González, et al., 2009), cattle (approximately 70-90%) (Špinka & Illmann, 1992; Waltl, Appleby, & Sölkner, 1995) and red deer (Bartoš, Vaňková, Šiler, et al., 2001). The perpendicular and parallel positions were generally adopted by NF calves in camels (100%) (Brandlová et al., 2013), fallow deer (56%) (Ekvall, 1998; Pélabon et al., 1998), cattle (approximately 53-85%) (Špinka & Illmann, 1992; Waltl et al., 1995), in river buffalo (Murphey et al., 1995) and guanacos (Zapata, González, et al., 2009). NF red deer calves, which were composed of two groups based on non-maternal dams adopting NF calves, adopted the antiparallel position in 49% of NF bouts (Bartoš, Vaňková, Šiler, et al., 2001). Adopted NF red deer calves generally approached in the antiparallel position, while non-adopted NF calves generally approached in the parallel or perpendicular positions (Bartoš, Vaňková, Šiler, et al., 2001). However, the proportions of antiparallel positions adopted by reindeer calves were higher for F than NF calves in our study, which was consistent with the milk-theft hypothesis. A similar result could occur if does were allonursing NF calves to compensate for growth and/or nutritional deficiency by letting down milk surplus with lower intensity than they nurse their own calf. If mismothering or compensation with equal intensity of allonursing NF calves and nursing F calves were occurring, the proportions of antiparallel positions adopted by F and NF reindeer calves should not have differed. The risk for NF reindeer calves of being discriminated by sniffing the ano-genital region was low due to limited attempts by the does to sniff the ano-genital region of NF calves. Reindeer does may have tolerated NF solicitations, since ending an

F bout with NF solicitations would have penalized the doe's own calf. Supplemental feeding may have reduced the cost of allonursing and milk-theft. Selective allonursing, such as reciprocal allonursing or compensation to particular calves, based on a kin-recognition mechanism other than sniffing the ano-genital region of calves may account for the function of not sniffing the ano-genital region. Reindeer mothers and offspring may recognize each other's vocalizations by direct familiarity (Espmark, 1971c; West et al. 2007), which does not support a lack of efficient kin recognition mechanisms (i.e. mismothering). It was possible that reindeer does generally did not have sufficient time to smell the ano-genital region of their own calf and that of NF calves, since the mean duration of allobouts was shorter than F bouts. When two calves were beside each other and both adopted an antiparallel position on the same side of the doe, the ano-genital region of the calf furthest from the doe was often not accessible. Due to all of these arguments, we argue that our results concerning the likelihood of a successful allobout based on positions adopted, provided limited support for the mismothering hypothesis in our study.

Allosuckling in this study group of reindeer was not a function of kin-selection. Allonursing studies of river buffalo (Murphey et al., 1995), evening bats, *Nycticeius humeralis* (Wilkinson, 1992), grey seals (McCulloch et al., 1999; Perry, Boness, & Fleischer, 1998) and polar bears, *Ursus maritimus,* (Lunn et al., 2000), did not support the kin-selection hypothesis. In contrast, allosuckling/allonursing was a function of kin-selection in dwarf mongooses (Creel et al., 1991), mice (König, 1994b), grey mouse lemurs (Eberle & Kappeler, 2006) and fallow deer (Ekvall, 1998). Female mice had higher lifetime reproductive success by communally nesting with a familiar sister than with a familiar unrelated female (König, 1994b). Reindeer does in Kutuharju generally give birth to 1 calf every year, and most calves are slaughtered in autumn (Weladji et al., 2006), which would not increase the lifetime reproductive success of does by communally rearing in groups of closely related does. Adult mortality rates, mainly due to predation, are high in grey mouse lemurs and adoption of close relatives increases inclusive fitness (Eberle & Kappeler, 2006). Predators rarely enter the research station, and the slaughter of adult does often occurs prior to senescence (Weladji et al., 2010). In contrast to studies of allonursing in species in which cooperative breeding groups are likely composed of closely related individuals, when cooperative breeding groups are not all composed of closely related individuals, lactating females do not certainly prefer to allonurse closely related offspring (see review by Roulin, 2002). Our study group was not all composed of closely related does. The association between reindeer females, other than calves, during calving was reported to not be influenced by relatedness (Hirotani, 1989, 1990). We did not find support for the kin-selection hypothesis.

Reindeer calves that weighed less at birth were not allosuckling to compensate for lower birth mass. The prediction that NF calves can successfully allosuckle by arriving before the F calf could fit equally well to the compensation hypothesis (Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005), and this prediction could be supported in favour of the compensation hypothesis even if reindeer does discriminated F from NF calves. Reindeer does could have selectively allonursed particular calves for compensation. However, reindeer does rarely allowed NF calves to allosuckle when arriving 1st, and the odds of successfully allosuckling were significantly greater for NF calves arriving 2nd than NF calves arriving 1st. Thus, there was no evidence to support this prediction in favour of the compensation hypothesis. However, we could not discount the possibility that allosuckling calves were compensating for growth deficiency, poor maternal milk production and/or low maternal body mass, such as reported in previous studies of red deer (Bartoš, Vaňková, Hyánek, et al., 2001), cows (Víchová & Bartoš, 2005), river buffalo (Paranhos da Costa et al., 2000), and guanacos (Zapata et al., 2010). We could not discount the possibility that reindeer does allowed particular NF calves to adopt any position while allosuckling for compensation. This prompts for research to be conducted to further investigate the compensation hypothesis.

Our study documented allosuckling in reindeer, as well as its pattern. This current study's F and NF bout functions were similar to that reported in reindeer (Espmark, 1971c; Marken, 2003; White & Luick, 1984), but the bout functions were dissimilar to the strong increase in the F pattern from months 4 to 10 and bimodal NF pattern in capuchin monkeys (*Cebus nigritus*) (Baldovino & Di Bitetti, 2008), as well as being dissimilar to the red deer NF bouts increase as milk production decreased in later stages of lactation (Landete-Castillejos, García, Garde, et al., 2000). The F suckling frequency for farmed red deer calves gradually decreased after 14 days of age, when the calves started grazing (Bartoš, Vaňková, Hyánek, et al., 2001). Allosuckling is a form of cooperative breeding (Lewis & Pusey, 1997), which can be costly to the individual providing alloparental care and beneficial to the receiver (Clutton-Brock et al., 1998). Allosuckling may be costly for NF offspring. Reindeer does were aggressive (e.g. kicking, threatening to kick, chasing, head threat, and displacing) toward NF calves in 2.0% of all NF solicitations. Reindeer does were agonistic toward NF calves 4243 times when the calves were within a body length of the doe's udders. We recorded a total of 55 agonistic interactions of reindeer does being agonistic toward their own calf. When Northern elephant seal mothers noticed NF offspring attempting to allosuckle, the mothers pursued and attempted to bite the NF offspring (Reiter et al., 1978). Mexican free-tailed bats, *Tadarida brasiliensis*, were reported to be occasionally aggressive toward NF allosuckling offspring (McCracken & Gustin, 1991). As a possible cause explaining allosuckling behaviour in reindeer, we found strong support for the milk-theft hypothesis. Allosuckling was not supported by the kin-selection hypothesis, and we found limited support for the mismothering hypothesis. The allosuckling/allonursing hypotheses are non-mutually exclusive, and as such they are not in conflict with each other (Roulin, 2002). Finding support for one hypothesized cause or function would not exclude finding support for another hypothesized cause or function. We did not investigate the reciprocity, learning to parent, milk evacuation, neuroendocrine and immunological hypotheses as causes and functions of allosuckling (Roulin & Heeb, 1999; Roulin, 2002, 2003). We did not investigate whether reindeer does were selectively allonursing, by allowing particular NF calves to allosuckle while rejecting the solicitations of other NF calves. Reindeer does may have selectively allonursed the calves of kin and non-kin reciprocal partners (Roulin, 2002) or allonursed particular NF offspring to compensate for growth and/or nutritional deficiency by letting down milk surplus (Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005). Our future research objectives include investigations of the reciprocity and compensation hypotheses to better explain the causes and functions of these behaviours.

# Chapter 4 Evidence of Reciprocal Allonursing in Reindeer, *Rangifer tarandus*.

This chapter is based on the published manuscript: Sacha C. Engelhardt, Robert B. Weladji, Øystein Holand, Knut H. Røed, Mauri Nieminen. 2015. Evidence of reciprocal allonursing in reindeer, *Rangifer tarandus*. Ethology 121: 245-259.

## 4.1 Abstract

The nursing of non-offspring is referred to as allonursing. Reciprocity is a hypothesized cause of allonursing, but previous studies have not strongly supported or found no evidence to support this hypothesis. Biological market theory was applied to 25 reindeer (*Rangifer tarandus*) does and their calves to investigate allonursing reciprocity across bouts and within dyads and assess the diversity of allonursing partners. We also investigated whether variation in allonursing would be associated to relatedness within dyads. We recorded both the occurrence and the duration of 1027 successful allonursing solicitations. All does allonursed, and only three of the 25 calves were not observed being allonursed. Throughout the study, 234 allonursing dyadic pairs were observed. Does allonursed the calves of several does but allonursing was not distributed evenly among all potential partners. Twenty does were members of at least 1 dyad with a high degree of reciprocity based on the number of allonursing bouts exchanged within the dyad. We found evidence of both relative and absolute allonursing reciprocity at the group level. Across bouts and within dyads the reciprocal allonursing indexes varied greatly both for frequency and for duration, with an average tendency toward unidirectionality. Evidence of strong reciprocity within dyads was found in 32 dyads for number of allonursing bouts and in 25 dyads for duration of allonursing bouts. Across bouts and within dyads, the number of allonursing bouts received was not influenced by relatedness, allonursing bouts given or absolute rank difference. Allonursing was not interchanged for rank related benefits. Our results provide evidence of reciprocal allonursing at the group level, across bouts and within dyads, and reciprocal allonursing among chosen partners. Our results point to the usefulness of applying the biological market theory to allonursing and of considering allonursing as a tradable commodity, exchanged among chosen partners.

Keywords: Allonursing, Reciprocity, Cooperation, Matrix correlations, Shannon-Wiener diversity index, Biological market theory.

### 4.2 Introduction

The nursing of non-offspring is referred to as allonursing. Reciprocal allonursing is hypothesized to occur when two females achieve a higher fitness when nursing each other's offspring to a similar extent than when they do not share milk (Pusey & Packer, 1994; Roulin, 2002). If a member of the reciprocal relationship cheats and provides less milk than the other member, reciprocal allonursing may be selected against. Due to the ease of cheating in reciprocal relationships, the benefits of reciprocating should outweigh the costs of cheating for reciprocity to be selected (Axelrod & Hamilton, 1981; Roulin, 2002). Allonursing may impose direct negative effects on the females that allonurse, such as increased maternal costs, increased mortality rates, and decreased amounts of nutrients available to an allonursing doe's own offspring (Packer et al., 1992). Additional negative effects of allonursing include undernourishment of a female's calf if the female produces more milk for her partner's offspring than her own offspring receives from her partner and reduced fitness for the partner producing more milk for the partner's offspring (Roulin, 2002), or an increased risk of pathogen transmission (Roulin & Heeb, 1999). Benefits of allonursing may include avoiding mastitis, inclusive fitness benefits, learning to parent, relieved temporarily of maternal care (see review by Roulin, 2002), transferring specific immune compounds not possessed by a mother (Roulin & Heeb, 1999), compensation for low calf birth mass or nutritional deficiencies (Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005; Zapata et al., 2010), and neuroendocrine benefits and inducing milk production (Roulin, 2003). Allonursing may be nonadaptive due to mismothering either due to milk-theft or hypothesized lack of kin recognition mechanisms (Engelhardt, Weladji, Holand, & Nieminen, 2014; Packer et al., 1992; Roulin, 2002; Zapata et al., 2009). The hypothesized causes and functions of allonursing are not mutually exclusive.

Kin-selection, reciprocity, and group selection are mechanisms for the evolution of cooperation (Axelrod & Hamilton, 1981; Hamilton, 1964a, 1964b; Trivers, 1971; Wilson, 1975). Natural selection promotes the evolution of altruism among relatives, whereby the relatedness of a pair of individuals is greater than the cost to the altruist divided by the benefit to the recipient (Hamilton, 1964a). Reciprocal allonursing may occur among kin, since a mother may share genes by common descent with a non-filial calf, and providing an opportunity for her to spread those genes in her population and increase her inclusive fitness (Pusey & Packer, 1994; Roulin, 2002). Reciprocal allonursing may provide greater flexibility in the timing and frequency of milk production and provisioning (Pusey & Packer, 1994). The reciprocity hypothesis has not received much support. In wild fallow deer (*Dama dama*), the duration of allonursing was exchanged in 4 pairs (possibly mother-daughter pairs, based on observations) of does composed of the 2 oldest females in each of four groups (Ekvall, 1998). These 4 pairs of fallow deer reciprocally allonursed each other's fawn with high index of reciprocity values (mean: 0.81 ± 0.07), while the index of reciprocity values for the remaining 21 dyads composed of younger fallow deer were much lower (mean: 0.12 ± 0.17) (Ekvall, 1998). Most other studies reported no evidence of reciprocal allonursing, for example in bats (*Tadarida brasiliensis*) (McCracken & Gustin, 1991), river buffalo (*Bubalus bubalis*) (Murphey et al., 1995), red deer (*Cervus elaphus*) (Bartoš, Vaňková, Šiler, et al., 2001), lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) (Pusey & Packer, 1994), and warthogs (*Phacochoerus africanus*) (Plesner Jensen, Siefert, Okori, & Clutton-Brock, 1999). Reciprocal altruism is defined as cooperation among non-relatives, and reciprocal altruism is selected for if the recipient returns the exchange (e.g. allonursing) and both individuals accumulate a net benefit (Trivers, 1971). By interacting repeatedly, reciprocal altruism can occur by use of conditional strategies (e.g. tit-for-tat or win-stay, lose-shift) whereby giving an allonursing bout depends on the probability of another interaction being sufficiently high and the outcome of previous solicitations for allonursing by a doe's own calf (Rand & Nowak, 2013).

Conditional altruism may explain the evolution of cooperation and may be limited to biological markets (Le Galliard & Ferrière, 2008), which are game theoretic models (Noë & Hammerstein, 1995). According to biological market theory, allonursing can be conceived as a tradable commodity governed by the laws of supply and demand, which determine the value of offered commodities and the rates of exchange and interchange for individuals belonging to different classes (Noë & Hammerstein, 1994, 1995; Noë, 2001). The two classes of traders exchange commodities to their mutual benefits (Noë & Hammerstein, 1995). Additional characteristics of markets include outbidding competition, partner choice, and conflicts over the value of tradable commodities (Noë & Hammerstein, 1995). Biological market theory has been successfully applied to the study of allogrooming reciprocity (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Leinfelder, de Vries, Deleu, & Nelissen, 2001; Newton-Fisher & Lee, 2011; Schino, Ventura, & Troisi, 2003), and investigating for evidence of reciprocal allonursing may benefit from applying biological market theory. Partner choice is a preference for a partner based on the tradable commodity's value, which can be relative or absolute (Noë & Hammerstein, 1995). A tradable commodity can be evenly spread by each individual to every other individual or restricted to a smaller number of partners (Silk, Robert, & Cheney, 1999). Reciprocal allogrooming among chosen partners is widespread among primates (Schino & Aureli, 2009). Based on the biological market model, where competition is high for monopolizable resources that can be traded as commodities and rank order is steep, dominant individuals will use their access to the monopolized resources as currency for which subordinates will attempt to outbid each other by increasing their allocation of the commodity (e.g. allonursing) to higher ranking individuals in order to have access to the monopolized resources (Barrett et al., 1999; Leinfelder et al., 2001). Social rank was shown to influence allonursing in dwarf mongooses (Creel et al., 1991) and allonursing frequency in tufted capuchin monkeys (Baldovino & Di Bitetti, 2008). However, success of dams during agonistic encounters was not shown to influence allonursing in guanacos (*Lama guanicoe*) (Zapata et al., 2010).

At the group level, relative and absolute forms of reciprocity can be considered as a model based on what is given and received by the same individual, and this approach is the actor-receiver model (Hemelrijk, 1990b). The actor-receiver model implies that each individual compares what it gave to other individuals with what it received from them, without having to take into account what these other individuals gave to others (Hemelrijk, 1990b). To guard against deception, individuals only have to keep track of what they received and what they gave (Hemelrijk, 1990b). In the relative form, each female gives relatively more to each partner's calf from whom her own calf received more in return, and only allonursing acts given or received by the same individual interacting with individuals are compared among one another (Hemelrijk, 1990b). Relative reciprocity occurs even if general tendencies differ between individual and allows for individual variation (Hemelrijk, 1990b). In the absolute form, each female gives allonursing received in a more exact way than in the relative form. Absolute reciprocity is a special case of the relative type of reciprocity with a fixed exchange rate of 1, and it is expected to occur when individuals do not differ substantively in their capacities and tendencies to allonurse (Hemelrijk, 1990b). Non-parametric matrix correlation tests are regularly used by primatologists to investigate allogrooming reciprocity at the group level (Arnold & Whiten, 2003; Cooper, Berntein, & Hemelrijk, 2005; Hemelrijk, 1994; Newton-Fisher & Lee, 2011; Watts, 2002).

We here test whether reindeer does regard allonursing as a tradable commodity. The aim of this study was to investigate the distribution of allonursing in order to evaluate whether reindeer reciprocally traded allonursing among preferred partners. To achieve this, we assessed: (1) the occurrence of reciprocal allonursing across bouts and dyads (i.e. at the group level) and dyadic reciprocal allonursing across bouts. At the group level, we predicted that each doe gave relatively more allonursing to each partner's calf from whom its own calf was allonursed more in return (i.e. the relative form), and we predicted that each doe gave exactly the allonursing received by its calf in return (i.e. the absolute form). Across bouts and within dyads, the objective was to report the occurrence or non-occurrence of reciprocal allonursing and to describe the patterns. (2) The diversity of allonursing partners (i.e. partner choice) to quantify how evenly allonursing was spread by each doe to every other potential doe's calf. If reideer allonurse reciprocally, they should have few reciprocal partners. We predicted that the number of partners with which does were strongly reciprocal (i.e. reciprocity index values $\geq 0.8$) will be lower than the number of partners with which does were weakly reciprocal (i.e. reciprocity index values $< 0.8$). (3) To investigate whether reciprocity would be kin-related. A positive relationship between the number of allonursing bouts received and the number of allonursing bouts given would vary as the relatedness within dyads increased. We predicted that for dyads showing a tendency to reciprocate, there was a strong positive correlation between relatedness within dyads and reciprocity index values. (4) To investigate reciprocal altruism, under the prediction that the more a doe allonursed a partner's calf, within a dyad, the more her calf was allonursed in return. (5) To investigate whether reciprocity would be rank-related. Reindeer does did have a steep dominance hierarchy, but natural forage, which was plentiful in summer, and supplemental forage could not be monopolized by dominant reindeer does. We predicted that allonursing was not influenced by social rank, and that allonursing would be traded for itself instead of being interchanged for rank-related benefits.

## 4.3 Materials and Methods

### *4.3.1 Study Area, Subjects and Management Practise*

This study was conducted at the Kutuharju Field Reindeer Research Station near Kaamanen, Finland (69º N, 27º E). The herd was established in the late 1960s with about 20 males and 60 females. Since 1969, there has been a systematic monitoring of the animals for several aspects of their biology (e.g. physiology, behaviour) (Eloranta & Nieminen, 1986). Does are slaughtered at the age of 10–12 yr, when they start showing signs of reproductive senescence (Eloranta & Nieminen, 1986). During this study, the age of does in the population ranged from 2-13 yr (mean ± SD = 7.32 ± 3.21 yr). Every year, male and female calves and adults are bought and brought into the population to introduce new genetic material in the herd and to avoid inbreeding depression. This project was in accordance with the Animal Ethics and Care Certificate provided by Concordia University (AREC-2010-WELA) and the Finnish National Advisory Board on Research Ethics. During calving all does of the experimental herd were confined to a paddock (approximately 10 ha), where data on the birth date, calf sex, and mother-calf assignments were obtained. Mother-calf pairs were assigned in the field within 48 hours. Date of calving for this study population began on May 4th, 2012, and the 25th parturition occurred on May 13th, 2012. The first 25 calves to be born and their mothers were selected for this study and separated from the herd for 10 weeks. Collar tags of different colours and with numbers inscribed were fixed to individuals for identification. There were 14 male and 11 females calves. The age of does in the study group ranged from 2-13 yrs (mean ± SD = 8.25 ± 2.96 yrs). The study group had access to free running water, natural forage and supplemental feed (i.e. lichen, pellets, and leaves of young shoots of birch. The paddock was characterized by generally flat and open area with birch (*Betula pendula*, *Betula pubescens*) and pine (*Pinus sylvestris*) trees. The daily mass of Rasio Mullin-Herkku 2 pellets provided ranged from 80 Kg to 120 Kg. From June 12th to July 20th, the study group was released in a large enclosure, after daily data collection was finished, and herded in the paddock the next morning at 6h00, in order to give the study group access to more natural forage: observations were recorded 60 to 90 minutes after the study group was herded in the paddock. At the end of the study, the study group was transferred back into their large fenced enclosure (approximately 15 $Km^2$) together with the rest of the animals.

Blood samples were obtained from all individuals and analysed for 16 DNA microsatellite loci as part of an ongoing progeny testing within this experimental herd (Røed et al., 2002). Parenthood assignments was analysed with the simulation program software CERVUS 3.0 (Kalinowski et al., 2007) which is based on likelihood ratios between candidate parents. Within the herd all microsatellites were in Hardy Weinberg equilibrium and no mismatches were detected for the assigned mother-calf combinations used in the present study. Relatedness (R) was estimated for all pairwise combinations of all females producing a calf by using the program GenAlEx v 6.4 (Peakall & Smouse, 2006). Queller and Goodnight (1989)'s methods-of-moments estimator of relatedness was used with jackknifing over all the loci generating standard errors for average relatedness values.

### *4.3.2 Behavioural Observations*

Behavioural observations were conducted between 7h00 and 20h30 from May 3rd to July 20th, 2012 over 65 days. All does were habituated to human presence. Observations were conducted by 3 trained observers, inside the paddock, at a distance ranging from 5 to 50 meters from animals. Binoculars were used to reliably record observations of solicitations, agonistic interactions, and identify of individuals. For each observation of an allonursing bout, the occurrence, duration, and the identity of the doe and calves were collected on data collection sheets using behaviour sampling with continuous recording (Martin & Bateson, 2007), and observations without all of this information collected were removed from the analyses. A solicitation was scored as a successful allobout when a calf suckled for 5 seconds or more and ended when the calf no longer grasped the doe's udder. A successful solicitation was considered terminated when a calf's muzzle and a doe's udder were not in contact for 20 seconds or more. There is variation in the determination of the cut-off duration for assigning a solicitation as successful, and the determination varies by species and researcher. We selected a 5 seconds cut-off based on previous suckling and allosuckling research with reindeer (Lavigueur & Barrette, 1992; Marken, 2003), and a 5 seconds cut-off has also been selected to study nursing and allonursing in red deer (Bartoš, Vaňková, Hyánek, et al., 2001; Drábková et al., 2008), fallow deer (Birgersson & Ekvall, 1994), cows (*Bos taurus*) (Víchová & Bartoš, 2005), bactrian camels

(*Camelus bactrianus*) (Brandlová et al., 2013), zebras (Olléová et al., 2012), big horn sheep (Hass, 1990).

The choice to use both the number and duration of allobouts as measures, instead of one or the other, was threefold. Firstly, reciprocity can involve exchange of the same behaviour (Noë & Hammerstein, 1994, 1995; Noë, 2001). Secondly, exchange of a tradable commodity (e.g. allonursing) is a form of reciprocity that can be quantified as a ratio measuring the degree of reciprocity within a dyad (Mitani, 2009). Thirdly, assessing the exchange of both the number and duration of allonursing bouts helps elucidate which commodities (e.g. number or length of allonursing) are being traded, since little is known concerning reciprocal allonursing. The number and length of allonursing bouts were not independent, since we could not collect data on length of allonursing bouts without collecting data on occurrence of allonursing bouts.

Four behaviour sampling sessions of agonistic interactions of one hour each, using continuous recording, were conducted daily (Martin & Bateson, 2007). An agonistic interaction was recorded as resolved when an individual showed a submissive behaviour ("lose"), and the other did not ("win"). Unresolved agonistic interactions were recorded as unresolved when neither animal showed a submissive behaviour. The agonistic interactions scored were displacement, head threat, push, chase, kick, boxing, and other interactions (Holand et al., 2004 adapted from Thomson, 1977), and their associated submissive behaviours were scored as 'flee' or 'walk away' if submission occurred. Throughout the rest of the day, agonistic interactions were opportunistically scored using ad libitum sampling and continuous recording methods. The rank of female reindeer is fairly stable throughout the year (Hirotani, 1990), except for a very short time immediately following the shedding of antlers (Espmark, 1971a; Thomson, 1977).

### *4.3.3 Statistical Analyses*

#### *4.3.3.1 Social Hierarchy*

Observations of agonistic interactions with a winner and loser being identified were used to generate a dominance hierarchy for adult female reindeer in the study group. Ranks were given values ranging 1 to 25, with 25 representing the most dominant doe and 1 representing the least dominant doe. The dominance hierarchy tended to be linear, with a Landau's index of linearity of 0.785 (de Vries, 1998).

### *4.3.3.2 Inter-Observer Reliability*

We used the data obtained when measuring the same observations simultaneously to assess the inter-observer reliability. To do this, we calculated the Pearson correlation coefficients between the 3 pairs of observers for the duration of allonursing, and we calculated the index of concordance between the 3 pairs of observers for the identities of the does and calves observed allonursing (Martin & Bateson, 2007).

### *4.3.3.3 Reciprocity at the Group Level*

At the group level, we investigated allonursing reciprocity among all pairs of group members as summed frequencies and durations of allonursing bouts during 10 weeks of study (Hemelrijk, 1990b). An investigation of reciprocity at the group level is limited to general patterns across dyads. Evidence of "relative" and "absolute" allonursing reciprocity at the group level, across bouts and dyads, were tested for with matrix correlations of matrices of summed frequencies and durations of successful allonursing bouts with their respective transposed matrix. For a detailed description of the actor-receiver model and the statistical methodology to test for the relative and absolute types of reciprocity across bouts and dyads (i.e. at the group level) using the $K_r$, tau $K_r$, Mantel Z and the R tests refer to Hemelrijk (1990a, 1990b). These non-parametric rank-based tests are regularly used by primatologists investigating allogrooming reciprocity at the group level (K. Arnold & Whiten, 2003; Cooper et al., 2005; Hemelrijk, 1994; Newton-Fisher & Lee, 2011; Watts, 2002). Matrix correlation tests were performed using the program MatrixTester with the right-tailed test for the probability level based on 2000 permutations (Hemelrijk, 1990a, 1990b). In matrix correlation tests for reciprocity at the group level, only right-sided one-tailed probability values are of interest, since left-sided probability values indicate a negative correlation, which reflect the opposite of reciprocity (Hemelrijk, 1990b). The Kr test and tau Kr test are analogous to the Kendall rank correlation test (Hemelrijk, 1990b). Unlike Kendall's rank correlation test, the Kr and tau Kr tests do not assume independence of data since we repeatedly measured the same individuals (Hemelrijk, 1990b). The Kr statistic measures the correlation within rows between two matrices. The Kr statistic is derived from the

S statistic in Kendall's rank correlation coefficient, where the S statistic is calculated per row and summed over all rows (Hemelrijk, 1990b). Analogous to Kendall's tau, the tau Kr statistic for squared matrices is divided by the total number of pairs of cells, which depends on the number of rows, the number of columns, the presence of empty diagonal cells, and the presence or absence of ties (Hemelrijk, 1990b). Absolute reciprocity is examined by testing the symmetry of a matrix, and it can be verified with the Mantel Z test (Hemelrijk, 1990b). However, the Mantel Z test results are dependent on the measure used and outliers, which could strongly bias the results (Hemelrijk, 1990b). The Mantel Z test should be followed with an R test. The R statistic is a Mantel's Z statistic but calculated from within-matrix ranks (Hemelrijk, 1990b). Since the Mantel Z test for allonursing duration was not significant but the R test was significant, we used a Spearman rank correlation to test whether it was possible that per individual the one who allonursed calves longer also had the calf that received allonursing the longest by correlating per individual the allonursing given and received for duration. We performed separate partial tau Kr tests to control for relatedness and social rank (Hemelrijk, 1990a). We applied these methods and tests for both allonursing frequency and duration and set the right-tailed statistical significance level at 0.05.

#### *4.3.3.4 Dyadic Reciprocity across Bouts*

Observations of successful allonursing frequency and duration across bouts were summed within dyads. To assess dyadic reciprocity, we used the reciprocity index presented by (Mitani, 2009) to create the reciprocal allonursing duration index (RADI) and the reciprocal allonursing frequency index (RAFI).

**Equation 4.1** Reciprocal Index = $1 - \left| aAB/(aA + aB) - aBA/(aA + aB) \right|$

Where $aAB$ is the amount of allonursing that individual $A$ gave to individual $B$'s calf, $aBA$ is the amount of allonursing that individual $B$ gave to individual $A$'s calf, and $aA + aB$ is the total amount of allonursing between the two individuals. The reciprocity index quantifies the degree to which members of a dyad match one another's exchange of allonursing bouts. The reciprocal indexes range from 0 (no reciprocation and unidirectional, i.e. allonursing performed by only one individual) to 1 (complete reciprocation). Index values equal to or above 0.5 were interpreted as a tendency towards reciprocity; values below 0.5 were interpreted as a tendency towards unidirectionality; values of 0.8 or above were interpreted as strong reciprocity (Newton-Fisher & Lee, 2011). To assess the relationship between both indices, a Spearman rank correlation test was used, since the assumption of bivariate normality was violated after data transformation.

Four spearman rank correlations were performed. We correlated the number of allonursing bouts given to the mean RAFI index, the number of allonursing bouts received to the mean RAFI index, the duration of allonursing bouts given to the mean RADI index, and the duration of allonursing bouts received to the mean RADI index. These tests were used to assess whether reciprocal allonursing was an artefact of the total number or duration of allonursing performed and received by each individual. We ran two Spearman rank correlations for dyads with reciprocity index values ≥ 0.5 to correlate relatedness within dyads to RAFI and RADI, respectively.

A generalized linear mixed model (PROC GLIMMIX in SAS version 9.3, SAS Institute Inc. Carey, North Carolina, U.S.A.) (SAS, 2012) with a log link function, a negative binomial distribution, to correct for overdispersion, was conducted on the frequency data from 468 dyads to investigate whether the following variables influenced the allonursing bouts received. The variables investigated were allonursing bouts given, relatedness within dyads, absolute rank difference, the interaction between bouts given and relatedness. The identity of the individual giving was a random term, due to repeated measures. The predictor relatedness was centered on the mean. We first inspected for multicollinearity using the variation inflation factor (VIF), and the predictors were retained in the model since we found that VIF values were consistently smaller than 2.7 (Montgomery & Peck, 1992). Based on an information-theoretical approach, model selection was performed using Akaike's Information Criterion (AIC) with the smallest AIC value indicating the most parsimonious model, and we reported the differences between the AIC value of the best model and that of the other models (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). For the sake of pluralism and because we were also interested in effect size, direction, and parameter precision, we reported parameter estimates and their accompanying *P* values (Stephens, Buskirk, Hayward, & Martínez Del Rio, 2005) for models not distinguishable from the best model (i.e. $\Delta$ AIC < 2). An alpha of 0.05 was adopted.

#### *4.3.3.5 Diversity of Allonursing Partners*

We used the standardized Shannon-Wiener diversity index ($H'$) to quantify how evenly successful allonursing was spread by each individual to every other potential individual (C. J. Krebs, 1989; Silk et al., 1999):

**Equation 4.2** Shannon-Wiener diversity index = $H = - \Sigma p_{\mathrm{i}} (\ln p_{\mathrm{i}})$

**Equation 4.3** Maximum Shannon-Wiener diversity index = $H_{max} = \ln(n\text{-}1)$

**Equation 4.4** Standardized Shannon-Wiener diversity index = $H' = H/H_{max}$

where $p_i$ is the relative proportion of allonursing directed toward the $i$th individual's calf, and $n$ is the number of individuals in the group. The standardized index ($H'$) ranges from 0 (i.e. allonursing focused on a single partner's calf) to 1 (allonursing spread evenly across all potential partners' calves). We calculated these indexes for both frequency and duration of allonursing. All means are presented with their standard deviations (SD). Standardized diversity index values, ranging from 0 to 0.91, have been reported for allogrooming in Old World primate species (Cheney, 1992; Newton-Fisher & Lee, 2011; Silk et al., 1999).

We tested whether the number of partners with which does were members of strong reciprocal dyads (i.e. reciprocity index values $\geq 0.8$) was significantly lower than the number of partners does had with reciprocity index values less than 0.8 using two paired t-tests, one for the frequency data and one for the duration data. Prior to each paired t-test, the assumption of the normality of differences was tested with a Kolmogorov-Smirnov test, and the assumption was not violated.

Two generalized linear models (PROC GENMOD in SAS version 9.3, SAS Institute Inc. Carey, North Carolina, U.S.A.) (SAS, 2012) with log link function and a Poisson distribution were conducted on the frequency and duration data, respectively, for the 25 reindeer does to investigate whether the number and duration allonursing bouts given influenced the number of allonursing partners sampled. We used R version 3.0.1 (R Core Team, 2013) to assess the rationale of use a Poisson distribution for both models by evaluating distribution plots of the poissonness to plot the number of occurrences against the distribution metameter of the specified distribution, Q-Q plots of the models, goodness-of-fit tests for poisson distribution based on a likelihood ratio test, goodness-of-fit measures comparing deviance of both of our poisson distribution models versus a null model, deviance/model residual values and dispersion tests. The poisson distribution fitted the data for both models, and our data were underdispersed with deviance/model residual values of 0.235 and 0.338 for the frequency and duration data sets, respectively. Based on these results, we selected a poisson distribution for both models, and we scaled the deviance to correct for the underdispersion.

## 4.4 Results

We recorded 1027 allonursing bouts, and 1049 unsuccessful allonursing attempts. All does allonursed, and 3 of the 25 calves were not observed being allonursed. The mean number of allonursing bouts performed by does was 41.32 ± 16.52 (range: 13-75), and the mean number of allonursing bouts for calves was 41.12 ± 41.37 (range: 0-163). The mean duration of an allobout was 14.821 ± 9.179 s. All mother-calf assignments from field observations were supported by the DNA analyses. There were no occurrences of agonistic interactions between mothers and their calf during nursing, while reindeer does were agonistic toward non-filial calves on 45 occasions of all allosuckling solicitations. Reindeer does were agonistic toward their own calf 55 times when their own calf was within a body length of the doe's udders, while reindeer does were agonistic toward non-filial calves 4243 times when the calves were within a body length of the doe's udders. The Pearson correlation coefficients for the duration of observations measured between the 3 pairs of observers were 0.997 (N = 418), 0.969 (N = 217), and 0.999 (N = 45). All identities of does and calves were reliably measured between the 3 pairs of observers (indices of concordance = 1.0).

### *4.4.1 Reciprocity at the Group Level*

There was evidence of "relative" allonursing reciprocity at the group level (i.e. each doe gave relatively more allonursing to each partner's calf from whom its own calf was allonursed more in return) for both frequency and duration (Table 4.1). There was evidence of "absolute" allonursing reciprocity at the group level for frequency, but being only marginally significant (i.e. Mantel Z test) for duration (Table 4.1). However, there was no evidence that per individual the doe that allonursed more had the calf that received more allonursing for duration (Spearman rho test, $r_s = 0.101$, $P = 0.6358$, $df = 23$). The observed relation between the allonursing matrices did not disappear when controlling for either the social rank of does or relatedness (Table 4.1).

**Table 4.1** Matrix correlations for relative and absolute tests of allonursing. $N = 25$.

| Types reciprocity and associations | Tests statistics | *P* values |
|---|---|---|
| 1. Relative exchange of<br>the number of allonursing bouts | *Kr* = 505<br>*Tau Kr* = 0.120 | 0.0375 |
| Controlling for social rank | *Partial Tau Kr* = 0.121 | 0.0295 |
| Controlling for relatedness | *Partial Tau Kr* = 0.119 | 0.0415 |
| 2. Absolute exchange of<br>the number of allonursing bouts | *Mantel Z* = 2100<br>*R* = 56454549.5 | 0.0495<br>0.019 |
| 3. Relative exchange of<br>the duration of allonursing bouts | *Kr* = 528<br>*Tau Kr* = 0.114 | 0.0420 |
| Controlling for social rank | *Partial Tau Kr* = 0.118 | 0.0375 |
| Controlling for relatedness | *Partial Tau Kr* = 0.113 | 0.045 |

### *4.4.2 Dyadic Reciprocity across Bouts*

Within dyads and across bouts, the average degree to which members of a dyad matched one another's exchange of allonursing bouts tended towards unidirectionality for the reciprocal allonursing frequency index (RAFI) (mean: 0.283 ± 0.351, range = 0.000-1.000) and for the reciprocal allonursing duration index (RADI) (mean: 0.265 ± 0.340, range = 0.000-0.985). The average dyad displayed a lack of absolute allonursing reciprocity in the number and length of allonursing bouts, and 132 dyads (56.41%) had values equal to zero for both indices. The remaining 102 dyads had dyadic reciprocity values greater than zero for both indices. Most dyads (150/234; 64.10%) tended towards unidirectionality in their frequency of allonursing (RAFI < 0.50), while 84/234 (35.90%) dyads were more reciprocal in their allonursing (RAFI ≥ 0.50). Similarly, most dyads (162/234; 69.23%) tended towards unidirectionality in their duration of allonursing (RADI < 0.50), while 72/234 (30.77%) dyads were more reciprocal in their allonursing (RADI ≥ 0.50).

The degree to which members of a dyad matched one another's exchange of allonursing bouts was high in a subset of dyads. Evidence of strong reciprocity within dyads was found in 32/234 (13.68%) dyads (RAFI ≥ 0.80), while 37/234 (15.81%) dyads had RAFI values ≥ 0.70. Based on the frequency data, 20 of the does were members of at least one dyad with strong reciprocity (i.e. RAFI ≥ 0.80) or with RAFI values ≥ 0.70 (RAFI ≥ 0.80: mean number of partners: 3.200 ± 1.735, range = 1-7; RAFI ≥ 0.70: mean number of partners: 3.700 ± 2.105, range = 1-8) (Table 4.2). Evidence of strong reciprocity within dyads was found in 25/234 (10.68%) dyads (RADI ≥ 0.80), while 39/234 (16.67%) dyads had RADI values ≥ 0.70. Based on the duration data, 21 of the does were members of at least one dyad with strong reciprocity (RADI ≥ 0.80: mean number of partners: 2.381 ± 1.564, range = 1-7), while 22 of the does were members of at least one dyad with RADI values ≥ 0.70 (mean number of partners: 3.545 ± 2.324, range = 1-9) (Table 4.2). Most does had at least one partner with whom they strongly allonursed reciprocally. There was a strong positive correlation between the RAFI and RADI indices (Spearman rho test, $r_s = 0.960$, $P < 0.001$, $df = 232$), and the positive correlation continued after excluding the 132 points with a value of zero on both indices (Spearman rho test, $r_s = 0.596$, $P < 0.001$, $df = 100$) (Figure 4.1). For the dyads with reciprocity index values ≥ 0.5, both the RAFI values (Spearman rho test, $r_s = -0.005$, $P = 0.967$, $df = 82$) and the RADI values (Spearman rho test, $r_s = 0.031$, $P = 0.794$, $df = 70$) did not increase with increasing relatedness within dyads.

**Table 4.2** Reciprocal allonursing partnerships with reciprocal index values equal or greater to 0.8 for both indices. The allonursing partnerships for RAFI and RADI ≥ 0.7 range from 0.7 to less than 0.8. Lower rank value means the doe is higher in the social hieerarchy. Age was measured in years.

| Doe | | | Reciprocal allonursing partners based on indices | | | |
|---|---|---|---|---|---|---|
| ID | Rank | Age | RAFI ≥ 0.8 | RAFI ≥ 0.7 | RADI ≥ 0.8 | RADI ≥ 0.7 |
| V1 | 1 | 11 | 10 | | W5 | |
| P5 | 2 | 10 | Y2, B1, G6 | B8, 9V, P4 | P4, P2, 9V, Y2 | B8, G6 |
| W5 | 3 | 8 | BL | W6 | 10, V1, V2, BL | |
| P2 | 4 | 10 | P4, V2, P3 | V6 | B2, V6, P3, P4, P5 | |
| P3 | 5 | 10 | V6, P2, B2, 10 | W6 | P2, BL, P1 | W6, 10 |
| P1 | 6 | 10 | | G6 | P3 | |
| W6 | 7 | 7 | BL, 9V, B8, 10, 6V, V9, B5 | W5, P3 | B5, BL, 10, B2, B8, V9, 9V | P3 |
| 15 | 8 | 10 | | | | |
| 22 | 9 | 11 | | | | |
| B8 | 10 | 6 | W6, V6, 9V | P5 | V6, 9V, V2, W6 | P5 |
| 10 | 11 | 5 | P3, V6, W6, V1 | 9V, V2 | P4, W5, V6, 9V, W6 | V2, P3 |
| 14 | 12 | 10 | | | | |
| B5 | 13 | 6 | G6, W6 | P4, BL | W6, G6 | |
| V6 | 14 | 11 | P3, 10, B8 | G6, P2 | B8, P2, 10 | |
| P4 | 15 | 10 | P2 | B5, P5 | 10, P5, P2 | |

| | | | | | | |
|---|---|---|---|---|---|---|
| 6V | 16 | 11 | W6 | | | |
| Y2 | 17 | 2 | P5 | | P5 | |
| 9V | 18 | 11 | W6, B6, B8 | 10, P5 | B6, B8, 10, P5, W6 | |
| V9 | 19 | 11 | W6 | | W6 | |
| B6 | 20 | 6 | 9V | | 9V | |
| BL | 21 | 13 | W6, V2, G6, W5 | B5 | B2, P3, G6, W5, W6 | |
| B2 | 22 | 5 | P3 | G6 | BL, P2, V2, W6 | |
| V2 | 23 | 11 | BL, P2 | 10, G6 | B2, W5, B8 | 10 |
| B1 | 24 | 5 | P5 | | | |
| G6 | 25 | 3 | P5, B5, BL | V6, V2, P1, B2 | BL, B5 | P5 |

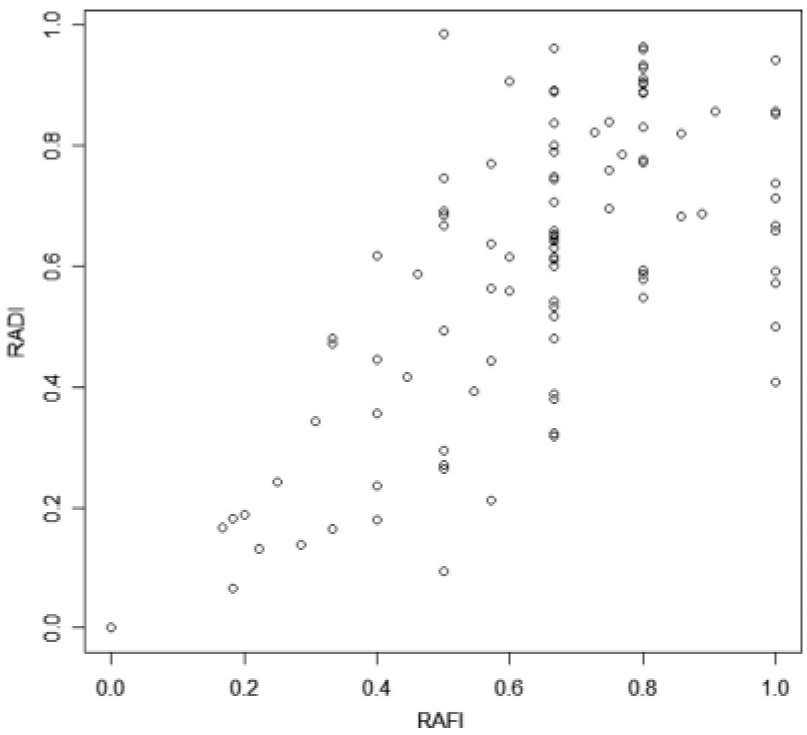

**Figure 4.1** The relationship between the frequency (RAFI) and duration (RADI) indices for reciprocity across bouts and within dyads.

The mean RAFI values for each doe were influenced by the number of allonursing bouts received (Spearman rho test: $r_s = 0.7713$, $P < 0.001$, $df = 23$), but they were not influenced by the number of allonursing bouts given (Spearman rho test: $r_s = 0.293$, $P = 0.155$, $df = 23$). The mean RADI values for each doe were influenced by the number of allonursing bouts received (Spearman rho test: $r_s = 0.7914$, $P < 0.001$, $df = 23$), but they were not influenced by the number of allonursing bouts given (Spearman rho test: $r_s = 0.2925$, $P = 0.155$, $df = 23$).

Results of the AIC-based selection revealed the most parsimonious model to include relatedness within allonursing dyads, with the only other model within 2 AIC units being the intercept-only model (Table 4.3). Across bouts and within dyads, there was a tendency for the number of allonursing bouts received by a doe's calf to increase with relatedness within allonursing dyads (PROC GLIMMIX, Estimate ± $SE = 1.1829 \pm 0.6287$, $F_{1,442} = 3.54$, $P = 0.061$) (Table 4.4). Number of allonursing bouts given, the interaction term between relatedness and number of allonursing bouts given, and absolute rank difference within dyads did not significantly influence the number of allonursing bouts received (Table 4.4), and these parameters were not included in the most parsimonious model or in any model within 2 AIC units of the most parsimonious model (Table 4.3).

**Table 4.3** Model selection based on the AIC criterion to predict the number of allonursing bouts received by a doe's own calf within dyads. Number given represents the number of allonursing bouts a doe gave to her dyadic partner's calf. The number of fitted parameters is represented by *k*.

| | Candidate Models | *k* | AIC | Δ*i* |
|---|---|---|---|---|
| 1 | relatedness + intercept | 2 | 1286.13 | |
| 2 | intercept | 1 | 1287.50 | 1.37 |
| 3 | number given + relatedness + intercept | 3 | 1292.36 | 6.23 |
| 4 | number given + relatedness + number given*relatedness + intercept | 4 | 1293.19 | 7.06 |
| 5 | number given + intercept | 2 | 1293.41 | 7.28 |
| 6 | relatedness + absolute rank difference + intercept | 2 | 1294.58 | 8.45 |
| 7 | absolute rank difference + intercept | 2 | 1295.81 | 9.68 |
| 8 | number given + relatedness + absolute rank difference + intercept | 4 | 1300.82 | 14.69 |
| 9 | number given + relatedness + number given*relatedness + absolute rank difference + intercept | 5 | 1301.61 | 15.48 |
| 10 | number given + absolute rank difference + intercept | 2 | 1301.76 | 15.63 |

**Table 4.4** Model parameter estimates ± *SE* for the parameters predicting the number of allonursing bouts received within dyads by a doe's calf.

| | Intercept | Number given | Relatedness | Number given*Relatedness | Absolute rank difference |
|---|---|---|---|---|---|
| 1 | 0.1299 ± 0.2820 | | 1.1829 ± 0.6287 | | |
| 2 | 0.0942 ± 0.2809 | | | | |
| 3 | 0.1241 ± 0.2841 | 0.0025 ± 0.0146 | 1.1727 ± 0.6320 | | |
| 4 | 0.1222 ± 0.2841 | 0.0036 ± 0.0156 | 1.0619 ± 0.8309 | 0.0559 ± 0.2745 | |
| 5 | 0.0833 ± 0.2831 | 0.0048 ± 0.0147 | | | |
| 6 | 0.1320 ± 0.2869 | | 1.1829 ± 0.6304 | | -0.0002 ± 0.0060 |
| 7 | 0.0911 ± 0.2857 | | | | 0.0004 ± 0.0060 |
| 8 | 0.1268 ± 0.2885 | 0.0025 ± 0.0147 | 1.1729 ± 0.6334 | | -0.0003 ± 0.0060 |
| 9 | 0.1240 ± 0.2887 | 0.0036 ± 0.0157 | 1.0644 ± 0.8355 | 0.0545 ± 0.2761 | -0.0002 ± 0.0061 |
| 10 | 0.0822 ± 0.2873 | 0.0048 ± 0.0148 | | | 0.0001 ± 0.0061 |

### *4.4.3 Diversity of Allonursing Partners*

The standardized Shannon-Wiener diversity index values were greater than 0.5 for both allonursing frequency (mean *H'*: 0.744 ± 0.085, $N = 25$) and duration (mean *H'*: 0.722 ± 0.085, $N = 25$) (Figure 4.2). One doe (i.e. Y2) had lower allonursing diversity values than all other does, and this doe was also the youngest (i.e. 2 years old) doe in the study group. Eight does had high standardized diversity index values for frequency (i.e. $H' \geq 0.80$), and of those eight does, five does had values above 0.80 for the duration index. Throughout the study, 234 allonursing dyadic pairs were observed of the potential 300 dyadic pairs. The 25 does had between 7 and 18 allonursing partners (mean: 13.440 ± 3.280).

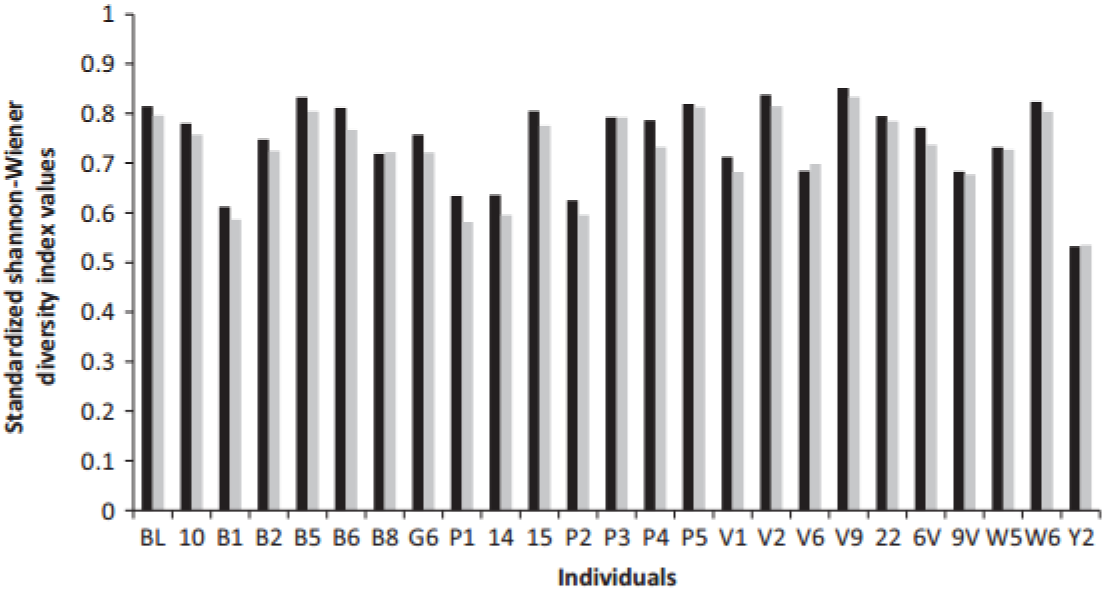

**Figure 4.2** Standardized Shannon-Wiener (*H'*) diversity indexes for frequency (black bars) and duration (grey bars).

For the frequency data, the number of partners with which does were members of reciprocal dyads (RAFI ≥ 0.8) was significantly lower than the number of partners does had ($t$ = -16.0719, $P$ < 0.001, $df$ = 24, mean difference = -11.36). For the duration data, the number of partners with which does were members of reciprocal dyads (RADI ≥ 0.8) was significantly lower than the number of partners does had ($t$ = -9.51, $P$ < 0.001, $df$ = 24, mean difference = -8.32).

Based on the frequency data, a one-unit increase in the number of allonursing bouts given had a multiplicative impact of 1.0073 on the estimated mean number of allonursing partners (Estimate ± $SE$: 0.0073 ± 0.0016, $P$ = < 0.001). Based on the duration data, a one-unit increase in the number of allonursing bouts given has a multiplicative impact of 1.0121 on the estimated mean number of allonursing partners (Estimate ± $SE$: 0.0120 ± 0.0020, $P$ = < 0.0001).

## 4.5 Discussion

With our sample size, this study provided evidence of reciprocal allonursing within a subset of dyads, with 84 dyads showing a tendency toward reciprocity and evidence of strong reciprocal allonursing in 32 dyads based on the occurrence of allonursing. This study presented patterns of reciprocal allonursing at both the group level (i.e. across bouts and dyads) and across bouts and within dyads. Our results were based on observed dyads. All the does were observed allonursing, and all but 3 calves were observed allosuckling successfully, which is in accordance with studies of allosuckling in reindeer that reported that most does and calves allonursed and allosuckled (Espmark, 1971c; Marken, 2003). The 3 does with calves that were not allonursed could not exchange the commodity of allonursing with other does. In contrast to wild fallow deer (i.e. 4 pairs of does with mean index values of 0.81 ± 0.07) (Ekvall, 1998), most reindeer does were members of at least one dyad with strong evidence of reciprocal allonursing. Compared to other studies, for example in bats (McCracken & Gustin, 1991), river buffalo (Murphey et al., 1995), red deer (Bartoš, Vaňková, Šiler, et al., 2001), lions and hyenas (Pusey & Packer, 1994), and warthogs, that did not find evidence in support of the reciprocal allonursing hypothesis, the evidence in support of reciprocal allonursing in wild fallow deer (Ekvall, 1998) and our results for reindeer may suggest that allonursing functions differently in different species and ecological conditions (see Chapters 1, 2 and 7).

We modelled allonursing interactions as a biological market place to test the suitability of the biological market theory to the behaviour of reciprocal allonursing (Noë & Hammerstein, 1994, 1995; Noë, 2001. Our results suggested that allonursing could be considered as a tradable commodity among chosen partners. We provided support for the inclusion of partner choice in modelling and testing for allonursing reciprocity. Partner choice for social interactions is common and biologically relevant for individuals living in social groups (Bshary & Grutter, 2002; Noë & Hammerstein, 1995). It was not possible to compare the diversity index values with those from other allonursing studies, since no other study has provided them. We found evidence that both the number and length of allonursing bouts are tradable commodities between lactating reindeer partners, and that both behaviours can be traded for themselves.

Our results did not support the evolution of reciprocal allonursing based on kin-selection or reciprocal altruism. We did not investigate for direct evidence of kin discrimination. There were two reasons why we could not argue that reindeer does would not have needed to evolve any specific mechanism to recognize relatives. During the calving period, the association between reindeer mothers and their adult daughters did not differ from a control sample of unrelated females (Hirotani, 1989, 1990). Secondly, rejection rates of filial and non-filial offspring were calculated as an indirect measure of calf discrimination by the lactating females (Zapata, González, et al., 2009), and the rejection rates of non-filial reindeer calves were significantly greater than those of filial calves (Engelhardt et al., 2014). Nonetheless, reciprocal allonursing was not influenced by relatedness (MacLeod & Lukas, 2014). Number of allonursing bouts received was not influenced by the number of allonursing bouts given or the interaction term between number of allonursing bouts given and relatedness, and there was no positive and strong correlation between the dyadic reciprocity index values and dyadic relatedness. That allonursing dyads interspersed non-reciprocal bouts between reciprocal bouts during the 10 weeks of study does not support the reciprocal altruism model, since non-reciprocation is defection and does not adhere to conditional strategies such as tit-for-tat or win-stay, lose-shift (Rand & Nowak, 2013). Reciprocal altruism models emphasize partner control (Rand & Nowak, 2013; Trivers, 1971), while our results supported the inclusion of partner choice as a mechanism in modeling reciprocal allonursing in reindeer. In addition, the short time frames between action and reciprocation and between successive interactions within dyads generally applied to the investigation of reciprocal altruism (Schino & Aureli, 2010) would not be suitable for the study of reciprocal allonursing. Longer time frames were needed to investigate reciprocal allonursing and partner choice, since allonursing did not occur within-bouts or in an alternated pattern.

Market selection of allonursing involves the ability to attract trading partners, and the ability to sample alternative partners efficiently (Noë & Hammerstein, 1995). An increase in the number of allonursing bouts given yielded an increase in the number of sampled partners, resulting from variation among individuals in their allonursing propensity. Large individual variations within allonursing have been reported, for example, in red deer (Drábková et al., 2008) and in guanacos (Zapata, González, et al., 2009). Sampling costs associated with potential partners were minimized for this study group compared to free-ranging reindeer, since the does were near each other over 10 weeks, which decreased the costs of searching (Noë & Hammerstein, 1995). As a consequence of sampling alternative partners, a decrease in sampling costs associated with potential partners and the ability to attract trading partners, reindeer does had a large number of partners with which they did not have a reciprocal partnership.

The temporal delay, between the costs of allonursing and the benefits when allonursing was returned, provided reindeer does the possibility of cheating without fully repaying the benefits received (Clutton-Brock, 2009). That the does directed thousands of agonistic interactions to the calves of other does while directing few to their own calf suggests that they have evolved a propensity to decrease the risk of cheating and reduce the costs, for the lactating females, of calves stealing milk. Punishment in the form of agonistic interactions directed to the calves of other does appeared to be a way to guard against cheating (Clutton-Brock & Parker, 1995).

The temporal delay may have introduced inflation into a biological market through potential devaluing of the commodity (e.g. occurrence and/or duration of allonursing) by giving reindeer does opportunities to accumulate proximate benefits from other partners before allonursing could be repayed, which could have led to shifts in the supply/demand ratio (i.e. reindeer does having to provide more allonursing than their calves received) (Newton-Fisher & Lee, 2011). Physiological and temporal variations in milk production can create individual and/or temporal high differences in milk availability, which can influence the time period between successive allonursing bouts, the occurrence and the duration of allonursing reciprocation. When any member of a reciprocal dyad required its offspring to be allonursed, due to its milk reserves having been depleted, the value of an allonursing bout may have increased, and the repaying of the altruistic act may have increased beyond the matching in occurrences and/or duration of allonursing. In addition to the devaluation of the allonursing currency due to the actions of other individuals, the repayment of the allonursing 'debt' may take the form of having to provide more allonursing than what was received by giving multiple allonursing bouts or a longer allonursing bout. The tendency for one member of each dyad to provide more of the allonursing (e.g. occurrences and duration) may be partially accounted for due to the high value placed on an allonursing bout, when a doe's calf was in high need for consuming milk, and the devaluation of the allonursing currency due to the actions of other individuals.

The results testing the milk-theft and mismothering hypotheses for allosuckling in reindeer provided support to the milk-theft hypothesis, whereas limited support for the mismothering hypothesis was found (Engelhardt et al., 2014). The hypotheses of milk evacuation (Roulin, 2002), milk-theft (Packer et al., 1992), and mismothering due to the hypothesized inability to discriminate their own calf from the calves of other does (Roulin, 2002) could lead our results of reciprocity and partner choice to be interpreted as an active or passive consequence of indiscriminate nursing and apparent reciprocal allonursing and partner choice. However, reindeer does actively rejected calves attempting to allonurse while allowing other calves to allonurse, and directed their agonistic interactions toward the calves of others, when within a body length of a doe's udders, instead of toward their own calf. Does rarely allonursed without nursing their own calf, which did not support the milk evacuation hypothesis (Roulin, 2002), and allosuckling in reindeer supported the milk-theft hypothesis (Engelhardt et al., 2014). Therefore, we argue that the evidence of reciprocal allonursing and partner choice was not due to indiscriminate allonursing. Although the evidence supports reciprocal allonursing, the results could be a consequence of pseudo-reciprocity due to a by-product of other causes and functions of allonursing. A higher number or duration of allonursing given within a dyad did not influence the number or duration of allonursing received, and as such did not artificially inflate the RAFI values. Therefore, we argue that the reciprocal allonursing across bouts and within dyads was not an artefact of the large sample size collected, or an arithmetic artefact resulting from the tendency of some does to allonurse large numbers of calves (Murphey et al., 1995), or the number or duration of allonursing bouts given within a dyad.

A number of non-mutually exclusive hypotheses have been proposed to explain the causes and functions of allonursing, which are not well understood. Our results provided evidence that allonursing was partially explained by reciprocity. The milk-theft (Engelhardt et al., 2014) and reciprocity hypotheses were non-mutually exclusive hypotheses that partially explained the causes and functions of allosuckling and allonursing in reindeer. The 132 dyads within which allonursing was unidirectional may be explained by the other non-mutually exclusive hypotheses, with the exception of milk evacuation since does rarely allonursed without nursing their own calf (Roulin, 2002). Females are hypothesised to allonurse to evacuate surplus milk that their own offspring did not consume, and the milk evacuation hypothesis does not apply when a female's offspring is still hungry (e.g. attempting to suckle from its mother) or attempting to allosuckle (Roulin, 2002). Evidence in support of the milk-theft hypothesis has been reported, among other studies, in red deer (Landete-Castillejos, García, Garde, et al., 2000), river buffalo (Murphey et al., 1995), guanacos (Zapata, González, et al., 2009), bactrian camels (Brandlová et al., 2013) and reindeer (Engelhardt et al., 2014). Lactating females may allonurse to compensate for growth and/or nutritional deficiency by letting down milk surplus, such as in red deer (Bartoš, Vaňková, Hyánek, et al., 2001), cows (*Bos taurus*) (Víchová & Bartoš, 2005) and guanacos (Zapata et al., 2010).

The marginally significant increase in the number of allonursing bouts received as relatedness within dyads increased may imply kin recognition mechanisms. The association between reindeer females, other than calves, during calving was reported not to be influenced by relatedness (Hirotani, 1989, 1990). Rejection rates were calculated as an indirect measure of offspring discrimination by lactating females in guanacos (Zapata, González, et al., 2009) and in reindeer (Engelhardt et al., 2014). The rejection rates of non-filial offspring were significantly greater than those of filial offspring in both guanacos (Zapata, González, et al., 2009) and reindeer (Engelhardt et al., 2014). Therefore, we could not argue that reindeer does did not need to evolve any specific mechanism to recognize relatives by kin recognition mechanisms. In contrast to reindeer in our study population, red deer hinds on the Isle of Rhum were reported to be more frequently associated with their female offspring than male offspring less than 2 years old (Guinness, Hall, & Cockerill, 1979), and may not have needed to evolve any specific mechanism to recognize relatives by kin recognition mechanisms (Bartoš, Vaňková, Hyánek, et al., 2001; Bartoš, Vaňková, Šiler, et al., 2001). Allonursing may function to increase inclusive fitness benefits (Roulin, 2002), as has been reported in studies of lions (*Panthera leo*) (Pusey & Packer, 1994), dwarf mongooses (*Helogale parvula*) (Creel et al., 1991), meerkats (*Suricata suricatta*) (MacLeod & Clutton-Brock, 2014), house mice (*Mus domesticus*) (König, 1994a; Wilkinson & Baker, 1988), grey mouse lemur (*Microcebus murinus*) (Eberle & Kappeler, 2006) and fallow deer (Ekvall, 1998). In wild fallow deer, successful allosuckling was common between members in a stable social unit but was not observed between groups, which may be due to kin-selection (Ekvall, 1998). That the effect of relatedness on the number of allonursing bouts received was only marginally significant may suggest that the function of inclusive fitness benefits on allonursing may be minimal in reindeer. In addition, the odds of a successful allosuckling bout were not influenced by the relatedness of reindeer does in the same study group (Engelhardt et al., 2014). Alternatively, this may suggest that allonursing functions differently in different species and ecological conditions. These findings prompt for studies designed to experimentally test for kin recognition mechanisms and the kin-selection allonursing hypothesis.

In the presence of a steep social hierarchy and high competition for monopolizable resources, a commodity would be predicted to be interchanged for rank-related benefits, such as access to the monopolized resources, and the distribution of the commodity would be influenced by the social rank (Barrett et al., 1999; Leinfelder et al., 2001). There were no apparent rank-related benefits associated with trading allonursing among chosen reindeer partners, and the distribution of allonursing was not influenced by social rank. Even though the social hierarchy among reindeer was steep, resources, such as natural and supplemental forage, could not be monopolized.

The mean duration of allonursing bouts was 36.78 ± 65.47 s in bactrian camels (Brandlová et al., 2013), 0.9 ± 0.06 min in zebu (Das, Redbo, & Wiktorsson, 2000), 41.7 ± 8.7 s in fallow deer (Ekvall, 1998), 67.52 ± 7.22 s in red deer (Drábková et al., 2008), 319 s in June and 405 s in September in cattle cows (Waltl et al., 1995), and 1.5 ± 0.54 min and 2.1 ± 0.80 min in guanacos (Zapata, González, et al., 2009). The mean duration of allonursing was lower in reindeer than in other species. This may have been due to the large number of allonursing attempts by calves and the large number of calves that attempted to allonurse when a doe's calf was being nursed: we recorded over 500 occurrences of 2, 3, 4, and 5 calves attempting to simultaneously allonurse from the same doe. With so many calves attempting to allonurse simultaneously, a doe’s lactation costs and the costs to her own calf increased, and this may have resulted in does terminating nursing and allonursing bouts earlier than in other species. Calves being allonursed were often displaced by other calves that were attempting to allonurse, which decreased the duration of allonursing bouts. The large number of agonistic interactions directed to non-filial calves within a body length of the doe’s udders may have acted as a deterrent and resulted in short allonursing bouts.

Our results provided evidence of reciprocal allonursing at the group level and reciprocal allonursing among chosen partners. The standardized diversity index values indicated that the relative proportions of allonursing duration and frequency were not distributed evenly among all potential partners, although the index values were relatively high. Across bouts and within dyads, the number of allonursing bouts received was only marginally influenced by relatedness. Subsequent research and data collection will be needed to assess the kin-selection allonursing hypothesis by implementing an experimental design with does and their calves categorized into study groups based on the relatedness of the does. Our results pointed to the usefulness of applying the biological market theory to study the evolution of cooperation for allonursing and for considering allonursing as a tradable commodity among chosen partners.

### 4.6 Appendices

Tables 4.5, 4.6 and 4.7 are the matrices for the matrix correlation tests.

**Table 4.5** Matrix of the number of allonursing given (vertical column of doe identity) to another doe's calf and received (horizontal row of doe identity) by a doe's own calf.

| Doe | V1 | P5 | W5 | P2 | P3 | P1 | W6 | 15 | 22 | B8 | 10 | 14 | B5 | V6 | P4 | 6V | Y2 | 9V | V9 | B6 | BL | B2 | V2 | B1 | G6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| V1 | 0 | 6 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 2 | 0 | 1 |
| P5 | 1 | 0 | 5 | 2 | 0 | 1 | 1 | 0 | 0 | 5 | 2 | 0 | 1 | 3 | 6 | 0 | 2 | 6 | 1 | 0 | 0 | 1 | 3 | 1 | 5 |
| W5 | 1 | 10 | 0 | 2 | 0 | 1 | 2 | 0 | 0 | 4 | 1 | 0 | 0 | 2 | 11 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 4 | 0 | 6 |
| P2 | 0 | 3 | 1 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 4 | 0 | 1 |
| P3 | 2 | 11 | 6 | 6 | 0 | 3 | 5 | 0 | 0 | 0 | 7 | 0 | 0 | 3 | 8 | 0 | 0 | 10 | 1 | 0 | 4 | 1 | 2 | 0 | 5 |
| P1 | 1 | 3 | 3 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 |
| W6 | 4 | 11 | 5 | 1 | 3 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 1 | 2 | 10 | 1 | 1 | 3 | 2 | 0 | 2 | 2 | 2 | 0 | 5 |
| 15 | 3 | 5 | 5 | 0 | 1 | 0 | 4 | 0 | 0 | 5 | 1 | 0 | 2 | 5 | 5 | 0 | 0 | 3 | 1 | 0 | 0 | 6 | 1 | 0 | 4 |
| 22 | 0 | 7 | 5 | 2 | 0 | 1 | 2 | 0 | 0 | 3 | 3 | 0 | 0 | 3 | 6 | 0 | 0 | 2 | 0 | 0 | 0 | 4 | 4 | 2 | 3 |
| B8 | 1 | 8 | 1 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 8 | 0 | 0 | 4 | 0 | 0 | 1 | 0 | 2 | 2 | 7 |
| 10 | 2 | 5 | 1 | 2 | 4 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 5 | 0 | 0 | 3 | 0 | 0 | 2 | 2 | 3 | 0 | 4 |
| 14 | 1 | 6 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 2 |
| B5 | 3 | 10 | 3 | 1 | 2 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 2 | 0 | 2 | 2 | 1 | 0 | 1 | 2 | 4 | 0 | 3 |
| V6 | 1 | 12 | 5 | 1 | 1 | 0 | 4 | 0 | 0 | 4 | 2 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 1 | 0 | 2 |
| P4 | 2 | 6 | 2 | 2 | 1 | 0 | 4 | 0 | 0 | 0 | 5 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 3 | 0 | 2 |
| 6V | 3 | 5 | 5 | 1 | 3 | 1 | 2 | 0 | 0 | 1 | 6 | 0 | 0 | 4 | 12 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 3 | 0 | 4 |
| Y2 | 1 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 9V | 2 | 9 | 5 | 1 | 3 | 0 | 2 | 0 | 0 | 3 | 2 | 0 | 0 | 7 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| V9 | 3 | 4 | 4 | 2 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 3 | 0 | 3 | 3 | 0 | 1 | 2 | 4 | 2 | 0 | 2 |
| B6 | 3 | 8 | 2 | 2 | 2 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 7 | 0 | 2 | 1 | 0 | 0 | 2 | 3 | 1 | 0 | 2 |
| BL | 2 | 7 | 3 | 0 | 3 | 0 | 3 | 0 | 0 | 2 | 4 | 0 | 2 | 4 | 9 | 0 | 3 | 3 | 0 | 0 | 0 | 3 | 7 | 0 | 3 |
| B2 | 0 | 10 | 2 | 1 | 2 | 1 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 6 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 1 | 2 |
| V2 | 10 | 9 | 5 | 2 | 4 | 1 | 1 | 0 | 0 | 3 | 5 | 0 | 2 | 7 | 8 | 0 | 3 | 4 | 0 | 0 | 3 | 3 | 0 | 1 | 1 |
| B1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 4 |
| G6 | 3 | 3 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 2 | 4 | 8 | 0 | 0 | 2 | 0 | 0 | 2 | 4 | 3 | 0 | 0 |

**Table 4.6** Matrix of the duration in seconds of allonursing given (vertical column of doe identity) to another doe's calf and received (horizontal row of doe identity) by a doe's own calf.

| Doe | V1 | P5 | W5 | P2 | P3 | P1 | W6 | 15 | 22 | B8 | 10 | 14 | B5 | V6 | P4 | 6V | Y2 | 9V | V9 | B6 | BL | B2 | V2 | B1 | G6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| V1 | 0 | 67 | 6 | 10 | 0 | 0 | 27 | 0 | 0 | 0 | 12 | 0 | 0 | 55 | 16 | 0 | 0 | 10 | 0 | 0 | 8 | 14 | 22 | 0 | 8 |
| P5 | 5 | 0 | 68 | 22 | 0 | 5 | 15 | 0 | 0 | 71 | 34 | 0 | 5 | 28 | 71 | 0 | 26 | 68 | 18 | 0 | 0 | 19 | 29 | 25 | 54 |
| W5 | 12 | 148 | 0 | 33 | 0 | 13 | 30 | 0 | 0 | 56 | 13 | 0 | 0 | 23 | 116 | 0 | 0 | 18 | 6 | 0 | 22 | 8 | 44 | 0 | 61 |
| P2 | 0 | 53 | 16 | 0 | 57 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 39 | 0 | 0 | 0 | 12 | 0 | 0 | 6 | 41 | 0 | 5 |
| P3 | 28 | 149 | 74 | 76 | 0 | 45 | 60 | 0 | 0 | 0 | 103 | 0 | 0 | 33 | 127 | 0 | 0 | 113 | 9 | 0 | 52 | 23 | 25 | 0 | 76 |
| P1 | 12 | 32 | 26 | 0 | 17 | 0 | 10 | 0 | 0 | 0 | 73 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 | 0 | 13 |
| W6 | 56 | 165 | 48 | 12 | 32 | 0 | 0 | 0 | 0 | 24 | 46 | 0 | 9 | 16 | 158 | 12 | 21 | 30 | 43 | 0 | 35 | 24 | 36 | 0 | 68 |
| 15 | 39 | 81 | 44 | 0 | 10 | 0 | 65 | 0 | 0 | 81 | 6 | 0 | 25 | 72 | 104 | 0 | 0 | 21 | 18 | 0 | 0 | 108 | 12 | 0 | 53 |
| 22 | 0 | 105 | 85 | 39 | 0 | 12 | 36 | 0 | 0 | 46 | 36 | 0 | 0 | 56 | 109 | 0 | 0 | 36 | 0 | 0 | 0 | 66 | 50 | 36 | 17 |
| B8 | 9 | 110 | 25 | 29 | 6 | 0 | 29 | 0 | 0 | 0 | 0 | 0 | 0 | 43 | 85 | 0 | 0 | 49 | 0 | 0 | 7 | 0 | 35 | 43 | 91 |
| 10 | 18 | 87 | 31 | 17 | 72 | 0 | 38 | 0 | 0 | 0 | 0 | 0 | 0 | 39 | 89 | 0 | 0 | 27 | 0 | 0 | 18 | 21 | 44 | 0 | 55 |
| 14 | 14 | 63 | 0 | 0 | 11 | 0 | 10 | 0 | 0 | 29 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 19 | 0 | 0 | 12 | 0 | 0 | 0 | 91 |
| B5 | 54 | 148 | 59 | 23 | 22 | 9 | 12 | 0 | 0 | 14 | 19 | 0 | 0 | 70 | 23 | 0 | 16 | 26 | 9 | 0 | 12 | 18 | 57 | 0 | 45 |
| V6 | 29 | 209 | 81 | 12 | 32 | 0 | 83 | 0 | 0 | 58 | 36 | 0 | 0 | 0 | 106 | 0 | 0 | 0 | 0 | 0 | 0 | 110 | 22 | 0 | 37 |
| P4 | 44 | 128 | 24 | 42 | 9 | 0 | 74 | 0 | 0 | 0 | 181 | 0 | 15 | 47 | 0 | 0 | 0 | 40 | 0 | 0 | 14 | 36 | 54 | 0 | 27 |
| 6V | 32 | 77 | 78 | 9 | 57 | 7 | 15 | 0 | 0 | 9 | 71 | 0 | 0 | 70 | 181 | 0 | 0 | 21 | 0 | 0 | 9 | 0 | 34 | 0 | 45 |
| Y2 | 6 | 31 | 0 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 7 | 0 | 0 | 0 | 11 | 10 | 0 | 0 |

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 9V | 27 | 107 | 57 | 9 | 47 | 0 | 26 | 0 | 0 | 34 | 17 | 0 | 0 | 96 | 103 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 0 | 0 |
| V9 | 58 | 63 | 61 | 27 | 0 | 0 | 54 | 0 | 0 | 6 | 35 | 0 | 0 | 27 | 48 | 0 | 36 | 48 | 0 | 8 | 20 | 48 | 36 | 0 | 24 |
| B6 | 39 | 154 | 23 | 23 | 14 | 16 | 0 | 0 | 0 | 52 | 6 | 0 | 37 | 26 | 144 | 0 | 32 | 9 | 0 | 0 | 21 | 55 | 12 | 0 | 27 |
| BL | 23 | 102 | 31 | 0 | 27 | 0 | 40 | 0 | 0 | 37 | 42 | 0 | 22 | 44 | 135 | 0 | 31 | 41 | 0 | 0 | 0 | 27 | 88 | 0 | 35 |
| B2 | 0 | 190 | 34 | 18 | 32 | 29 | 59 | 0 | 0 | 0 | 10 | 0 | 0 | 36 | 69 | 0 | 0 | 34 | 0 | 0 | 105 | 0 | 30 | 7 | 35 |
| V2 | 247 | 191 | 84 | 51 | 57 | 6 | 17 | 0 | 0 | 83 | 72 | 0 | 28 | 159 | 221 | 0 | 58 | 84 | 0 | 0 | 73 | 75 | 0 | 13 | 35 |
| B1 | 0 | 27 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 12 | 0 | 8 | 9 | 0 | 0 | 0 | 29 | 0 | 0 | 46 |
| G6 | 162 | 39 | 0 | 0 | 9 | 22 | 21 | 0 | 0 | 24 | 0 | 0 | 37 | 62 | 125 | 0 | 0 | 36 | 0 | 0 | 28 | 64 | 59 | 0 | 0 |

**Table 4.7** Matrix of dominance rank of the potential partners. Higher numbers equal higher rank.

| Doe | V1 | P5 | W5 | P2 | P3 | P1 | W6 | 15 | 22 | B8 | 10 | 14 | B5 | V6 | P4 | 6V | Y2 | 9V | V9 | B6 | BL | B2 | V2 | B1 | G6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| V1 | 0 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| P5 | 25 | 0 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| W5 | 25 | 24 | 0 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| P2 | 25 | 24 | 23 | 0 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| P3 | 25 | 24 | 23 | 22 | 0 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| P1 | 25 | 24 | 23 | 22 | 21 | 0 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| W6 | 25 | 24 | 23 | 22 | 21 | 20 | 0 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| 15 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 0 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| 22 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 0 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| B8 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 0 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| 10 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 0 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| 14 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 0 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| B5 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 0 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| V6 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 0 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| P4 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 0 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| 6V | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 0 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| Y2 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 0 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| 9V | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 0 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| V9 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 0 | 6 | 5 | 4 | 3 | 2 | 1 |
| B6 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 0 | 5 | 4 | 3 | 2 | 1 |
| BL | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 0 | 4 | 3 | 2 | 1 |
| B2 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 0 | 3 | 2 | 1 |
| V2 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 0 | 2 | 1 |
| B1 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 0 | 1 |
| G6 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 0 |

## Chapter 5 Allosuckling in Reindeer (*Rangifer tarandus*): A Test of the Improved Nutrition and Compensation Hypotheses.

This chapter is based on the published manuscript: Sacha C. Engelhardt, Robert B. Weladji, Øystein Holand, Mauri Nieminen. 2016. Allosuckling in reindeer (*Rangifer tarandus*): a test of the improved nutrition and compensation hypotheses. Mammalian Biology 81: 146-152.

### 5.1 Abstract

The hypothesized causes and functions of allosuckling can co-occur and influence each other (i.e. non-mutually exclusive). In our two previous studies of allosuckling in reindeer, *Rangifer tarandus*, the milk-theft and reciprocity hypotheses were supported; the mismothering hypothesis received partial support; and the kin-selection hypothesis was not supported. In this study we investigated: the compensation hypothesis, stating that offspring may allosuckle to compensate for low birth mass, insufficient maternal milk supply (i.e. high maternal rejection rates, low mass of mothers and a large number of allonursing bouts performed by a calf's mother) or inadequate growth; and the improved nutrition hypothesis, stating that offspring improve their nutrition, and hence mass gain, by ingestion of non-maternal milk in addition to maternal milk For the compensation hypothesis, we predicted that: 1) the cumulative number of allosuckling bouts performed by a calf (hereafter, number of allosuckling bouts) would increase due to low birth mass of calves and other measures of insufficient maternal milk supply; 2) the percentage of mass gain would not be related to the number of allosuckling bouts (i.e. calves that allosuckled often would have the same percentage of mass gain as calves that allosuckled less often) or would have a negative relationship with the number of allosuckling bouts (i.e. calves that allosuckled often would have a lower percentage of mass gain than calves that allosuckled less often); and 3) a negative relationship between the percentage of mass gain and the number of allosuckling bouts would vary with birth mass (i.e. interaction term). For the improved nutrition hypothesis, we predicted that the percentage of mass gain of calves that allosuckled often would increase more than for calves that allosuckled less often. We tested the compensation and improved nutrition hypotheses on 25 mother-calf pairs of semi-domesticated reindeer from parturition to 67 days of age of calves. The number of allosuckling bouts was not influenced by low birth mass of calves or other measures of insufficient maternal milk supply. Percentage of mass gain increased as the number of allosuckling bouts increased. Calves born heavier had a lower percentage of mass gain than calves born lighter. The relationship between percentage of mass gain and number of allosuckling bouts did not vary with birth mass. Our findings did not support the compensation hypothesis. Our results suggest that allosuckling functioned to improve nutrition by ingesting non-maternal milk in addition to maternal milk, which increased the percentage of mass gain.

Keywords: Allosuckling, Compensation, Improved nutrition, Cooperative breeding, Growth, *Rangifer tarandus*

### 5.2 Introduction

The suckling by offspring from females other than their own mother is referred to as allosuckling. The provision of milk to the offspring of other mothers is referred to as allonursing. A number of hypotheses that can co-occur and influence each other (i.e. non-mutually exclusive) have been proposed to explain the causes and functions of allonursing (Roulin, 2002, 2003; Víchová & Bartoš, 2005). The misdirected maternal care hypothesis (due to milk-theft or to a lack of efficient kin recognition mechanisms) (Engelhardt et al., 2014; Packer et al., 1992; Roulin, 2002) is maladaptive from the point of view of lactating females. The offspring parasitism strategy of milk-theft is adaptive from the point of view of offspring (Engelhardt et al., 2014; Packer et al., 1992; Zapata, González, et al., 2009). The kin-selection, reciprocity, learning to parent, milk evacuation (Roulin 2002), compensation (Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005), neuroendocrine (Roulin 2003) and improved nutrition hypotheses of allonursing are adaptive hypotheses. Kin-selection functions by increasing indirect fitness benefits if a lactating female shares genes by common descent, allowing her genes to spread in the population and increase her inclusive fitness (Roulin, 2002). Reciprocal allonursing functions when two females achieve a higher fitness when nursing each other's offspring to a similar extent than when they do not share milk (Engelhardt, Weladji, Holand, Røed, & Nieminen, 2015; Roulin, 2002). Learning to parent improves maternal skills (Roulin, 2002). Milk evacuation functions to allow lactating females evacuate milk that their own offspring did not drink, and it is caused by physiological mechanisms to avoid mastitis and to stimulate the teat for the synthesis and secretion of milk (Roulin, 2002). Offspring allosuckle to compensate for low offspring birth mass, insufficient maternal milk supply or inadequate growth (Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005). Teat stimulation by allonursing can optimally adjust prolactin concentration and induce milk production (e.i. the neuroendocrine hypothesis, Roulin, 2003). Lactating females improve immunocompetence by transferring specific immune compounds not possessed by a mother (Roulin & Heeb, 1999). Allonursing may be constrained by costs (i.e. occurring when the costs are likely the lowest) rather than explained by the likely benefits (MacLeod & Lukas, 2014). Allonursing may increase maternal costs (e.g. increasing the amount of time a mother has to forage to compensate for the losses of milk due to allonursing) (Packer et al., 1992), decrease amounts of nutrients available to an allonursing female's own offspring, which may reduce offspring growth gains (Packer et al., 1992), increase mortality rates due to the high costs of lactation (Clutton-Brock et al., 1989), and increase pathogen transmission between foster and genetic mothers implying costs to all allosuckling offspring and allonursing females (Roulin & Heeb, 1999). Pathogen transmission through milk transfer to allosuckling offspring may reduce the total net immunological benefits (Roulin & Heeb, 1999).

Allosuckling is hypothesized to function to improve offspring nutrition, and hence mass gain, by ingestion of non-maternal milk in addition to maternal milk (Packer et al., 1992; Riedman, 1982). In studies of laboratory rodents provided with unlimited access to food (König, 1993; Mennella et al., 1990; Sayler & Salmon, 1969; Werboff et al., 1970) and in red deer, *Cervus elaphus* (Landete-Castillejos et al., 2005), allosuckling offspring benefited in mass gain by ingesting milk surplus when compared to non-allosuckling offspring. However, the compensation hypothesis proposes that offspring allosuckle to compensate for deficiencies, i.e. low birth mass, inadequate growth or insufficient maternal milk supply (Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005) and was supported by 9 studies (see Table 5.1). Maternal suckling rate, mass of mothers, cumulative number of allonursing bouts performed by an offspring's mother (hereafter, number of allonursing bouts), and milk availability were predictors used as proxies of maternal milk supply in previous studies assessing the compensation hypothesis (Bartoš, Vaňková, Hyánek, et al., 2001; Murphey et al., 1995; Réale, Boussès, & Chapuis, 1999; Víchová & Bartoš, 2005; Zapata et al., 2010). Offspring allosuckled to compensate for inadequate growth in red deer (Bartoš, Vaňková, Hyánek, et al., 2001), cattle, *Bos taurus* (Víchová & Bartoš, 2005), and mouflon, *Ovis orientalis* (Réale et al., 1999) (see Table 5.1). For example, frequently allosuckling cattle calves tended to grow less and tended to reach lower weaning masses than calves that allosuckled less often (Víchová & Bartoš, 2005).

In guanacos, *Lama guanicoe* allosuckling and non-allosuckling calves had similar daily mass gains and mass at 60 days of age, and daily mass gains and mass at 60 days of age were not related to the percentage of allosuckling and allonursing (Zapata et al., 2010) (see Table 5.1).

**Table 5.1** List of studies and species for which authors concluded that observations of allosuckling supported the compensation hypothesis, and the evidence that supported the compensation hypothesis.

| Species | Allosuckling to compensate for | | | | | Allosuckling to compensate for | |
|---|---|---|---|---|---|---|---|
| | low birth mass | low maternal acceptance rate | low mass of mother | allonursing performed by offspring's mother | insufficient maternal milk availability | Lower mass at weaning, lower percentage of mass gain, and/or lower growth rate | Allosuckling offspring achieved similar daily mass gains and similar mass as offspring that did not allosuckle |
| *Bos taurus* | Víchová and Bartoš (2005) | Víchová and Bartoš (2005) | | | Nicoll (1982a, 1982b),<br>Waltl et al. (1995) | Víchová and Bartoš (2005) | |
| *Cervus elaphus* | | | | Bartoš, Vaňková, Hyánek, et al. (2001) | | Bartoš, Vaňková, Hyánek, et al. (2001) | |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Lama guanicoe* | | Zapata et al. (2010) | Zapata et al. (2010) | | | *Zapata et al. (2010) |
| *Dama dama* | Pélabon et al. (1998) | | | | | |
| *Bubalus bubalis* | | | | Murphey et al. (1995) | Murphey et al. (1995) | |
| *Ovis orientalis* | | Réale et al. (1999) | | | Réale et al. (1999) | |

*Allosuckling and non-allosuckling guanaco calves had similar daily mass gains and mass at 60 days of age, and daily mass gains and mass at 60 days of age were not related to the percentage of allosuckling and allonursing (Zapata et al., 2010). Allosuckling guanaco calves did not have greater daily mass gains than non-allosuckling calves (Zapata et al., 2010).

In this study, we tested two hypotheses: the compensatory (i.e. to assess whether allosuckling calves were compensating for low birth mass, insufficient maternal milk supply or inadequate growth) and improved nutritional functions of allosuckling in reindeer, *Rangifer tarandus*. High maternal rejection rates, low mass of mothers after parturition and a large number of allonursing bouts performed by a calf's mother were indirect measures of insufficient maternal milk supply. We tested the compensation hypothesis with 3 predictions: 1) the number of allosuckling bouts would increase due to low birth mass of calves and other measures of insufficient maternal milk supply; 2) the percentage of mass gain would not be related to the number of allosuckling bouts (i.e. calves that allosuckled often would have the same percentage of mass gain as calves that allosuckled less often) or would have a negative relationship with the number of allosuckling bouts (i.e. calves that allosuckled often would have a lower percentage of mass gain than calves that allosuckled less often); and 3) a negative relationship between the percentage of mass gain and the number of allosuckling bouts would vary with birth mass (i.e. interaction term). We tested the hypothesized improved nutritional function of allosuckling with the prediction: 1) the percentage of mass gain of calves that allosuckled often would increase more than for calves that allosuckled less often.

## 5.3 Materials and Methods

### *5.3.1 Study Area and Study Population*

This study was conducted at the Kutuharju Field Reindeer Research Station near Kaamanen, Finland (69º N, 27º E). Most of the methods have been previously reported (Engelhardt et al., 2014, 2015). This research project was in accordance with the Animal Ethics and Care Certificate provided by Concordia University (AREC-2010-WELA) and the Finnish National Advisory Board on Research Ethics.

Reindeer females are plural breeders (i.e. several breeding females that cooperatively breed with low reproductive skew and no reproductive suppression) (Mumme, 1997). Reindeer calves are gradually weaned, and the lactation cycle usually ends in September to October during rut (Eloranta et al., 1990; White & Luick, 1984). The first 25 calves to be born (14 males and 11 females) and their mothers were selected for this study and separated from the herd for 10 weeks. The birth mass of the calves in this study was recorded within 48 h after parturition to the nearest

0.1 Kg with a hand-held scale. The mass of mothers in this study was recorded after parturition on May 15th (i.e. May 15th: this mass was correlated to the pre-parturition mass of April 24th, $r$ = 0.89), by herding individual reindeer to walk onto an electronic scale, and the mass was recorded to the nearest 1 Kg. The mass of the calves and mothers was recorded near the end of the study, July 18th 2012, by herding individual reindeer to walk onto an electronic scale, and the mass was recorded to the nearest 0.1 Kg.

Mother-calf pairs were assigned in the field within 48 h. To assess the mother-calf assignments in the field and the precision of the designation of allosuckling/allonursing bouts collected in the field as allosuckling/allonursing bouts, blood samples were obtained from all individuals and analysed for 16 DNA microsatellite loci as part of an ongoing progeny testing within this experimental herd (Pintus et al., 2015; Røed et al., 2002). Parenthood assignments were analysed with the simulation program software CERVUS 3.0 (Kalinowski et al., 2007), which is based on likelihood ratios between candidate parents. Within the herd all microsatellites were in Hardy Weinberg equilibrium, and no mismatches were detected for the assigned mother-calf combinations used in the present study. All mother-calf assignments from field observations were supported by the DNA analyses (Engelhardt et al., 2014, 2015).

### *5.3.2 Behavioural Observations*

The methods used for behavioural observations were previously published (Engelhardt et al., 2014, 2015). The occurrence of a supplemental feeding bout was recorded when a calf was filling its mouth with pellets, lichen or birch leaves, and one supplemental feeding bout could consist of a calf filling its mouth several times with either pellets, lichen or birth leaves. An occurrence of a supplemental feeding bout was completed when a calf walked away from the supplemental feed. Using a stopwatch, the duration of a supplemental feeding bout was recorded as the cumulative time a calf spent filling its mouth with supplemental feed.

### *5.3.3 Statistical Analyses*

Following a recommendation by Kline (2009), all continuous variables were standardized to z-scores to detect outliers with absolute z-score values greater than 3. There were no outliers for the variables percentage of mass change, number of supplemental feeding bouts, mass of mothers after parturition (i.e. May 15th), maternal rejection rates and number of allonursing bouts. There was 1 outlier for birth mass and 1 outlier for number of allosuckling bouts, and both outliers came from the same calf. The outlier for birth mass was not replaced, since heavier reindeer calves are expected and have been recorded in the population (i.e. this is a natural aspect of the variable birth mass). Based on the birth mass of 2860 reindeer calves collected between 1970 and 2012 at the Kutuharju Field Reindeer Research Station, the mean ± SD birth mass was 5.63 ± 1.06 Kg, and the birth mass of calves ranged from 1.8 Kg to 10.4 Kg. This calf with 221 allosuckling bouts was successful on 221 occurrences, and this data point was not erroneous. If this calf with outlier scores was not from the same population as the rest of the calves, then it may have been best to remove that case from the sample (Kline, 2009). This calf did belong to the population, and it was not best to remove this individual from the sample. The outlier for number of allosuckling bouts was converted to a value that equalled the next most extreme score that was within 3 standard deviations of the mean (i.e. a z-score of 1.917, and the value of the number of allosuckling bouts for the individual calf with a z-score of 1.917 was 153) (Kline, 2009). Therefore, we replaced the value of number of allosuckling bouts from 221 to 153.

To test our prediction 1 of the compensation hypothesis, a generalized linear model with a negative binomial distribution and log link function was conducted to assess how the number of allosuckling bouts of the individual calves was influenced by birth mass of calves, mass of mothers after parturition (i.e. May 15th), number of allonursing bouts by the mother to another offspring, sex of calves and maternal rejection rates. Sex of calves was added as a covariate since male river buffalo, *Bubalus bubalis*, calves allosuckled longer and had higher mass gain than female calves (Paranhos da Costa et al., 2000) and female cattle calves had a higher incidence of allosuckling than male calves (Víchová & Bartoš, 2005). The number of allonursing bouts, maternal rejection rates and the number of allosuckling bouts were adjusted additively from birth of each calf to 67 days of age. The age of 67 days for calves was selected, since it was the age of the youngest calf on July 18th 2012, which was the last day of weighing.

To test our predictions 2 and 3 of the compensation hypothesis and the prediction for the improved nutrition hypothesis, a general linear model was conducted to assess how the percentage of mass gain of calves was influenced by the number of allosuckling bouts, birth mass, the interaction term birth mass x number of allosuckling bouts, cumulative number of supplemental feeding bouts (i.e. pellets, lichen, birch leaves) (hereafter, number of supplemental feeding bouts) and calf sex as predictors on the response variable percentage of mass gain of calves. Sex of calves was added as a covariate. The number of supplemental feeding bouts (i.e. pellets, lichen, birch leaves) was added as a covariate, since the calves had access to supplemental feeding. The percentages of mass gain were adjusted using classical least squares model for each calf to predict the percentage of mass gain of each calf at the age of 67 days. The number of supplemental feeding bouts was adjusted additively from birth of each calf to 67 days of age. We conducted a general linear model to assess how the mass of calves was influenced by the same predictors as those in the model with percentage of mass gain as the response.

All models were analysed in R version 3.0.1 (R Core Team, 2013), using the MASS, car, and MuMin packages. The Mass package was used to run the negative binomial regression with the glm.nb function (Venables & Ripley, 2002). The car package was used to inspect for multicollinearity of the first-order terms using the variation inflation factor with the VIF function (Fox & Weisberg, 2011). The MuMin package was used to assess the full model-averaged coefficients (with shrinkage) and relative importance of variables using the dredge function (Barton, 2013). The MuMin's dredge function was also used to generate the values of multiple R2, the adjusted R2, the AICc values, the delta AICc, and the model weights for all possible models. For all models, we first inspected for multicollinearity of the first-order terms using the variation inflation factor, and the values were less than 5 (Montgomery & Peck, 1992). Based on an information-theoretical approach, model selection for all models was performed using Akaike's Information Criterion (AICc) with the smallest AICc value indicating the best-fit model, and we reported the differences between the AICc value of the best model and that of seven other models, the Akaike weights, and the evidence ratios (*ER*) (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). For each variable, a model weight was calculated by summing the Akaike weight of each model in which the variable appeared in order to estimate the relative importance of the variable (Symonds & Moussalli, 2011). Due to model selection uncertainty, we performed model averaging using the full set of models and reported the estimates for the parameters of the global model and the unconditional variance (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). For the sake of pluralism and because we were also interested in effect size, direction, and parameter precision, we reported parameter estimates and their accompanying $P$ values (Stephens et al., 2005) for models not distinguishable from the best model (i.e. $\Delta$ AICc < 2). An alpha of 0.05 was adopted.

## 5.4 Results

### *5.4.1 Descriptive Statistics*

From birth to 67 days of age for the calves, we recorded 1299 allosuckling bouts. All females allonursed, and 23 of the 25 calves were observed allosuckling. The mean ± standard deviation (*SD*) of the number of allosuckling bouts for calves aged 67 days was 52 ± 53 (range: 0-221). The mean ± *SD* number of allonursing bouts was 52.12 ± 19.29 (range: 15-91). The mean ± *SD* birth mass of calves was 5.8 ± 0.7 Kg (range: 4.4-7.9 Kg). The mean ± *SD* maternal rejection rate was 0.29 ± 0.06 (range: 0.14-0.41). The mean ± *SD* mass of mothers on May 15th was 81.6 ± 7.9 Kg (range: 68.0-98.0 Kg). The mean ± *SD* number of supplemental feeding bouts for calves was 143 ± 37 (range: 97-215).

### *5.4.2 Cumulative Number of Allosuckling Bouts over 67 Days*

The number of allosuckling bouts performed by individual calves was not significantly influenced by birth mass of calves, maternal rejection rates, mass of mothers on May 15th and the number of allonursing bouts by the mother to another offspring or sex, according to model averaging (Table 5.2 and Table 5.3). The most parsimonious model had sex as a predictor with an $R^2$ value of 0.10 (Table 5.2). The most parsimonious model had *ER* values of 1.06 and 1.84 compared to the 2 models, respectively, within 2 AICc units of the most parsimonious model (Table 5.2). The second most parsimonious model was the intercept-only model. All other models had model weights below 0.06 (Table 5.2). Across all models considered, the relative importance of sex and mass of mothers was 0.48 and 0.29, respectively (Table 5.3). The number of allosuckling bouts was not significantly lower for males than female calves (estimated difference = -0.76, *SE* = 0.46, *P* = 0.092). For the first prediction of this study, we found that the number of allosuckling bouts did not increase due to low birth mass of calves and other measures of insufficient maternal milk supply, which contradicted our prediction.

**Table 5.2** Model selection based on the AICc criterion to predict the cumulative number of allosuckling bouts performed by individual reindeer calves from birth to 67 days of age. The first 8 models with the lowest AICc values are presented. Allonursing represents the cumulative number of allonursing bouts performed by a calf's mother to other offspring. Mass of mothers represents the mass of mothers after parturition on May 15th. *ER*, *wi*, and *k* represent the evidence ratio, the Akaike weight for a given model, and the number of fitted parameters, respectively.

| | Candidate Models | *k* | AICc | Δ*i* | w*i* | *ER* | $R^2$ |
|---|---|---|---|---|---|---|---|
| 1 | sex + intercept | 2 | 248.28 | | 0.17 | | 0.10 |
| 2 | intercept | 1 | 248.41 | 0.12 | 0.16 | 1.06 | 0.00 |
| 3 | mass of mothers + intercept | 2 | 249.50 | 1.22 | 0.09 | 1.84 | 0.06 |
| 4 | mass of mothers + sex + intercept | 3 | 250.53 | 2.24 | 0.06 | 3.07 | 0.12 |
| 5 | birth mass + intercept | 2 | 250.55 | 2.27 | 0.06 | 3.11 | 0.02 |
| 6 | allonursing + intercept | 2 | 250.59 | 2.30 | 0.05 | 3.17 | 0.02 |
| 7 | maternal rejection rates + intercept | 2 | 250.85 | 2.57 | 0.05 | 3.61 | 0.01 |
| 8 | allonursing + sex + intercept | 3 | 250.93 | 2.65 | 0.05 | 3.766 | 0.11 |

**Table 5.3** Model averaging estimates for the parameters predicting the cumulative number of allosuckling bouts performed by individual reindeer calves from birth to 67 days of age. Parameter estimates (± *SE*) are shown for each of the 8 models with the lowest AICc values, and weighted averages for estimates are shown at the bottom of the table. Mass of mothers represents the mass of mothers after parturition on May 15th. Female calf is the reference category for the predictor sex. The symbols *w* and *β* represent the model weights as summed Akaike's weight across all models and the parameter estimates for all variates of the global model, respectively.

| | Intercept | Number of allonursing bouts | Birth mass | Maternal rejection rates | Sex | Mass of mothers |
|---|---|---|---|---|---|---|
| 1 | 4.25 (0.34) | | | | -0.76 (0.45) | |
| 2 | 3.90 (0.24) | | | | | |
| 3 | 0.66 (2.44) | | | | | 0.04 (0.03) |
| 4 | 2.14 (2.37) | | | | -0.65 (0.45) | 0.02 (0.03) |
| 5 | 1.80 (2.70) | | 0.08 (0.34) | | -0.64 (0.45) | 0.02 (0.03) |
| 6 | 3.39 (0.69) | 0.01 (0.01) | | | | |
| 7 | 3.51 (1.11) | | | 1.32 (3.74) | | |
| 8 | 3.91 (0.79) | 0.01 (0.01) | | | -0.74 (0.47) | |
| *w* | | 0.22 | 0.21 | 0.20 | 0.44 | 0.29 |
| *β* | 2.94 | 0.002 | 0.03 | 0.108 | -0.32 | 0.01 |

### *5.4.3 Percentage of Mass Gain*

The percentage of mass gain of reindeer calves was positively influenced by how often they allosuckled, negatively influenced by mass at birth, and male calves gained more percentage of mass than female calves, according to model averaging. The most parsimonious model had birth mass, number of allosuckling bouts and sex as predictors with a multiple $R^2$ value of 0.65 ($F_{3,21} = 12.81$, $P = < 0.001$) (Table 5.4). The most parsimonious model had an *ER* value of 2.66 compared to the model with the second lowest AICc value, which had an AICc value less than 2 AICc units of the most parsimonious model and a multiple $R^2$ value of 0.57 (Table 5.4). There were no other models within 2 AICc units of the most parsimonious model. The second most parsimonious model had birth mass, and sex as predictors. All other models had model weights equal to or less than 0.10 (Table 5.4). Across all models considered, the relative importance of birth mass, number of allosuckling bouts, sex, number of supplemental feeding bouts and the interaction between birth mass and number of allosuckling bouts were 1.00, 0.67, 0.82, 0.16, and 0.10, respectively (Table 5.5). It appeared from the most parsimonious model that for every 1.0 Kg increase in calf birth mass, there was a 68.45 % decrease in mass gain from birth to the age of 67 days (Table 5.6; Figure 5.1). We found that for every 1 allosuckling bout, there was a 0.46 % increase in mass gain from birth to the age of 67 days (Table 5.6; Figure 5.2; see Appendices 4.6 for Figure 5.2's R codes). From birth to the age of 67 days, the percentage of mass gain of male calves was 51.11% greater than that of females (Table 5.6; Figure 5.1). The interaction term of number of allosuckling bouts and birth mass of calves, and number of supplemental feeding bouts did not significantly influence the percentage of mass gain from birth to the age of 67 days (Table 5.4 and Table 5.5). For the second prediction of this study, we found that the relationship between percentage of mass gain and number of allosuckling bouts was positive (i.e. the percentage of mass gain increased as the number of allosuckling bouts increased), which was opposite to our prediction (Table 5.6; Figure 5.2). For the third prediction, we found that the relationship between percentage of mass gain and number of allosuckling bouts did not vary with birth mass, which contradicted our prediction. See Appendices section 4.6.1 and Appendices Table 5.7, Table 5.8 and Table 5.9 for the additional mass gain model selection, model averaging and most parsimonious model results.

**Table 5.4** Model selection based on the AICc criterion to predict the percentage of mass gain for reindeer calves from birth to 67 days of age. The first 8 models with the lowest AICc values are presented. Allosuckling represents the cumulative number of allosuckling bouts. Allonursing represents the cumulative number of allonursing bouts performed by a calf's mother. Allosuckling:birth mass represents the interaction between the cumulative number of allosuckling bouts and birth mass. Supplemental feed represents the cumulative number of supplemental feeding bouts (i.e. lichen, pellets, leaves). *ER*, *wi*, and *k* represent the evidence ratio, the Akaike weight for a given model, and the number of fitted parameters, respectively.

| | Candidate Models | *k* | AICc | $\Delta i$ | w*i* | *ER* | $R^2$ |
|---|---|---|---|---|---|---|---|
| 1 | allosuckling + birth mass + sex + intercept | 4 | 265.08 | | 0.45 | | 0.65 |
| 2 | birth mass + sex + intercept | 3 | 267.04 | 1.96 | 0.17 | 2.66 | 0.57 |
| 3 | birth mass + intercept | 2 | 268.12 | 3.04 | 0.10 | 4.57 | 0.49 |
| 4 | allosuckling + birth mass + sex + allosuckling:birth mass + intercept | 5 | 26858 | 3.50 | 0.08 | 5.76 | 0.65 |
| 5 | allosuckling + birth mass + supplemental feed + sex + intercept | 5 | 268.59 | 3.51 | 0.08 | 5.77 | 0.65 |
| 6 | birth mass + supplemental feed + sex + intercept | 4 | 269.78 | 4.70 | 0.04 | 10.50 | 0.57 |
| 7 | allosuckling + birth mass + intercept | 3 | 269.95 | 4.87 | 0.04 | 11.40 | 0.51 |
| 8 | birth mass + supplemental feed + intercept | 3 | 270.93 | 5.84 | 0.02 | 18.59 | 0.49 |

**Table 5.5** Model averaging estimates for the parameters predicting the percentage of mass gain for reindeer calves from birth to 67 days of age. As in Table 5.4, parameter estimates (± *SE*) are shown for each of the 8 models with the lowest AICc values, and weighted averages for estimates are shown at the bottom of the table. Female calf is the reference category for sex. The symbols *w* and *β* represent the model weights as summed Akaike's weight across all models and the parameter estimates for all variates of the global model, respectively.

| | Intercept | Number of allosuckling bouts | Birth mass | Sex | Number of supplemental feeding bouts | Interaction between number of allosuckling bouts: birth mass |
|---|---|---|---|---|---|---|
| 1 | 841.46 (71.01) | 0.46 (0.21) | -68.45 (12.28) | 51.11 (18.13) | | |
| 2 | 841.47 (76.85) | | -62.93 (13.01) | 34.50 (17.81) | | |
| 3 | 871.82 (79.62) | | -64.84 (13.73) | | | |
| 4 | 847.58 (113.42) | 0.38 (1.15) | -69.52 (19.78) | 51.23 (18.65) | | 0.01 (0.19) |
| 5 | 842.75 (79.29) | 0.45 (0.22) | -68.41 (12.63) | 51.15 (18.60) | -0.01 (0.24) | |
| 6 | 860.62 (84.49) | | -62.75 (13.21) | 36.53 (18.40) | -0.15 (0.25) | |
| 7 | 878.50 (80.05) | 0.21 (0.22) | -69.79 (14.09) | | | |
| 8 | 879.62 (89.38) | | -64.82 (14.02) | | -0.06 (0.26) | |
| *w* | | 0.67 | 1.00 | 0.82 | 0.16 | 0.10 |
| *β* | 848.63 | 0.29 | -68.55 | 38.60 | -0.008 | -0.0009 |

**Table 5.6** The fixed effects of birth mass, number of allosuckling bouts (i.e. adjusted from birth to 67 days) and sex on the percentage of mass gain of reindeer calves from birth to 67 days of age, based on a general linear model with Gaussian distribution and identity link function. Female sex is the reference category for the variable sex. This is the most parsimonious model after model averaging (see Table 5.4 for model selection based on the AICc criterion and Table 5.5 for model averaging estimates).

| Variables | Estimate | *SE* | *t* | *P* |
|---|---|---|---|---|
| Intercept | 841.46 | 71.01 | 11.85 | < 0.001 |
| Birth mass | -68.45 | 12.28 | -5.57 | < 0.001 |
| Number of allosuckling bouts | 0.46 | 0.21 | 2.18 | 0.041 |
| Sex | 51.11 | 18.13 | 2.82 | 0.010 |

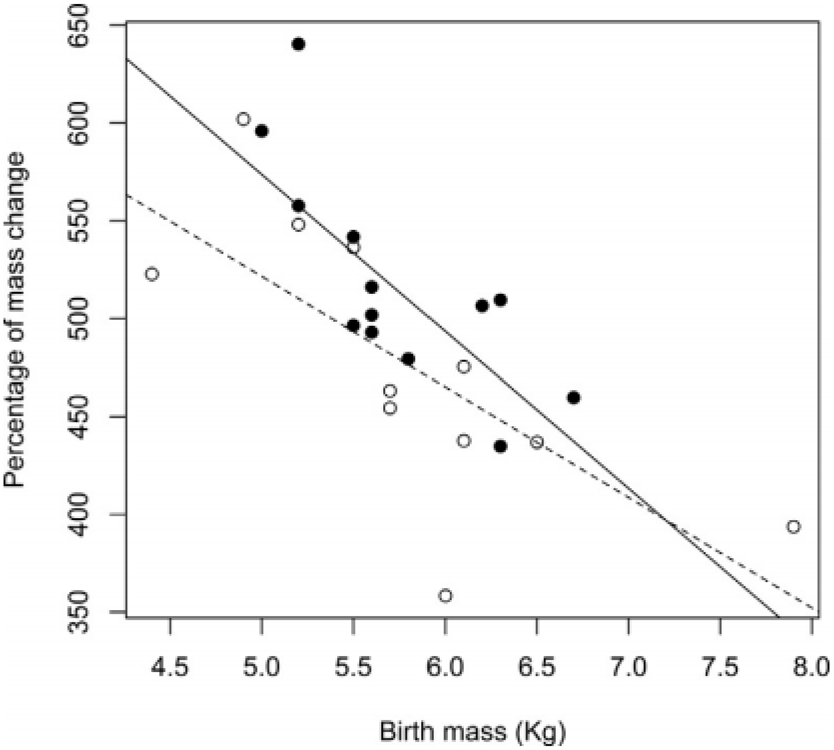

**Figure 5.1** The relationship between birth mass of calves and percentage of mass gain of reindeer calves aged 67 days by sex. Open circles represent female calves, and the dotted line is the line of best fit for the female calves. Filled circles represent male calves, and the solid line is the line of best fit for the male calves.

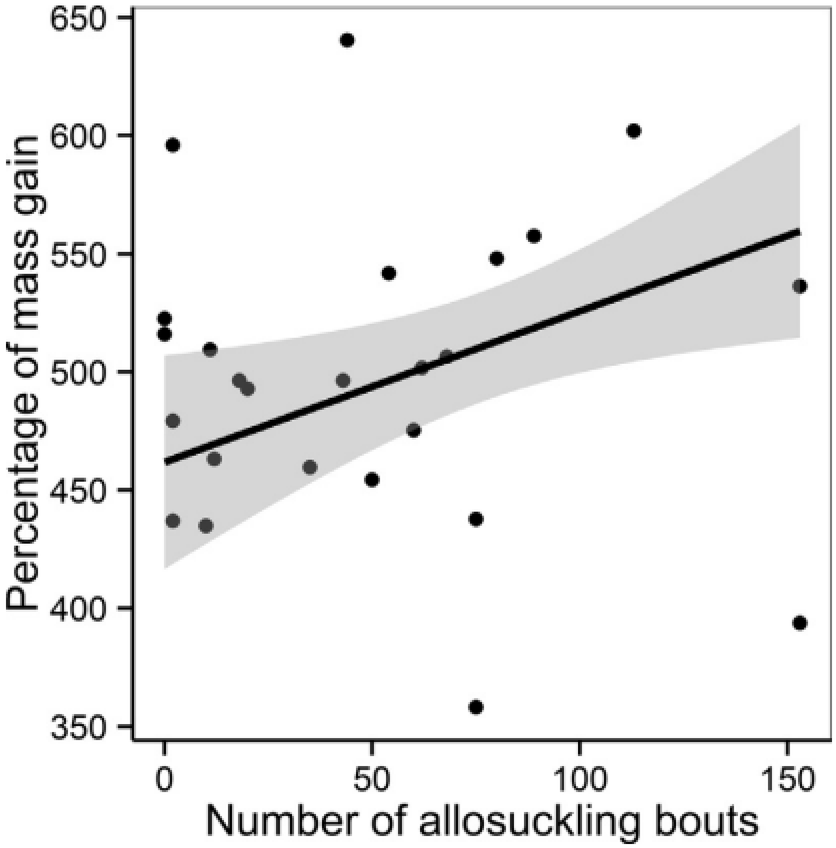

**Figure 5.2** The relationship between number of allosuckling bouts and percentage of mass gain of reindeer calves from birth to 67 days of age. The solid line is the line of best fit ± 1 *SE* (shaded areas).

### 5.5 Discussion

As proposed by Packer et al. (1992) and Riedman (1982), our results suggest that allosuckling functioned to improve nutrition by ingesting non-maternal milk in addition to maternal milk, which increased the percentage of mass gain of reindeer calves over 67 days. The hypothesized improved nutritional function of allosuckling was also supported by studies in Norway rats, *Rattus norvegicus* (Mennella et al., 1990), house mice, *Mus musculus* (König, 1993; Sayler & Salmon, 1969; Werboff et al., 1970) and red deer (Landete-Castillejos et al., 2005). Our results did not support the hypothesis that reindeer calves allosuckled to compensate for low calf birth mass, insufficient maternal milk supply (high maternal rejection rates, number of allonursing bouts, and low mass of mothers) or inadequate growth. Our three predictions for the compensation hypothesis were not supported. Our results were different from 9 studies that supported the compensation hypothesis in 6 species (see Table 5.1).

In this study, calves with low birth mass did not allosuckle more often than reindeer calves born heavier, which did not support the compensation hypothesis. The birth mass of reindeer calves in our sample might not have been so low that calves had to compensate by allosuckling. Early-born red deer calves are heavier than late-born red deer calves (Fisher, Fennessy, & Davis, 1989; Landete-Castillejos, García, & Gallego, 2001), and allosuckling was predominantly performed by early-born red deer calves on the hinds of late-born calves (Landete-Castillejos et al., 2005), which could explain the positive correlation between allosuckling bouts and calf birth mass in red deer (Landete-Castillejos, García, Garde, et al., 2000). The milk-theft hypothesis was supported in reindeer, based on the same data used for this study (Engelhardt et al., 2014), and in red deer (Landete-Castillejos, García, Garde, et al., 2000), which suggests that milk-theft may better explain the cause of allosuckling in our study sample reindeer and a population of farmed red deer in Spain than the compensation hypothesis. However, the occurrence of allosuckling increased with low birth mass in cattle (Víchová & Bartoš, 2005) and fallow deer, *Dama dama* (Pélabon et al., 1998) (see Table 5.1), which suggests that insufficient offspring growth during gestation, as measured as low birth mass, induces the hypothesized compensatory function of allosuckling.

In this study, measures of insufficient maternal milk supply (i.e. high maternal rejection rates, low mass of mothers and a large number of allonursing bouts performed by a calf's mother) did not increase the number of allosuckling bouts, which did not support the compensation hypothesis. Similar to our findings, red deer calves did not allosuckle to compensate for insufficient maternal milk supply, since the percentage of allosuckling bouts performed by each red deer calf did not correlate with its mother's body mass, total milk production or percentage of body mass loss (i.e. total milk production and percentage of body mass loss are proxies of maternal milk supply) (Landete-Castillejos, García, Garde, et al., 2000). In Norway rats allosuckling was linked to birth synchrony and reciprocal allonursing, and allosuckling was not linked to insufficient maternal milk supply (Mennella et al., 1990). Insufficient maternal milk supply has been suggested to induce allosuckling in 7 studies across 4 species (see Table 5.1). If offspring cannot acquire their nutritional needs from their mother, offspring have to solicit allosuckling bouts to complete their nutritional requirements (Víchová & Bartoš, 2005). In guanacos, mothers of calves that allosuckled had lower body mass and lower percentages of suckling acceptance than calves that suckled exclusively from their mothers, and both of these measures were indirect indicators of poor maternal milk supply (Zapata et al., 2010). Cattle calves that had lower maternal suckling rates allosuckled more often than calves with higher maternal suckling rates, and birth mass and maternal suckling rates influenced allosuckling occurrence interactively (Víchová & Bartoš, 2005). Maternal milk supply in our study was not found to be insufficient or poor. In addition, the body mass of lactating reindeer females in May did not influence milk production (Gjøstein, Holand, & Weladji, 2004), which may explain why reindeer calves did not allosuckle to compensate for low body mass of their mother in this study. Mass of lactating females could be important in other artiodactyls (Zapata et al., 2010).

In this study, reindeer calves that allosuckled more often had greater increases in percentage of mass gain than those that allosuckled less often. The percentage of mass change of calves increased as birth mass decreased, and this result, in itself, does not provide sufficient evidence to support the compensation hypothesis. For the hypothesized compensatory function of allosuckling to be supported by the finding that calves born lighter gained more mass than calves born heavier, the relationship between percentage of mass gain and number of allosuckling bouts would have to vary with birth mass, which it did not in our study, and/or calves born lighter would have to allosuckle more often than calves born heavier, which did not occur in our study. Therefore, the increase in percentage of mass gain due to an increase in the number of allosuckling bouts suggests that allosuckling functioned to improve nutrition by ingesting non-maternal milk in addition to maternal milk (Packer et al., 1992; Riedman, 1982). Early-born red deer calves stole milk during the late stages of lactation from hinds with late-born calves that produced excess milk to ensure a surplus of milk for their own late-born calves in order to make-up for milk-theft, which could explain why late-born calves grew more than predicted by the milk production of their mother (Landete-Castillejos, García, Garde, et al., 2000; Landete-Castillejos et al., 2005). Communal nursing in house mice (König, 1993; Sayler & Salmon, 1969; Werboff et al., 1970) and Norway rats (Mennella et al., 1990) and reciprocal allonursing in house mice (König, 1993), Norway rats (Mennella et al., 1990) and in our previous study of reindeer (Engelhardt et al., 2015) may increase milk production due to improved teat stimulation, which could explain the increase in mass at weaning or percentage of mass gain and suggests the hypothesized neuroendocrine function of allosuckling (Roulin, 2003). If the hypothesized compensatory function of allosuckling is effective, offspring that allosuckle to compensate should grow at least at the same rate and reach the same final mass as offspring satisfied by maternal milk, as was reported in guanacos (Zapata et al., 2010) (see Table 5.1). The effectiveness of the compensatory function of allosuckling was less effective in other ungulate species: mass at weaning, percentage of mass gain and/or growth rates were lower for calves that allosuckled often compared to calves that allosuckled less often, in cattle (Nicoll, 1982a, 1982b; Víchová & Bartoš, 2005) and red deer (Bartoš, Vaňková, Hyánek, et al., 2001), and for river buffalo calves whose mothers allonursed often (Murphey et al., 1995) (see Table 5.1). Mouflon lambs had lower growth rates, allosuckling solicitations increased, and maternal suckling rates were low in a year when food resources were limited and maternal expenditure was limited (Réale et al., 1999) (see Table 5.1). Frequently allosuckling cattle calves tended to grow less and tended to reach lower weaning masses than calves that allosuckled with lower frequency, and birth mass significantly influenced the percentage of mass gain, weaning mass and the occurrence of allosuckling bouts (Víchová & Bartoš, 2005) (see Table 5.1).

To explain why reindeer calves did not allosuckle to compensate for low birth mass, insufficient maternal milk supply or inadequate growth, whereas almost all other studies of artiodactyls supported the compensation hypothesis, we provide some additional explanations. We have investigated the hypothesized causes and functions of allosuckling and allonursing in reindeer in two previous studies (Engelhardt et al., 2014, 2015). The causes of allosuckling in our study sample of 25 mother-calf pairs of reindeer may be better explained by milk-theft

(Engelhardt et al., 2014) and reciprocal allonursing (Engelhardt et al., 2015) than by the compensation hypothesis. The reciprocal allonursing hypothesis has received little support in ungulates and in other mammals (Roulin, 2002). The mismothering hypothesis (i.e. allonursing due a lack of efficient kin recognition mechanisms) received marginal support (Engelhardt et al., 2014), while the kin-selection and milk evacuation hypotheses were not supported (Engelhardt et al., 2014, 2015). Therefore, the hypothesized causes and functions of allosuckling and allonursing are non-mutually exclusive (Roulin, 2002).

Our results did not support the hypothesis that reindeer calves allosuckled to compensate for low birth mass, insufficient maternal milk supply or inadequate growth. Instead, our results suggest that allosuckling in reindeer calves functioned to improve nutrition by ingesting non-maternal milk in addition to maternal milk, which increased the percentage of mass gain over 67 days (Packer et al., 1992; Riedman, 1982). This study suggests that the hypothesized causes and functions of allosuckling and allonursing differ by species and ecological conditions.

## 5.6 Appendices

### R codes for Figure 5.2

```
fit1<- lm(Percentmasschangeat67days~Birthmass+Alloboutsat67days+ Sex)
summary(fit1)
s<-qplot(Alloboutsat67days,Percentmasschangeat67days,data=a, xlab="Number of allosuckling
bouts",ylab="Percentage of mass gain")
grid2<-with(a,expand.grid(
 Alloboutsat67days=seq(min(Alloboutsat67days),max(Alloboutsat67days),length=25)))
grid2$Percentmasschangeat67days<-stats::predict(fit1,newdata=grid2)
u<-s+stat_smooth(colour="black",method="lm",formula = y ~ x,se=TRUE, size =
1,data=grid2)+ theme_bw() + theme(panel.grid.major = element_blank(),
panel.grid.minor = element_blank(), axis.line = element_line(colour = "black"))
```

### *5.6.1 Additional Results for Mass Gain*

The mass of reindeer calves was positively influenced by how often they allosuckled, and the mass of male calves was greater than the mass of female calves aged 67 days, according to model averaging. The most parsimonious model had number of allosuckling bouts and sex as predictors with a multiple $R^2$ value of 0.33 ($F_{3,21} = 12.81$, $P = < 0.013$) (Table 5.7). The most parsimonious model had an evidence ratio (*ER*) value of 1.99 compared to the model with the second lowest AICc value, which had an AICc value less than 2 AICc units of the most parsimonious model and a multiple $R^2$ value of 0.37 (Table 5.7). There were no other models within 2 AICc units of the most parsimonious model. The second most parsimonious model had number of allosuckling bouts, birth mass, and sex as predictors. All other models had model weights equal to or less than 0.10 (Table 5.7). Across all models considered, the relative importance of sex, number of allosuckling bouts, birth mass, number of supplemental feeding bouts and the interaction between birth mass and number of allosuckling bouts were 0.89, 0.68, 0.40, 0.18, and 0.04, respectively (Table 5.8). It appeared from the most parsimonious model that for every 1 allosuckling bout, there was a 0.03 Kg increase in mass at the age of 67 days (Table 5.9; Figure 5.3). We found that the mass of male calves was 3.05 Kg greater than the mass of female calves at the age of 67 days (Table 5.8). Birth mass, the interaction term of number of allosuckling bouts and birth mass of calves, and number of supplemental feeding bouts did not significantly influence the mass of calves at the age of 67 days (Table 5.7, Table 5.8 and Table 5.9). We found that the relationship between mass at 67 days of age and number of allosuckling bouts was positive (i.e. the mass of calves that allosuckled more often was greater than the mass of calves that allosuckled less often). We found that the relationship between mass at the age of 67 days and number of allosuckling bouts did not vary with birth mass.

**Table 5.7** Model selection based on the AICc criterion to predict the mass of reindeer calves at 67 days of age. The first 8 models with the lowest AICc values are presented. Allosuckling represents the cumulative number of allosuckling bouts. Allosuckling:birth mass represents the interaction between the cumulative number of allosuckling bouts and birth mass. Supplemental feed represents the cumulative number of supplemental feeding bouts (i.e. lichen, pellets, leaves). *ER*, *wi*, and *k* represent the evidence ratio, the Akaike weight for a given model, and the number of fitted parameters, respectively.

| | Candidate Models | *k* | AICc | $\Delta i$ | w*i* | *ER* | $R^2$ |
|---|---|---|---|---|---|---|---|
| 1 | allosuckling + sex + intercept | 3 | 117.74 | | 0.37 | | 0.33 |
| 2 | allosuckling + birth mass + sex + intercept | 4 | 119.12 | 1.37 | 0.17 | 1.99 | 0.37 |
| 3 | sex + intercept | 2 | 120.12 | 2.37 | 0.10 | 3.28 | 0.17 |
| 4 | birth mass + sex + intercept | 3 | 120.26 | 2.52 | 0.10 | 3.52 | 0.25 |
| 5 | allosuckling + supplemental feed + sex + intercept | 4 | 120.83 | 3.08 | 0.07 | 4.67 | 0.33 |
| 6 | intercept | 1 | 122.13 | 4.39 | 0.04 | 8.97 | 0.00 |
| 7 | allosuckling + birth mass + allosuckling:birth mass + sex + intercept | 5 | 122.34 | 4.59 | 0.03 | 9.94 | 0.38 |
| 8 | allosuckling + birth mass + supplemental feed + sex + intercept | 5 | 122.60 | 4.85 | 0.03 | 11.32 | 0.37 |

**Table 5.8** Model averaging estimates for the parameters predicting the mass of reindeer calves at 67 days of age. Parameter estimates (± *SE*) are shown for each of the 8 models with the lowest AICc values, and weighted averages for estimates are shown at the bottom of the table. Female calf is the reference category for the predictor sex. The symbols *w* and *β* represent the model weights as summed Akaike's weight across all models and the parameter estimates for all variates of the global model, respectively.

| | Intercept | Number of allosuckling bouts | Birth mass | Sex | Number of supplemental feeding bouts | Interaction between number of allosuckling bouts: birth mass |
|---|---|---|---|---|---|---|
| 1 | 25.45 (1.03) | 0.03 (0.01) | | 3.05 (0.99) | | |
| 2 | 20.84 (3.83) | 0.02 (0.01) | 0.83 (0.66) | 3.03 (0.98) | | |
| 3 | 27.23 (0.73) | | | 2.10 (0.97) | | |
| 4 | 20.84 (4.08) | | 1.10 (0.69) | 2.22 (0.95) | | |
| 5 | 24.94 (2.29) | 0.03 (0.01) | | 3.04 (1.01) | 0.00 (0.01) | |
| 6 | 27.40 (0.52) | | | | | |
| 7 | 18.59 (6.09) | 0.05 (0.06) | 1.22 (1.06) | 2.99 (1.00) | | -0.00 (0.01) |
| 8 | 20.58 (4.28) | 0.02 (0.01) | 0.82 (0.68) | 3.02 (1.00) | 0.00 (0.01 | |
| *w* | | 0.68 | 0.40 | 0.89 | 0.18 | 0.04 |
| *β* | 24.01 | 0.02 | 0.38 | 2.49 | 1.30e-4 | -2.09e-4 |

**Table 5.9** The fixed effects of number of allosuckling bouts (i.e. adjusted from birth to 67 days) and sex on the mass of reindeer calves at 67 days of age, based on a general linear model with Gaussian distribution and identity link function. Female sex is the reference category for the variable sex. This is the most parsimonious model after model averaging (see Table 5.7 for model selection based on the AICc criterion and Table 5.8 for model averaging estimates).

| Variables | Estimate | *SE* | *t* | *P* |
|---|---|---|---|---|
| Intercept | 25.45 | 1.03 | 24.60 | < 0.001 |
| Number of allosuckling bouts | 0.03 | 0.11 | 2.26 | 0.034 |
| Sex | 3.05 | 0.99 | 3.08 | 0.005 |

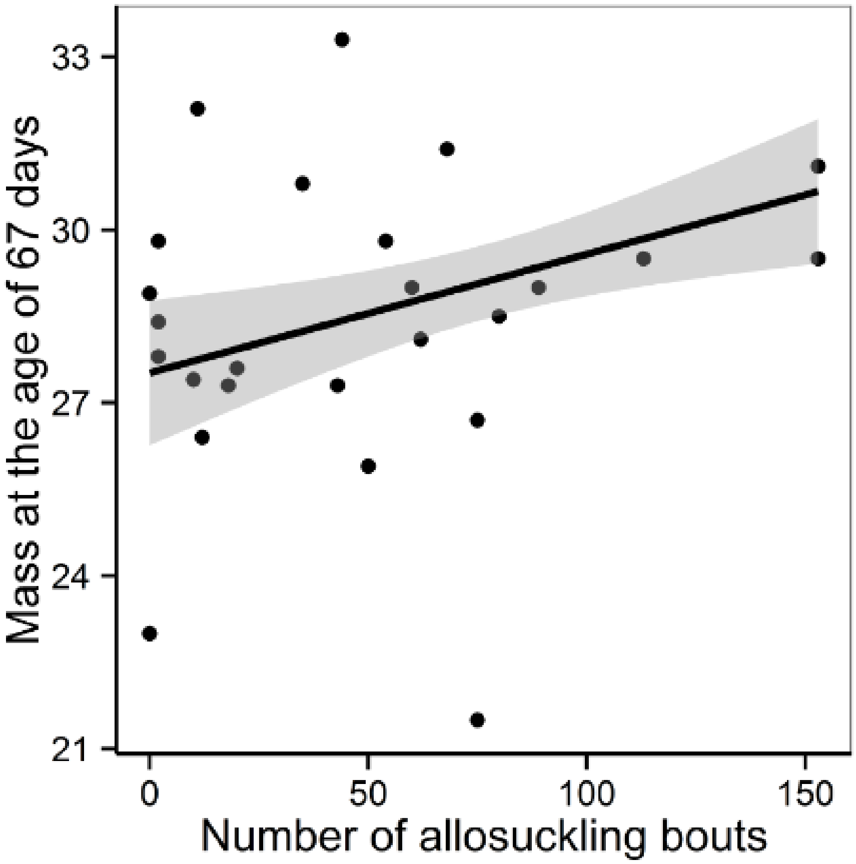

**Figure 5.3** The relationship between number of allosuckling bouts and percentage of mass gain of reindeer calves from birth to 67 days of age. The solid line is the line of best fit ± 1 *SE* (shaded areas).

### R codes for Figure 5.3

```
fit2<- lm(Massofcalfatage67days~ Alloboutsat67days+Sex)
summary(fit2)
r<-qplot(Alloboutsat67days, Massofcalfatage67days,data=a, xlab="Number of allosuckling
bouts",ylab="Mass at the age of 67 days")
grid2<-
with(a,expand.grid(Alloboutsat67days=seq(min(Alloboutsat67days),max(Alloboutsat67days),length=25)))
grid2$ Massofcalfatage67days<-stats::predict(fit2,newdata=grid2)
r+stat_smooth(colour="black",method="lm",formula = y ~ x,se=TRUE, size = 1,data=grid2)+
theme_bw() + theme(panel.grid.major = element_blank(),
panel.grid.minor = element_blank(), axis.line = element_line(colour = "black"))
```

## Chapter 6 Allonursing in Reindeer, *Rangifer tarandus*: A Test of the Kin-selection Hypothesis.

This chapter is based on the accepted manuscript: Sacha C. Engelhardt, Robert B. Weladji, Øystein Holand, Knut H. Røed, Mauri Nieminen. First published online on March 10th 2016. DOI: 10.1093/jmammal/gyw027. Allonursing in reindeer, *Rangifer tarandus*: a test of the kin-selection hypothesis. Journal of Mammalogy.

### 6.1 Abstract

Allonursing, the nursing of non-offspring, is a form of cooperative breeding. To test the kin-selection allonursing hypothesis, we selected 2 experimental groups, based on genetic relatedness, to assess whether evidence of individual and daily patterns of kin-related allonursing would emerge. Each group consisted of 8 mother-offspring pairs, and observers monitored each group over 5 weeks, starting when the offspring were between 8 and 23 days old. One group of 8 mothers was selected to be closely related, and the other group of 8 mothers was selected to be distantly related, based on genetic relatedness. We recorded 1652 solicitations, of which 869 were nursing bouts and 161 were allonursing bouts. All mothers nursed their own offspring, and 15 of the 16 mothers allonursed. In both groups, 7 of the 8 offspring were allonursed. The offspring of closely related mothers were allonursed more often than the offspring of distantly related mothers, and we found evidence for this pattern at the individual level and daily over 5 weeks. Our results supported the kin-selection hypothesis but not the compensation hypothesis. We suggest that allonursing may have provided adaptive related to kin-selection, and offspring from the closely related group may have gained more nutritional benefits and more mass than offspring from the distantly related group. We presented evidence that allonursing contributions detected can depend upon the research design. Furthermore, we suggest that the indirect fitness benefits of alloparental care may have been overestimated, and that kin-selection alone is not sufficient to explain alloparental care in cooperative breeding social systems.

Keywords: Alloparental care; Compensation; Cooperative breeding.

### 6.2 Introduction

Cooperative breeding is a social system in which members of the social group provide parental care to the offspring of other parents (Cant, 2012; Solomon & French, 1997).

Researchers have reported cooperative breeding social systems in insects (Wilson, 1971), crustaceans (Duffy & Macdonald, 2010), arachnids (Salomon & Lubin, 2007), fish (Wisenden, 1999), birds (Cockburn, 1998) and mammals (Riedman, 1982). Alloparents typically assist parents in the care of offspring (Brown, 1987). Alloparents retain the potential to reproduce in the present and in the future (Cant, 2012), and alloparents may be nonbreeding adults or subadults, or reproductive adults that provide alloparental care (Solomon & French, 1997). Endocrinological changes of alloparents and the responsiveness of alloparents to infants are proximate causes of alloparental care (Mumme, 1997; Solomon & Hayes, 2012). Ultimate causes of alloparental care may be adaptive or nonadaptive (Emlen et al., 1991; Jamieson, 1989; Mumme, 1997). Adaptive hypotheses of alloparental care postulate that alloparents gain future direct fitness, and present and future indirect fitness (Mumme, 1997; Solomon & Hayes, 2012). Alloparents may incur short-term-costs, such as increased energy expenditure, reduced body mass or growth, and decreased foraging efficiency (Russell, Sharpe, et al., 2003; Tardif, 1997). Alloparents may incur long-term fitness costs, such as decreased survival (Rabenold, 1990) and decreased future reproductive success (Reyer, 1984; Stiver & Alonzo, 2010).

Lactating females providing milk to the offspring of other mothers is referred to as allonursing, and allonursing is a type of cooperative breeding (Roulin, 2002). Researchers have reported that allonursing occurrs in over 68 mammalian species and across most mammalian families (Packer et al., 1992). Animals that are in captivity and with larger litter sizes allonurse more often (Packer et al., 1992). Monotocous (i.e., giving birth of 1 offspring per parturition) species tend to allonurse more often when group size is large, while polytocous (i.e., giving birth to more than one offspring per parturition) species tend to allonurse more often when group size is small (Packer et al., 1992). The occurrence of allonursing varies between taxa (Packer et al., 1992).

Lactation is the most energetically expensive aspect of mammalian reproduction and increases the energetic costs, metabolic demands, and weight loss of lactating females (Gittleman & Thompson, 1988; König et al., 1988). Lactating females lose energy and resources during nursing ( i.e. lactation is a depreciable form of investment; Clutton-Brock, 1991). In the first few days or weeks after parturition, milk is the exclusive source of nutrients for new-born mammals (Clutton-Brock, 1991). Lactation can have important implications for the survival and subsequent reproductive success of mothers and their offspring, with greater risks of mortality

(Clutton-Brock et al., 1989) and lower future fecundity (Clutton-Brock et al., 1989; Huber et al., 1999) in lactating than non-lactating females. Allonursing is an additional lactation cost for several species (Roulin, 2002). Allonursing may increase nursing loads, and females with heavier nursing loads may incur greater risks of mortality and lower future fecundity than those with lighter nursing loads (Clutton-Brock et al., 1989). Allonursing may increase the risk of pathogen transmission, which could cause haemolitic diseases and infections (Roulin & Heeb, 1999; Roulin, 2002). The transfer of antibodies during allonursing could retard the maturation of offspring (Carlier & Truyens, 1995). Alternatively, offspring that allosuckle may obtain a greater diversity of antibodies and improve resistance against pathogens (Roulin & Heeb, 1999). Immunodeficient laboratory mice, *Mus musculus*, survived and grew in nonsterile conditions only when immunocompetent females allonursed them (Gustafsson et al., 1994).

Researchers have proposed a number of non-mutually exclusive hypotheses to explain the causes and functions of allonursing (Roulin, 2002, 2003; Víchová & Bartoš, 2005). The misdirected paternal care hypothesis postulates that mothers inadvertently transfer milk to offspring that steal milk (i.e., milk-theft), or mothers lack efficient kin-recognition mechanisms (i.e., mismothering) (Packer et al., 1992; Roulin, 2002). Researchers have proposed that the misdirected parental care hypothesis is maladaptive from the point of view of lactating females, because of a potential reduction in fitness, when mothers transfer milk to unrelated offspring during milk-theft or mismothering (Packer et al., 1992). The offspring parasitism strategy of milk-theft is adaptive from the point of view of the offspring stealing milk (Brandlová et al., 2013; Engelhardt et al., 2014; Packer et al., 1992). For example in red deer, *Cervus elaphus*, early-born offspring stole milk during the late stages of lactation from mothers with late-born offspring (Landete-Castillejos, García, Garde, et al., 2000; Landete-Castillejos et al., 2005).

The reciprocity hypothesis proposes that 2 females achieve a higher fitness when allonursing each other's offspring to a similar extent than when they do not share milk (Roulin, 2002). Most studies of allonursing report that mothers do not reciprocate allonursing (see Gerlach & Bartmann, 2002; Roulin, 2002). Only 2 studies have supported the reciprocity hypothesis (Ekvall, 1998; Engelhardt et al., 2014). Many reindeer, *Rangifer tarandus* (Engelhardt et al., 2014), and 4 fallow deer, *Dama dama* (Ekvall, 1998) reciprocally allonursed, but there is yet no evidence to support that 2 females achieve a higher fitness when allonursing reciprocally than when they do not. Reciprocal allonursing between unrelated mothers only increases the direct fitness of mothers (Roulin, 2002). The learning to parent hypothesis predicts that inexperienced females will allonurse to improve their maternal skills, which may increase their current and/or future direct fitness (Roulin, 2002). Females are thought to allonurse to evacuate surplus milk that their own offspring did not consume, however, the milk evacuation hypothesis does not apply when the offspring of a female is still attempting to consume milk or forage (Roulin, 2002). Females may allonurse to improve the stimulation of their teats, to optimally adjust prolactin concentrations, to enhance their immunocompetence, and to increase the quantity and quality of milk produced (Roulin, 2003). The learning to parent, reciprocity, milk evacuation and neuroendocrine hypotheses are adaptive hypotheses.

The kin-selection allonursing hypothesis postulates that lactating females preferentially allonurse offspring with whom they share genes by common descent, allowing lactating females to spread their genes in the population and increase their inclusive fitness (Roulin, 2002). Studies of allonursing in lions, *Panthera leo* (Pusey & Packer, 1994), dwarf mongooses, *Helogale parvula* (Creel et al., 1991), fat dormice, *Glis glis* (Pilastro, 1992), fallow deer (Ekvall, 1998), prairie dogs, *Cynomys ludovicianus* (Hoogland, Tamarin, & Levy, 1989), grey mouse lemurs, *Microcebus murinus* (Eberle & Kappeler, 2006), and meerkats, *Suricata suricatta* (MacLeod et al., 2013) have reported that lactating females preferentially allonursed the offspring of close kin. In contrast, studies of allonursing in river buffalo, *Bubalus bubalis* (Murphey et al., 1995), evening bats, *Nycticeius humeralis* (Wilkinson, 1992), house mice (König, 2006), wood mice, *Apodemus sylvaticus* (Gerlach & Bartmann, 2002), Mexican free-tailed bats, *Tadarida brasiliensis* (McCracken & Gustin, 1991; McCracken, 1984), wedge-capped capuchin monkeys, *Cebus olivaceus* (O'Brien & Robinson, 1991), grey seals, *Halichoerus grypus* (Perry et al., 1998) and polar bears, *Ursus maritimus* (Lunn et al., 2000) have not supported the kin-selection hypothesis. More recently, we directly tested the effect of genetic relatedness on the odds of successfully allosuckling (Engelhardt et al., 2014) and reciprocal allonursing (Engelhardt et al., 2015) as opposed to comparing 2 groups based on their genetic relatedness. However, Hirotani (1990) reported that the association between adult female reindeer (hereafter, females) and their adult daughters during calving did not differ from a control sample of unrelated females, which may explain our previous findings (Engelhardt et al., 2014, 2015). Researchers have often attributed the evolution of cooperative breeding primarily to kin-selection (Brown, 1987; Emlen, 1997), but researchers have also questioned whether the indirect fitness benefits of alloparental care may be overestimated (Clutton-Brock, 2002; Cockburn, 1998). Our previous findings supported the milk-theft (Engelhardt et al., 2014), reciprocity (Engelhardt et al., 2015) and improved nutrition (Engelhardt, Weladji, Holand, & Nieminen, 2016) hypotheses. In our 3 previous studies, we selected the first 25 reindeer mothers to give birth, and we observed them over 10 weeks (Engelhardt et al., 2014, 2016, 2015). We thought that allonursing in reindeer functioned similarly all the time, but the detected results may depend upon research design. Before suggesting an overestimation of the indirect fitness benefits of allonursing (Clutton-Brock, 2002; Cockburn, 1998), we wanted to experimentally test for kin-selection allonursing at the two extremes of genetic relatedness, while controlling for group size.

Allosuckling is hypothesized to function to improve offspring nutrition, and hence mass gain, by ingestion of non-maternal milk in addition to maternal milk (Packer et al., 1992; Riedman, 1982). Offspring that allosuckle may improve their nutrition, and hence gain mass (Engelhardt et al., 2016; Landete-Castillejos et al., 2005; Mennella et al., 1990), or offspring may allosuckle to compensate for low birth mass, insufficient maternal milk supply (i.e., high maternal rejection rates, low mass of mothers and a large number of allonursing bouts performed by the mother of an offspring) or inadequate growth (Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005, but see Engelhardt et al., 2016). The compensation and improved nutrition hypotheses are adaptive hypotheses. When allonursing females associate with close kin or vary their allonursing contributions with genetic relatedness, kin-selection may play a role in the behaviour of offspring that allosuckle to compensate for deficiencies or improve their nutrition and mass gain (Bartoš, Vaňková, Hyánek, et al., 2001). There may be adaptive benefits of allonursing relative to kin-selection.

We manipulated the association of reindeer mothers on the basis of genetic relatedness to assess the kin-selection allonursing hypothesis in reindeer. We predicted that the offspring of genetically, closely related reindeer mothers (hereafter, closely related) allonursed more often than the offspring of genetically, distantly related reindeer mothers (hereafter, distantly related). If there was a pattern of kin-selection allonursing, we suggested that the pattern should be apparent over time, and we suggested that on average the daily ratios of the cumulative number of allonursing bouts among closely related mothers over the cumulative number of allonursing bouts among closely and distantly related reindeer mothers (hereafter, daily ratios of allonursing bouts) should be greater than 0.5. We tested the compensation hypothesis, and we predicted that the number of allonursing bouts received by each offspring would increase because of the low birth mass of offspring, high maternal rejection rates, and a high number of allonursing bouts performed by the mother of the offspring.

### 6.3 Materials and Methods

We conducted this study at the Kutuharju Field Reindeer Research Station near Kaamanen, Finland (69º N, 27º E), a 45 $km^2$ fenced enclosure. We followed the guidelines of the American Society of Mammalogists for care and use of live animals (Sikes, Gannon, & the Animal Care and Use Committee of the American Society of Mammalogists, 2011), and we designed this study in accordance with the Animal Ethics and Care Certificate of Concordia University (AREC-2010-WELA) and the Finnish National Advisory Board on Research Ethics. The Finnish Reindeer Herding Association established the herd in the late 1960s with about 20 males and 60 females. The reindeer population at the Kutuharju Field Reindeer Research Station is semi-domesticated and free-ranging within the enclosure. During this study, the manager of the herd maintained a population of females ranging between 2-12 yr ($\bar{X} \pm SD = 5.93 \pm 3.76$ yr), and we selected mothers with ages ranging from 3-11 yr (see Table 6.1). Females in the herd began giving birth on 4 May 2013, and the manager recorded the last birth on 11 June 2013. Female reindeer are monotocous, giving birth to 1 offspring in May-June, and they are plural breeders. Mothers gradually wean their offspring, and the lactation cycle usually ends in September to October during rut (White & Luick, 1984). During calving, the manager of the herd confined all females to a paddock (approximately 10 ha), where we obtained data on the birth date, offspring sex, birth mass, and mother-offspring assignments. The manager of the herd recorded the birth mass of the offspring to the nearest 0.1 kg with a hand-held scale. We characterised the paddocks as generally flat and open area with birch (*Betula pendula*, *Betula pubescens*) and pine (*Pinus sylvestris*) trees. The study animals drank free running water, and ate natural forage and supplemental feed (i.e., pellets). Daily, the manager of the herd provided between 10-40 Kg of Rasio Mullin-Herkku 2 pellets to each group (see Appendices 5.6). The manager adjusted the daily mass of the pellets based on how many pellets remained in the feed-troughs. Reindeer offspring depend on the milk of their mother for nutrition during the first few weeks and do not eat the pellets provided during this time. Offspring could reach the pellets from the feed-troughs on the ground, and mothers ate pellets in the ground feed-troughs and in the raised feed-troughs. Metallic roofs sheltered the pellets from rain. The manager provided pellets to the reindeer at times ranging from 0700 to 1530 h ($\bar{X}$ = 9:13; *SE* = 15 min; see Appendices 5.6). For the research protocol, the manager provided supplemental feed only because we thought that the natural forage within the paddock could not sustain the density of reindeer and to avoid restricting the nutrition of mothers. Mothers with restricted nutrition may increase maternal rejection rates and reduce the occurrence of allonursing (e.g., no allonursing bouts, Réale et al., 1999). Extremely high maternal rejection rates increase the risk of offspring mortality (Réale et al., 1999). The manager herded individuals we did not select for this study into Lauluvaara, a 13.6 km$^2$ fenced enclosure within the Kutuharju Field Reindeer Research Station, where the manager did not provide supplemental feed. At the end of the study, the study individuals joined the rest of the herd in Lauluvaara. Researchers fixed collar tags of different colours, with numbers inscribed, to individuals for identification. To avoid potential allonursing effects because of primiparous mothers learning to parent (e.g., allonursing performed mainly by inexperienced mother) (Roulin, 2002), we did not select primiparous mothers for this study.

We collected blood samples from all individuals and analyzed for 16 DNA microsattelite loci as part of an on-going progeny testing within this experimental herd (Røed et al., 2002). We analyzed the following DNA microsatellite loci: NVHRT-01, NVHRT-03, NVHRT-16, NVHRT-31, NVHRT-48, NVHRT-66, NVHRT-73, NVHRT-76 (Røed & Midthjell, 1998), RT-1, RT-5, RT-6, RT-7, RT-9, RT-30 (Wilson, Strobeck, Wu, & Coffin, 1997), OarFCB193 (Buchanan & Crawford, 1993), and BM4513 (Bishop et al., 1994). We assessed parenthood assignments with the simulation program software CERVUS 3.0 (Kalinowski et al., 2007), which is based on likelihood ratios between candidate parents. We found all microsatellites within the herd to be in Hardy Weinberg equilibrium and detected no mismatches in the assigned mother-offspring combinations. Indeed, the DNA analyses supported all mother-offspring assignments from field observations. We used the program GenAlEx v 6.4 (Peakall & Smouse, 2006) to generate estimates of methods-of-moments estimator of pairwise relatedness, QGM (Queller & Goodnight, 1989), and of methods-of-moments estimator of pairwise relatedness, LRM (Lynch & Ritland, 1999). We selected groups based on the pairwise relatedness estimators QGM and LRM (Table 6.1). We selected 1 group of 8 mothers to be closely related, and we selected the other group of 8 mothers to be distantly related. We selected study animals for both groups with similar birth masses, ages of offspring, ages of mothers and the numbers of male and female offspring (Table 6.1). We obtained 2 groups consisting of 8 mother-offspring pairs, and we separated the study individuals from the herd for 5 weeks.

**Table 6.1** Mean ± standard deviation (*SD*) for birth mass in kg, age of reindeer (*Rangifer tarandus*) offspring at the end of the study in days, and age of mothers in yr, of the closely and distantly related groups. The numbers of male and female reindeer offspring per group are reported for the closely and distantly related groups. The 95% confidence intervals of the pairwise relatedness estimators of QGM and LRM are reported. This study was conducted at the Kutuharju Field Reindeer Research Station near Kaamanen, Finland (69º N, 27º E) between 30 May and 25 June 2013.

| Groups | Birth mass | Age of offspring | Age of mothers | Number of males and females | QGM | LRM |
|---|---|---|---|---|---|---|
| Closely related | 5.9 ± 0.7 | 41.6 ± 2.4 | 6.0 ± 2.5 | 4:4 | (0.063 - 0.18) | (0.00059 - 0.047) |
| Distantly related | 6.0 ± 0.6 | 41.3 ± 5.2 | 8.1 ± 2.4 | 5:3 | (−0.13 - −0.048) | (-0.038 - −0.0090) |

### *6.3.1 Behavioural Observations*

We collected data from 30 May to 25 June 2013 over 25 observation days. We confined each group to separate fenced areas (approximately 5 ha) within the paddock. We started to collect data when offspring were between 8-23 days old. We monitored each group for 5 h/d, generally between 0700 and 2000 h, and recorded observations, inside the paddocks, at a distance ranging from 5 to 50 meters from animals. Observers used binoculars to reliably record observations of solicitations, agonistic interactions, and identify individuals. Observers collected observations of nursing and allonursing solicitations using behaviour sampling with continuous recording (Martin & Bateson, 2007). For each solicitation, observers recorded the occurrence of nursing and allonursing and the identity of the female and offspring. Observers scored a solicitation as an attempt when an offspring brought its muzzle within a head from the udders of a female and the female did not allow the offspring to suckle (e.g., walking away, kicking offspring, head threat to offspring, chasing offspring). Observers scored a solicitation as a rejection when an offspring suckled for less than 5 seconds (Víchová & Bartoš, 2005). Observers scored a solicitation as successful or as an allonursing bout when an offspring suckled for 5 seconds or more, and observers scored a bout as ended when the offspring no longer grasped the udder of the female. We selected a 5-second cut-off based on previous nursing and allonursing research in reindeer (Engelhardt et al., 2014, 2016, 2015; Espmark, 1971c; Marken, 2003). Observers collected information concerning which individual ended a solicitation, and they scored these observations as offspring or female. We calculated rates of maternal rejection for each offspring as the number of unsuccessful maternal solicitations divided by the total number of maternal solicitations, and the maternal rejection rates ranged from 0.00 to 1.00 (Zapata, González, et al., 2009). Observers opportunistically scored the supplemental feeding bouts of offspring using ad libitum sampling (Martin & Bateson, 2007), but we did not score the supplemental feeding bouts of mothers.

Observers opportunistically scored agonistic interactions using ad libitum sampling and continuous recording methods (Martin & Bateson, 2007). Observers recorded agonistic interaction as resolved when an individual showed a submissive behaviour (“lose”), and the other individual did not (“win”). Observers scored unresolved agonistic interactions as unresolved when neither animal showed a submissive behaviour. Observers scored agonistic interactions as displacement, head threat, push, chase, kick, boxing, and other interactions (Holand et al., 2004 adapted from Thomson, 1977), and they scored associated submissive behaviours as ‘flee’ or ‘walk away’, if submission occurred. The rank of female reindeer is fairly stable throughout the year (Hirotani, 1990), except for a very short time immediately following the shedding of antlers (Espmark, 1971a; Thomson, 1977).

Our study did not measure the actual milk consumption. Cameron (1998) found positive relationships between estimated milk intake and suckling bout frequency and total time suckling, based on mass gain. However, Cameron (1998) argued that assuming milk transfer based on behavioural sampling methods, such as time spent suckling, had inadequate empirical foundation because these variables explained less than 15% of the variation in estimated milk intake, and he reported significant heterogeneity between studies and between species. Reindeer offspring require rapid milk ejection, because they suckle frequently and for short durations (White & Luick, 1984). Researchers readily drew milk by hand from each of the 4 udders of reindeer mothers within 1 minute prior to experimental treatments in a study of milk ejection both in the presence and absence of the offspring of the mother and with and without the use of oxytocin (Gjøstein, Holand, Bolstad, et al., 2004). Therefore, we assumed that milk transfer occurred, and other studies made a similar assumption (Drábková et al., 2008; Paranhos da Costa et al., 2000; Víchová & Bartoš, 2005).

### *6.3.2 Statistical Analyses*

We ran a generalized linear model in R version 3.1.2 (R Development Core Team, 2014), using Mass and lsmeans packages, with a log link function and a negative binomial distribution, to assess the predictor variables group, birth mass, sex, the cumulative number of allonursing bouts performed by the mother of the offspring, age of offspring at the end of the study and the maternal rejection rate on the response variable, cumulative number of allonursing bouts received by each offspring. We designed the predictor group as a categorical variable with 2 categories, closely related group and distantly related group, and we designated the distantly related group as the reference group. We included age of offspring (Ekvall, 1998; Landete-Castillejos, García, Garde, et al., 2000) and sex (Paranhos da Costa et al., 2000; Víchová & Bartoš, 2005) as covariates, because studies reported that these predictors influenced the occurrence of allonursing. We included the predictors birth mass (Paranhos da Costa et al., 2000; Víchová & Bartoš, 2005), maternal rejection rates (Víchová & Bartoš, 2005; Zapata, González, et al., 2009), and the cumulative number of allonursing bouts performed by the mother of the offspring (Bartoš, Vaňková, Hyánek, et al., 2001; Murphey et al., 1995) as covariates in our model, since studies reported that these predictors influenced the occurrence of allonursing as part of the compensation hypothesis (Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005). We adopted an alpha of 0.05. We reported the effect size for each parameter as the inverse function of the log of each estimate. We generated the 95% confidence intervals (*CI*s) around the least square means of the predictor group and averaged them over the levels of sex.

We calculated the daily ratios of allonursing bouts for the 25 observation days. These daily ratios quantified how equivalent the degree to which the daily cumulative number of allonursing bouts was performed in each group. The daily ratio values ranged from 0.00 (i.e., mothers in the distantly related group performed all the observed allonursing bouts during the day) to 1.00 (i.e., mothers in the closely related group performed all the observed allonursing bouts during the day). A daily ratio value equal to 0.50 indicated that both groups equally allonursed during the day. We constructed the 95% *CI* around the mean daily ratio value to assess whether the daily ratios of the cumulative number of allonursing bouts among closely related mothers over the cumulative number of allonursing bouts among closely and distantly related reindeer mothers were greater than 0.50.

We generated a dominance hierarchy for reindeer mothers in the study group using observations of agonistic interactions with a winner and loser identified. The dominance hierarchy in the closely related group tended to be linear, with a Landau linearity index of 0.857 (de Vries, 1998). The dominance hierarchy in the distantly related group was linear, with a Landau linearity index of 0.988 (de Vries, 1998).

To compare the daily mass of pellets in the closely and distantly related groups, we ran a Mann Whitney *U* test since the assumption of normality was not met. To assess the influence of supplemental feed on maternal body condition, we ran a Student *t*-test to compare the mass change of mothers with and without access to supplemental feed. The manager recorded the mass of mothers in the herd on 29 May and on 16 September. Mothers selected for this study had access to both supplemental feed and natural forage for 5 weeks. The manager could not round up the entire herd for both weighing dates, and he recorded the mass of 41 (i.e., 14 study animals) of the 50 mothers in the herd on both dates.

### 6.4 Results

We recorded a total of 1652 solicitations, of which 869 were nursing bouts and 161 were allonursing bouts (Table 6.2). All mothers nursed their own offspring, and 15 of the 16 mothers successfully allonursed (i.e., 1 mother in the distantly related group did not allonurse) (Table 6.2). In each group mothers allonursed 7 of the 8 offspring (Table 6.3). None of the mothers or offspring died, and mothers did not adopt offspring.

**Table 6.2** Data for mothers. Mother identity, age of mother in yr, rank, offspring ID, group and observed number of solicitations by category. CR represents the closely related group, and DR represents the distantly related group. Ranks were given values ranging 1 to 8 in each group, with 8 representing the most dominant mother and 1 representing the least dominant mother. This study was conducted at the Kutuharju Field Reindeer Research Station near Kaamanen, Finland (69º N, 27º E) between 30 May and 25 June, 2013.

| ID | Age | Rank | Offspring ID | Group | Nursing bouts | Nursing rejections | Nursing attempts | Allonursing bouts | Allonursing rejections | Allonursing attempts |
|---|---|---|---|---|---|---|---|---|---|---|
| Va64 | 8 | 8 | 33 | CR | 52 | 10 | 14 | 31 | 2 | 9 |
| Ru7 | 7 | 7 | 15 | CR | 46 | 16 | 18 | 17 | 0 | 9 |
| Va63 | 8 | 6 | 57 | CR | 61 | 7 | 19 | 21 | 4 | 7 |
| Va60 | 8 | 5 | 12 | CR | 47 | 17 | 23 | 16 | 5 | 5 |
| Ne27 | 3 | 4 | 66 | CR | 46 | 13 | 22 | 8 | 5 | 10 |
| Ne29 | 3 | 3 | 18 | CR | 53 | 9 | 12 | 9 | 1 | 6 |
| Va66 | 8 | 2 | 13 | CR | 37 | 9 | 29 | 6 | 0 | 6 |
| Ne24 | 3 | 1 | 10 | CR | 52 | 6 | 17 | 5 | 3 | 3 |
| Pi19 | 10 | 8 | 4 | DR | 27 | 3 | 9 | 7 | 0 | 11 |
| Va61 | 8 | 7 | 0 | DR | 73 | 10 | 15 | 18 | 2 | 13 |
| Pi5 | 11 | 6 | 7 | DR | 59 | 2 | 20 | 2 | 0 | 6 |
| Ru1 | 7 | 5 | 5 | DR | 55 | 3 | 4 | 5 | 1 | 9 |
| Va65 | 8 | 4 | 3 | DR | 60 | 7 | 17 | 0 | 2 | 6 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Pi14 | 11 | 3 | 1 | DR | 104 | 17 | 48 | 4 | 6 | 11 |
| Vi2 | 5 | 2 | 6 | DR | 48 | 15 | 9 | 11 | 1 | 5 |
| Vi3 | 5 | 1 | 2 | DR | 49 | 10 | 36 | 1 | 1 | 7 |
| Total | | | | | 869 | 154 | 312 | 161 | 33 | 123 |

**Table 6.3** Offspring data. Offspring identity, date of birth, birth mass in Kg, sex, group and observed number of solicitations by category. CR represents the closely related group, and DR represents the distantly related group. This study was conducted at the Kutuharju Field Reindeer Research Station near Kaamanen, Finland (69º N, 27º E) between 30 May and 25 June, 2013.

| Offspring ID | Birth Date | Birth mass | Sex | Group | Nursing bouts | Nursing rejections | Nursing attempts | Allonursing bouts | Allonursing rejections | Allonursing attempts |
|---|---|---|---|---|---|---|---|---|---|---|
| 12 | 15/05/2013 | 6.1 | F | CR | 47 | 17 | 23 | 25 | 3 | 16 |
| 57 | 15/05/2013 | 5.8 | F | CR | 61 | 7 | 19 | 9 | 5 | 5 |
| 33 | 19/05/2013 | 6.9 | M | CR | 52 | 10 | 14 | 0 | 0 | 1 |
| 13 | 15/05/2013 | 5.6 | F | CR | 37 | 9 | 29 | 14 | 5 | 8 |
| 15 | 18/05/2013 | 6.4 | M | CR | 46 | 16 | 18 | 19 | 3 | 12 |
| 10 | 14/05/2013 | 5.2 | M | CR | 52 | 6 | 17 | 37 | 2 | 8 |
| 66 | 16/05/2013 | 6.1 | M | CR | 46 | 13 | 22 | 7 | 2 | 4 |
| 18 | 11/05/2013 | 4.7 | F | CR | 53 | 9 | 12 | 2 | 0 | 1 |
| 4 | 08/05/2013 | 6.3 | M | DR | 27 | 3 | 9 | 2 | 0 | 2 |
| 7 | 20/05/2013 | 5.6 | F | DR | 59 | 2 | 20 | 8 | 3 | 25 |
| 1 | 18/05/2013 | 6.5 | M | DR | 104 | 17 | 48 | 10 | 1 | 4 |
| 6 | 10/05/2013 | 5.5 | M | DR | 48 | 15 | 9 | 0 | 0 | 0 |
| 2 | 23/05/2013 | 4.8 | M | DR | 49 | 10 | 36 | 2 | 2 | 5 |
| 5 | 14/05/2013 | 6.5 | M | DR | 55 | 3 | 4 | 20 | 5 | 12 |
| 0 | 19/05/2013 | 6.3 | F | DR | 73 | 10 | 15 | 5 | 1 | 13 |

|  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
| 3 | 13/05/2013 | 6.4 | F | DR | 60 | 7 | 17 | 1 | 1 | 7 |
| Total |  |  |  |  | 869 | 154 | 312 | 161 | 33 | 123 |

We recorded a total of 370 supplemental feeding bouts (See Appendices 5.6). Per observation day, offspring cumulatively ate supplemental feed between 0-56 occasions ($\bar{X} \pm SD$ = 15 ± 13) (See Appendices 5.6). Over the 25 observation days, each offspring cumulatively ate supplemental feed between 7-48 times ($\bar{X} \pm SD$ = 23 ± 11) (See Appendices 5.6). Offspring ate supplemental feed for a cumulative total duration of 1071 s ($N = 63$) (See Appendices 5.6). Offspring ate supplemental feed for short durations ($\bar{X} \pm SD$: 17 ± 24 s; range: 1-107 s), and only 5 bouts were longer than 60 s (See Appendices 5.6). Reindeer in the closely and distantly related groups had access to the same mass of supplemental feed ($U = 273.0$, *d.f.* = 1, $P = 0.438$). The mass change of mothers with and without access to supplemental feed did not significantly differ ($\bar{X} \pm SE$ mass change of the mothers we selected = 9.6 ± 1.1 kg; $\bar{X} \pm SE$ mass change of the mothers we did not select = 6.4 ± 1.1 kg; $t = 1.86$, *d.f.* = 39, $P = 0.07$).

The difference in the logs of the expected cumulative number of allonursing bouts received by each offspring was 2.43 units higher for the closely related group compared to the distantly related group, while holding the other variables constant in the model ($P < 0.001$; Table 6.4; Figure 6.1). The effect of age of offspring at the end of the study was significant ($P = 0.049$; Table 6.4). Offspring born heavier were allonursed more often than offspring born lighter ($P = 0.024$; Table 6.4), and offspring with lower maternal rejection rates were allonursed less often ($P = 0.052$; Table 6.4). Sex and the cumulative number of allonursing bouts performed by the mother of an offspring did not significantly influence the cumulative number of allonursing bouts received by each offspring (Table 6.4).

The average daily ratio of allonursing bouts for the 25 observation days was greater than 0.50 ($\bar{X} \pm SD$ = 0.68 ± 0.28; 95% *CI* range = 0.55-0.81; Figure 6.2). We recorded allonursing bouts on 21 observation days (21/25; 84.00%), and the values of the daily ratios of allonursing bouts ranged from 0.00 to 1.00.

**Table 6.4** Parameter estimates of a generalized linear model, with a log link function and a negative binomial distribution, of the cumulative number of allonursing bouts received by each reindeer (*Rangifer tarandus*) offspring as the response variable. The effect size for each parameter was reported as the inverse function of the log of each estimate. The distantly related group was the reference category for the predictor Group. Allonursing performed by the mother of an offspring represented the cumulative number of allonursing bouts performed by the mother of an offspring. The male sex was the reference category for the predictor Sex. This study was conducted at the Kutuharju Field Reindeer Research Station near Kaamanen, Finland (69º N, 27º E) between 30 May and 25 June 25, 2013.

| Variables | Estimate | *SE* | *z* | *P* | Effect size |
|---|---|---|---|---|---|
| Intercept | 3.49 | 3.50 | 0.99 | 0.320 | 32.79 |
| Group | 2.43 | 0.68 | 3.59 | <0.001 | 11.36 |
| Birth mass | 0.91 | 0.41 | 2.25 | 0.024 | 2.48 |
| Age of offspring at the end of the study | -0.14 | 0.07 | -1.97 | 0.049 | 0.87 |
| Maternal rejection rates | -4.52 | 2.32 | -1.94 | 0.052 | 0.01 |
| Allonursing performed by the mother of an offspring | -0.06 | 0.04 | -1.45 | 0.146 | 0.94 |
| Sex | 0.22 | 0.40 | 0.56 | 0.579 | 1.25 |

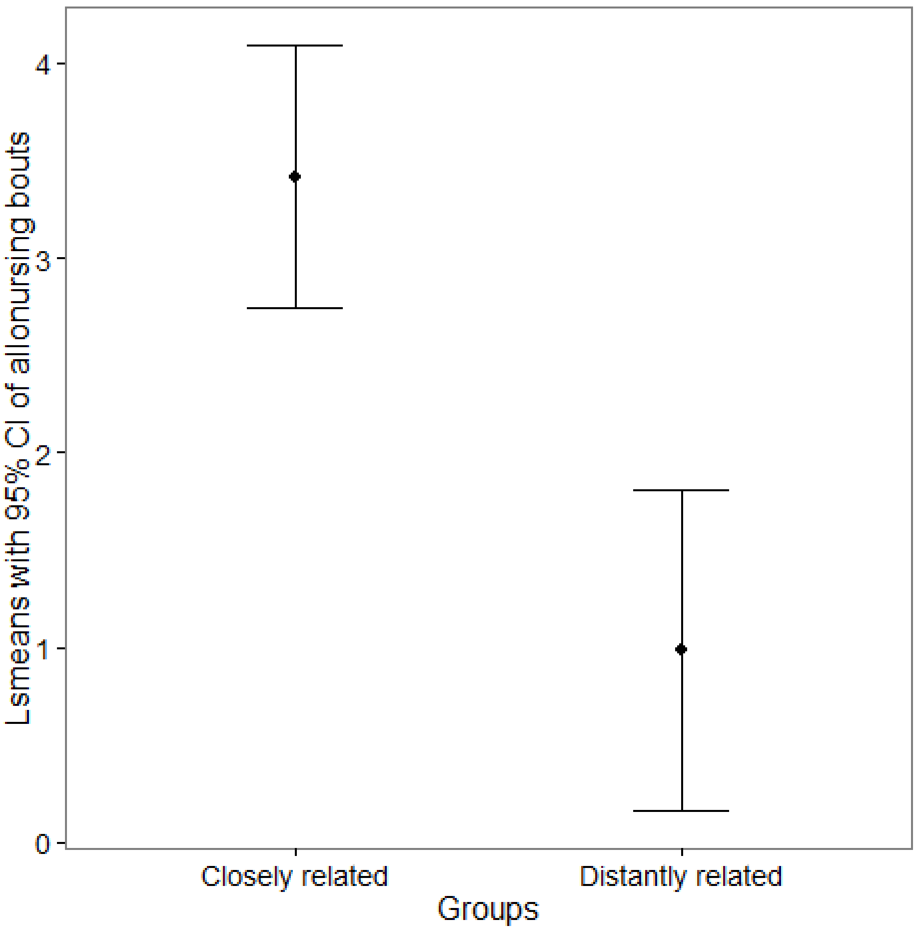

**Figure 6.1** The least square means with 95% confidence intervals of the cumulative number of allonursing bouts received by each reindeer (*Rangifer tarandus*) offspring for groups of closely and distantly related females, based on a generalized linear model, with a log link function and a negative binomial distribution. The selection of the closely and distantly related groups was based on the pairwise genetic relatedness of mothers. The values of the least square means and 95% confidence intervals were averaged over the levels of the predictor sex. This study was conducted at the Kutuharju Field Reindeer Research Station near Kaamanen, Finland (69º N, 27º E) between 30 May and 25 June 2013.

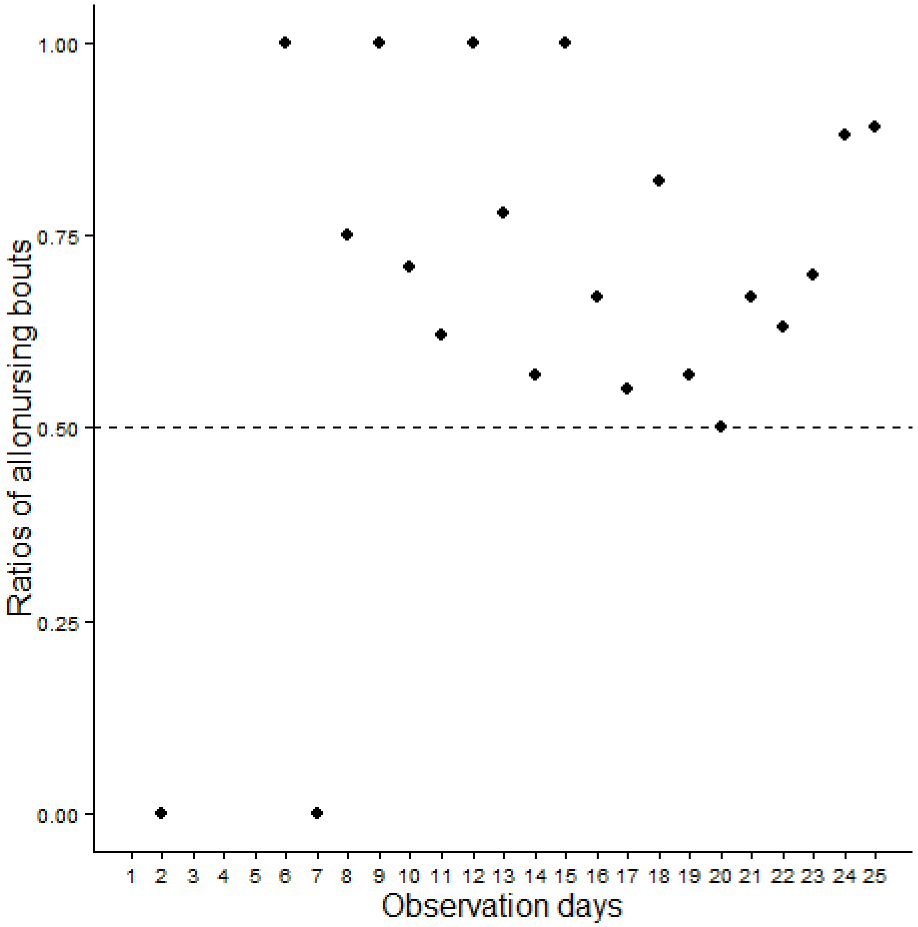

**Figure 6.2** Daily ratios of allonursing bouts estimated as the daily cumulative number of allonursing bouts among closely related mothers over the daily cumulative number of allonursing bouts among closely and distantly related reindeer (*Rangifer tarandus*) mothers. The selection of the closely and distantly related groups was based on the pairwise genetic relatedness of mothers. The daily ratios of allonursing bouts were calculated for the 25 observation days. This study was conducted at the Kutuharju Field Reindeer Research Station near Kaamanen, Finland (69º N, 27º E) between 30 May and 25 June 2013.

We recorded a total of 2,228 agonistic interactions between mothers, between females and offspring, and between offspring. Of the 2,228 agonistic interactions, we recorded 2,185 agonistic interactions with a winner and loser being identified. Observers recorded 1152 and 1076 resolved and unresolved agonistic interactions in the closely and distantly related groups, respectively. Observers recorded 1130 and 1055 resolved agonistic interactions in the closely and distantly related groups, respectively (Table 6.5). We recorded 149 and 171 agonistic interactions performed at the feeding troughs in the closely and distantly related groups, respectively (Table 6.5). Agonistic interactions in both groups were similar (Table 6.5). In the closely related group, 5 mothers performed between 2 and 6 agonistic interactions towards their own offspring, for a cumulative total of 22 agonistic interactions. In the distantly related group, 7 mothers performed between 1 and 5 agonistic interactions towards their own offspring, for a cumulative of 17 agonistic interactions.

**Table 6.5** Resolved agonistic interactions within the enclosures and at the feeding troughs between mothers, between females and offspring, and between offspring of reindeer (*Rangifer tarandus*) in the closely and distantly related groups. Mothers represent the number of agonistic interaction between mothers. Females and offspring represent the number of agonistic interactions between females and offspring. Offspring represent the number of agonistic interactions between offspring. Mothers at feeding trough represent the number of agonistic interaction between mothers at the feeding troughs. Females and offspring at feeding trough represent the number of agonistic interactions between females and offspring at the feeding troughs. Offspring at the feeding troughs represent the number of agonistic interactions between offspring at the feeding troughs. This study was conducted at the Kutuharju Field Reindeer Research Station near Kaamanen, Finland (69º N, 27º E) between 30 May and 25 June 2013.

| Groups | Mothers | Females and offspring | Offspring | Mothers at feeding trough | Females and offspring at feeding trough | Offspring at feeding trough |
|---|---|---|---|---|---|---|
| Closely related | 463 | 613 | 54 | 54 | 88 | 7 |
| Distantly related | 535 | 446 | 74 | 92 | 73 | 6 |

### 6.5 Discussion

We manipulated maternal groups of reindeer based on genetic relatedness and demonstrated that mothers allonursed the offspring of closely related mothers more often than the offspring of distantly related mothers. A group of closely related reindeer mothers allonursed more frequently than a group of distantly related mothers. The allonursing contributions of mothers varied with genetic relatedness, which supported the kin-selection hypothesis (Roulin, 2002). The results of this study, compared to our 3 previous studies of allonursing in reindeer (Engelhardt et al., 2014, 2016, 2015), suggest that allonursing functions similarly all the time, but the detected results depend upon research design. The results of our study suggest a causal relationship between allonursing contributions and 2 extremes of genetic relatedness. However, in our 2 previous studies, allonursing contributions did not vary with genetic relatedness, and distantly related mothers invested as much as closely related mothers (Engelhardt et al., 2014, 2015).

Females in many social species tend to associate non-randomly, and kinship is the main mechanism that shapes these associations (Djaković et al., 2012). In several species, alloparents are more likely to associate with and assist close kin (Emlen, 1991). Studies of free-ranging wildlife have reported that females that allonurse associate with close kin and allonurse the offspring of close kin (Creel et al., 1991; Eberle & Kappeler, 2006; Ekvall, 1998; Hoogland et al., 1989; MacLeod et al., 2013; Marin & Pilastro, 1994; Pilastro, 1992; Pusey & Packer, 1994). Some studies reported that allonursing contributions varied with relatedness (Creel et al., 1991; MacLeod et al., 2013; Pusey & Packer, 1994). Female dwarf mongooses breed communally with close relatives, and pregnant dwarf mongoose subordinates and spontaneous lactators allonursed close relatives (Creel et al., 1991). Females dwarf mongoose that spontaneously lactate generally remain in their natal pack, and the dominant female is often succeeded by a related female (Creel et al., 1991). Lion prides consist of closely related females, and the proportion of allonursing by lion mothers increased as the probability that all females in a crèche were first order relatives (Pusey & Packer, 1994). Within-group female relatedness in meerkats is high (0.41 ± 0.17), and the proportion of pregnant and recently pregnant females allonursing increased as the relatedness to the litter mother increased (MacLeod et al., 2013). However, others studies have reported that females that allonurse do not associate more strongly with close kin than with unrelated females, and do not preferentially allonurse the offspring of close kin

(Engelhardt et al., 2014, 2015; Gerlach & Bartmann, 2002; Lunn et al., 2000; McCracken & Gustin, 1991; McCracken, 1984; O'Brien & Robinson, 1991; Wilkinson, 1992). Feral river buffalo form maternal groups (Shackleton & Harestad, 2003). However, domesticated river buffalo mothers did not direct their allonursing contributions to close kin, and their allonursing contributions did not vary with kinship (Murphey et al., 1995). Female reindeer do not prefer to associate with kin during calving (Hirotani, 1990), which likely influenced the detected results in our 2 previous studies (Engelhardt et al., 2014, 2015). Reindeer mothers and yearling daughters associate more during the rut than during non-rut periods (Hirotani, 1989, 1990). Female reindeer preference for kin, male-male competition and male age influenced female association during rut (Djaković et al., 2012). Reindeer mothers and yearling daughters tend to associate throughout the year, except during calving when their associations did not differ from a control sample of unrelated females (Hirotani, 1990).

The results of this study, our previous findings (Engelhardt et al., 2014, 2016, 2015) and several other studies (e.g. Gerlach & Bartmann, 2002; König, 2006; McCracken & Gustin, 1991) support the suggestions that the relative importance of indirect fitness benefits of cooperative breeding may have been overestimated, and that kin-selection alone is not sufficient to explain allonursing in cooperative breeding social systems (Bergmüller et al., 2007; Clutton-Brock, 2002; Cockburn, 1998). Researchers have found that singular cooperative breeders, which have greater mean within-group relatedness than non-singular cooperative breeders, did not allonurse more than non-singular cooperative breeders, and the incidence of allonursing was not associated with relatedness in these groups (MacLeod & Lukas, 2014). Study animals with different motivations, other than motivated by indirect fitness benefits, may have influenced the detected results.

Scientists have proposed alternative explanations, other than kin-selection, for the expression of allonursing. Instead of supporting the kin-selection hypothesis, several studies supported the misdirected parental care hypothesis because of milk-theft (Engelhardt et al., 2014; Murphey et al., 1995; Zapata, González, et al., 2009) and because of a lack of efficient kin-recognition mechanisms (e.g. König, 2006; Manning et al., 1995; McCulloch et al., 1999). Four pairs of fallow deer mothers (Ekvall, 1998) and a large subset of reindeer mothers (Engelhardt et al., 2015) allonursed reciprocally. It is thought that mothers of evening bats may evacuate milk to reduce their mass and increase their hunting success, to induce their neuroendocrine system to adjust prolactin concentrations, or to increase the size of the colony and their future acquisition of foraging or roosting site information (Wilkinson, 1992). Allonursing may be a by-product of female sociality, such as communal defense against infanticide (Pusey & Packer, 1994) or reduction of the risk of infanticide (Manning et al., 1995).

Several studies of artiodactyls have supported the compensation hypothesis (e.g. Bartoš, Vaňková, Hyánek, et al., 2001; Víchová & Bartoš, 2005; Zapata et al., 2010). In a study of farmed red deer in the Czech Republic, the number of allonursing bouts performed by the mother of the offspring increased the number of allosuckling bouts performed by the offspring of the mother, and offspring that allosuckled more often had lower percentages of mass gain and mass at weaning than offspring that allosuckled less often (Bartoš, Vaňková, Hyánek, et al., 2001). In contrast, studies of laboratory rodents provided with unlimited access to food (König, 1993; Mennella et al., 1990; Sayler & Salmon, 1969; Werboff et al., 1970), and of red deer (Landete-Castillejos et al., 2005) supported the improved nutrition hypothesis, by demonstrating that allosuckling offspring improved their nutrition and mass gain by ingesting maternal as well as the milk of other mothers. In a previous study, reindeer offspring that allosuckled improved their nutrition and mass gain (Engelhardt et al., 2016), and we found no evidence to support the compensation hypothesis in 2 previous studies (Engelhardt et al., 2014, 2016). Researchers estimated the mean caloric value of reindeer milk to be 8.7 kJ/g, and the caloric value of reindeer milk increased by 66.7% throughout lactation (at week 3, $\bar{X} \pm SE = 6.8 \pm 0.4$ kJ/g; at week 24, $\bar{X} \pm SE = 11.4 \pm 0.6$ kJ/g), which is mainly because of an increased fat content (Gjøstein, Holand, & Weladji, 2004). Engelhardt et al. (2016) also reported that offspring gained 0.46% in mass from birth to 67 days of age per allosuckling bout, and offspring gained 0.03 kg per allosuckling bout. Therefore, allonursing in our study may provide adaptive and nutritional benefits relative to genetic relatedness, and offspring from the closely related group may have gain more nutritional benefits and more mass than offspring in the distantly related group. Our study did not support the compensation hypothesis, since reindeer offspring born lighter were not allonursed more often than offspring born heavier, and offspring with higher maternal rejection rates were not allonursed more often than offspring with lower maternal rejection rates.

Reindeer mothers and offspring did consume supplemental feed, and the closely and distantly related groups both had access to the same daily mass of supplemental feed. We contend that access to forage in paddocks (i.e., the restrictions of the research protocol on natural forage with supplemental feed) was similar to that for wild reindeer, reindeer in cooperatives and reindeer in Lauluvaara, since natural forage in the wild and in the cooperatives was easily accessible, instead of restrictive, during the 2013 calving season. Therefore, we suggest that reindeer were not habituated to supplemental feed. Captivity increases the occurrence of allonursing, and this increase may be because of crowding, disturbance, or access to unlimited food (Packer et al., 1992). Captive guanacos, with access to both natural forage and supplemental feed, allonursed more often than free-ranging guanacos (Zapata, Gaete, et al., 2009; Zapata, González, et al., 2009). Several weeks with access to supplemental forage, along with access to natural forage, may not significantly alter allonursing behaviour. The mass change of mothers with and without access to supplemental feed did not significantly differ. Our results could have been more convincing if we had data to compare the occurrence of allonursing with and without supplemental feed. In one of our previous studies, we found that the number of supplemental feeding bouts performed by each offspring did not influence the percentage of mass gain or the mass of the offspring at the end of the study (Engelhardt et al., 2016).

Demonstrating that lactating females associate strongly with close kin and preferentially allonurse closely related offspring are not, in themselves, sufficient evidence for the primary role of indirect fitness by kin-selection (Clutton-Brock, 2002; Griffin & West, 2002), because allonursing the offspring of close kin may not result in enhanced indirect fitness benefits. Only a few studies have calculated the indirect fitness benefits of allonursing (Creel et al., 1991; Gerlach & Bartmann, 2002; König, 2006), and not all allonursing females improved their inclusive fitness (Gerlach & Bartmann, 2002; König, 2006). For example, non-breeding, spontaneously lactating female dwarf mongoose increased their own inclusive fitness by the equivalent of 0.79 offspring (Creel et al., 1991), and only dominant wood mice mothers of mother-daughter pairs increased their inclusive fitness by the equivalent of 3.2 offspring (Gerlach & Bartmann, 2002). In contrast, dominant and subordinate wood mice mothers that communally nested and nursed with related or unrelated mothers had decreased inclusive fitness (Gerlach & Bartmann, 2002). Researchers found that familiarity overrode the effects of relatedness in house mice, and once mothers established an egalitarian relationship, they gained direct benefits by increasing the number of offspring weaned, irrespective of familiarity and relatedness (König, 2006). In addition, the average kinship between communally nesting house mice mothers was 0.16 ± 0.03

and ranged from 0 to 0.54 (Auclair et al., 2014). Therefore, future research should assess the indirect fitness benefits of allonursing.

The kin-selection benefits of altruism can be reduced by competition among relatives (Griffin & West, 2002; West, Pen, & Griffin, 2002). Limited dispersal of individuals from the natal group, as is the case in our study population, was suggested to increase the relatedness between individuals and to favor altruism (Hamilton, 1964b; West et al., 2002). West et al. (2002) suggest that limited dispersal also increases the relatedness between competitors, opposing the kin-selected benefits of altruism. In our study, there was no evidence that competition (i.e., agonistic interactions) was stronger in the closely related group than in the distantly related group, since agonistic interactions in the closely and distantly related groups were similar throughout the study and at the feeding troughs. Although interactions between closely related individuals do not, in themselves provide sufficient evidence for kin-selection (Griffin & West, 2002), allonursing interactions in our study may be consistent with kin-selection.

To demonstrate support for the kin-selection allonursing hypothesis in social groups of allonursing females, in which all females are not closely related, researchers should assess whether allonursing contributions vary with known coefficient of relationship derived from a pedigree or with genetic relatedness (Clutton-Brock, 2002). Future studies should estimate the indirect fitness benefits of allonursing females, which would provide stronger evidence of kin-selection rather than relying on the known association of lactating females. Social groups in which all allonursing females are closely related can only direct allonursing to close kin, but calculations of inclusive fitness may reveal that researchers have overestimated the relative importance of indirect fitness benefits (Clutton-Brock, 2002; Cockburn, 1998), such as finding no appreciable indirect fitness benefits or indirect fitness costs (Gerlach & Bartmann, 2002). A limitation of our study was that there were not replicates. We provided evidence that the ability to detect relationships within the same system can depend upon research design, an outcome indicating that future research should be cautious when interpreting relationships associated with allonursing and relatedness (e.g. Mumme, 1997; Roulin, 2002, 2003; Solomon & Hayes, 2012).

## 6.6 Appendices

**Table 6.6** Supplemental feeding. Over the first 6 observation days, the manager was attempting to estimate the mass of supplemental feed to provide. The mass of supplemental feed provided was higher on observation days 1 to 4 than throughout the remaining observation days.

| Date | Observation Day | Supplemental Feed (Kg) | Time of Provision | Related=1,Unrelated=2 |
|---|---|---|---|---|
| 30/05/2013 | 1 | 40 | 9:00 | 1 |
| 30/05/2013 | 1 | 40 | 9:00 | 2 |
| 31/05/2013 | 2 | 40 | 9:00 | 1 |
| 31/05/2013 | 2 | 40 | 9:00 | 2 |
| 01/06/2013 | 3 | 40 | 8:15 | 1 |
| 01/06/2013 | 3 | 40 | 8:15 | 2 |
| 02/06/2013 | 4 | 40 | 7:00 | 1 |
| 02/06/2013 | 4 | 40 | 7:00 | 2 |
| 03/06/2013 | 5 | 15 | 9:55 | 1 |
| 03/06/2013 | 5 | 15 | 9:55 | 2 |
| 04/06/2013 | 6 | 15 | 9:00 | 1 |
| 04/06/2013 | 6 | 15 | 9:00 | 2 |
| 05/06/2013 | 7 | 15 | 9:00 | 1 |
| 05/06/2013 | 7 | 15 | 9:00 | 2 |

|  |  |  |  |  |
|---|---|---|---|---|
| 06/06/2013 | 8 | 15 | 9:15 | 1 |
| 06/06/2013 | 8 | 15 | 9:15 | 2 |
| 07/06/2013 | 9 | 10 | 9:00 | 1 |
| 07/06/2013 | 9 | 10 | 9:00 | 2 |
| 09/06/2013 | 10 | 15 | 9:30 | 1 |
| 09/06/2013 | 10 | 10 | 9:30 | 2 |
| 10/06/2013 | 11 | 15 | 9:00 | 1 |
| 10/06/2013 | 11 | 10 | 9:00 | 2 |
| 11/06/2013 | 12 | 25 | 15:30 | 1 |
| 11/06/2013 | 12 | 28 | 15:30 | 2 |
| 12/06/2013 | 13 | 25 | 9:00 | 1 |
| 12/06/2013 | 13 | 25 | 9:00 | 2 |
| 13/06/2013 | 14 | 15 | 9:20 | 1 |
| 13/06/2013 | 14 | 27 | 9:20 | 2 |
| 14/06/2013 | 15 | 20 | 8:00 | 1 |
| 14/06/2013 | 15 | 27 | 8:00 | 2 |
| 15/06/2013 | 16 | 22 | 8:30 | 1 |
| 15/06/2013 | 16 | 27 | 8:30 | 2 |
| 16/06/2013 | 17 | 27 | 7:20 | 1 |
| 16/06/2013 | 17 | 27 | 7:20 | 2 |
| 17/06/2013 | 18 | 27 | 9:00 | 1 |
| 17/06/2013 | 18 | 32 | 9:00 | 2 |

| | | | | |
|---|---|---|---|---|
| 18/06/2013 | 19 | 27 | 10:00 | 1 |
| 18/06/2013 | 19 | 27 | 10:00 | 2 |
| 20/06/2013 | 20 | 25 | 13:00 | 1 |
| 20/06/2013 | 20 | 20 | 13:00 | 2 |
| 21/06/2013 | 21 | 10 | 9:20 | 1 |
| 21/06/2013 | 21 | 25 | 9:20 | 2 |
| 22/06/2013 | 22 | 25 | 7:30 | 1 |
| 22/06/2013 | 22 | 25 | 7:30 | 2 |
| 23/06/2013 | 23 | 27 | 7:30 | 1 |
| 23/06/2013 | 23 | 31 | 7:30 | 2 |
| 24/06/2013 | 24 | 30 | 7:10 | 1 |
| 24/06/2013 | 24 | 35 | 7:10 | 2 |
| 25/06/2013 | 25 | 20 | 11:20 | 1 |
| 25/06/2013 | 25 | 20 | 11:20 | 2 |

**Table 6.7** Daily, pooled supplemental feeding bouts. The number of supplementary feeding bouts performed by offspring per observation day. Data is pooled to include both the related and unrelated groups.

| Observation Day | Number of supplemental feeding bouts |
|---|---|
| 1 | 1 |
| 2 | 3 |
| 3 | 2 |
| 4 | 9 |
| 5 | 0 |
| 6 | 6 |
| 7 | 13 |
| 8 | 7 |
| 9 | 11 |
| 10 | 7 |
| 11 | 12 |
| 12 | 1 |
| 13 | 14 |
| 14 | 27 |
| 15 | 16 |
| 16 | 13 |
| 17 | 24 |
| 18 | 32 |
| 19 | 56 |
| 20 | 6 |
| 21 | 28 |
| 22 | 22 |
| 23 | 25 |
| 24 | 13 |
| 25 | 22 |

**Table 6.8** Cumulative supplemental feeding bouts per offspring. We did not collect data on the number of supplemental feeding bouts performed by mothers.

| Offspring ID | Number of supplemental feeding bouts |
|---|---|
| 12 | 12 |
| 57 | 18 |
| 33 | 8 |
| 13 | 12 |
| 15 | 16 |
| 10 | 7 |
| 66 | 19 |
| 18 | 21 |
| 4 | 34 |
| 7 | 31 |
| 1 | 26 |
| 6 | 48 |
| 2 | 36 |
| 5 | 23 |
| 0 | 24 |
| 3 | 35 |

**Table 6.9** Occurrences and durations of supplemental feeding bouts. Data collected per offspring per observation day. Duration of supplemental feeding bouts were in recorded to the nearest second.

| Date | Observation days | Related=1,Unrelated=2 | Offspring ID | Occurrences | Duration1 | Duration2 | Duration3 |
|---|---|---|---|---|---|---|---|
| 30/05/2013 | 1 | 2 | 3 | 1 | | | |
| 31/05/2013 | 2 | 2 | 3 | 1 | 5 | | |
| 31/05/2013 | 2 | 2 | 4 | 1 | 15 | | |
| 31/05/2013 | 2 | 2 | 6 | 1 | | | |
| 01/06/2013 | 3 | 1 | 18 | 1 | | | |
| 01/06/2013 | 3 | 1 | 66 | 1 | | | |
| 02/06/2013 | 4 | 2 | 0 | 1 | 2 | | |
| 02/06/2013 | 4 | 2 | 4 | 1 | | | |
| 02/06/2013 | 4 | 2 | 5 | 1 | | | |
| 02/06/2013 | 4 | 2 | 7 | 3 | 12 | | |
| 02/06/2013 | 4 | 1 | 13 | 1 | | | |
| 02/06/2013 | 4 | 1 | 15 | 1 | | | |
| 02/06/2013 | 4 | 1 | 18 | 1 | | | |
| 04/06/2013 | 6 | 2 | 2 | 1 | | | |
| 04/06/2013 | 6 | 2 | 4 | 1 | | | |
| 04/06/2013 | 6 | 2 | 5 | 1 | | | |
| 04/06/2013 | 6 | 2 | 6 | 1 | | | |

| | | | | | |
|---|---|---|---|---|---|
| 04/06/2013 | 6 | 2 | 7 | 1 | |
| 04/06/2013 | 6 | 1 | 10 | 1 | |
| 05/06/2013 | 7 | 2 | 0 | 1 | |
| 05/06/2013 | 7 | 2 | 2 | 1 | |
| 05/06/2013 | 7 | 2 | 3 | 1 | |
| 05/06/2013 | 7 | 2 | 5 | 1 | |
| 05/06/2013 | 7 | 2 | 4 | 2 | 6 |
| 05/06/2013 | 7 | 2 | 6 | 2 | |
| 05/06/2013 | 7 | 2 | 7 | 4 | |
| 05/06/2013 | 7 | 1 | 13 | 1 | 15 |
| 06/06/2013 | 8 | 2 | 1 | 1 | |
| 06/06/2013 | 8 | 2 | 3 | 1 | |
| 06/06/2013 | 8 | 2 | 5 | 1 | |
| 06/06/2013 | 8 | 2 | 6 | 1 | |
| 06/06/2013 | 8 | 2 | 7 | 1 | |
| 06/06/2013 | 8 | 1 | 18 | 1 | |
| 06/06/2013 | 8 | 1 | 57 | 1 | |
| 07/06/2013 | 9 | 2 | 3 | 1 | |
| 07/06/2013 | 9 | 2 | 4 | 1 | |
| 07/06/2013 | 9 | 2 | 6 | 1 | |
| 07/06/2013 | 9 | 2 | 7 | 1 | |
| 07/06/2013 | 9 | 1 | 10 | 1 | |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| 07/06/2013 | 9 | 1 | 12 | 1 |  |
| 07/06/2013 | 9 | 1 | 57 | 1 |  |
| 07/06/2013 | 9 | 1 | 66 | 1 |  |
| 07/06/2013 | 9 | 1 | 33 | 1 |  |
| 07/06/2013 | 9 | 1 | 18 | 2 |  |
| 09/06/2013 | 10 | 1 | 13 | 1 |  |
| 09/06/2013 | 10 | 1 | 15 | 1 |  |
| 09/06/2013 | 10 | 1 | 57 | 1 |  |
| 09/06/2013 | 10 | 1 | 66 | 1 |  |
| 09/06/2013 | 10 | 1 | 33 | 1 |  |
| 09/06/2013 | 10 | 1 | 12 | 2 |  |
| 10/06/2013 | 11 | 2 | 0 | 1 |  |
| 10/06/2013 | 11 | 2 | 1 | 1 |  |
| 10/06/2013 | 11 | 2 | 3 | 1 |  |
| 10/06/2013 | 11 | 2 | 4 | 1 |  |
| 10/06/2013 | 11 | 2 | 5 | 1 |  |
| 10/06/2013 | 11 | 2 | 7 | 1 |  |
| 10/06/2013 | 11 | 1 | 18 | 1 | 2 |
| 10/06/2013 | 11 | 1 | 66 | 2 |  |
| 10/06/2013 | 11 | 1 | 15 | 3 | 3 |
| 11/06/2013 | 12 | 2 | 3 | 1 |  |
| 12/06/2013 | 13 | 2 | 6 | 1 |  |

| | | | | | |
|---|---|---|---|---|---|
| 12/06/2013 | 13 | 2 | 2 | 3 | |
| 12/06/2013 | 13 | 1 | 18 | 1 | |
| 12/06/2013 | 13 | 1 | 15 | 2 | |
| 12/06/2013 | 13 | 1 | 66 | 2 | |
| 12/06/2013 | 13 | 1 | 33 | 2 | |
| 12/06/2013 | 13 | 1 | 13 | 3 | |
| 13/06/2013 | 14 | 2 | 5 | 1 | |
| 13/06/2013 | 14 | 2 | 6 | 2 | |
| 13/06/2013 | 14 | 2 | 0 | 3 | |
| 13/06/2013 | 14 | 2 | 1 | 3 | 3 |
| 13/06/2013 | 14 | 2 | 3 | 3 | 2 |
| 13/06/2013 | 14 | 2 | 4 | 3 | |
| 13/06/2013 | 14 | 2 | 7 | 3 | 2 |
| 13/06/2013 | 14 | 2 | 2 | 5 | 3 |
| 13/06/2013 | 14 | 1 | 13 | 1 | |
| 13/06/2013 | 14 | 1 | 18 | 1 | |
| 13/06/2013 | 14 | 1 | 57 | 1 | 3 |
| 13/06/2013 | 14 | 1 | 66 | 1 | 2 |
| 14/06/2013 | 15 | 2 | 0 | 1 | |
| 14/06/2013 | 15 | 2 | 2 | 2 | |
| 14/06/2013 | 15 | 2 | 3 | 2 | 2 |
| 14/06/2013 | 15 | 2 | 4 | 2 | |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| 14/06/2013 | 15 | 2 | 5 | 2 |  |  |  |
| 14/06/2013 | 15 | 2 | 6 | 2 | 2 |  |  |
| 14/06/2013 | 15 | 2 | 7 | 3 |  |  |  |
| 14/06/2013 | 15 | 1 | 18 | 1 |  |  |  |
| 14/06/2013 | 15 | 1 | 57 | 1 |  |  |  |
| 15/06/2013 | 16 | 2 | 0 | 1 |  |  |  |
| 15/06/2013 | 16 | 2 | 3 | 1 |  |  |  |
| 15/06/2013 | 16 | 2 | 5 | 1 |  |  |  |
| 15/06/2013 | 16 | 2 | 1 | 2 |  |  |  |
| 15/06/2013 | 16 | 2 | 4 | 2 |  |  |  |
| 15/06/2013 | 16 | 2 | 6 | 3 |  |  |  |
| 15/06/2013 | 16 | 2 | 7 | 3 |  |  |  |
| 16/06/2013 | 17 | 2 | 0 | 1 | 1 |  |  |
| 16/06/2013 | 17 | 2 | 5 | 1 | 3 |  |  |
| 16/06/2013 | 17 | 2 | 2 | 2 | 2 |  |  |
| 16/06/2013 | 17 | 2 | 3 | 4 | 3 | 10 |  |
| 16/06/2013 | 17 | 2 | 4 | 5 | 6 | 5 | 7 |
| 16/06/2013 | 17 | 2 | 6 | 5 | 44 | 18 |  |
| 16/06/2013 | 17 | 1 | 10 | 1 |  |  |  |
| 16/06/2013 | 17 | 1 | 12 | 1 |  |  |  |
| 16/06/2013 | 17 | 1 | 13 | 1 | 41 |  |  |
| 16/06/2013 | 17 | 1 | 15 | 1 |  |  |  |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| 16/06/2013 | 17 | 1 | 18 | 1 | 63 |  |  |
| 16/06/2013 | 17 | 1 | 57 | 1 |  |  |  |
| 17/06/2013 | 18 | 2 | 4 | 1 |  |  |  |
| 17/06/2013 | 18 | 2 | 7 | 1 |  |  |  |
| 17/06/2013 | 18 | 2 | 0 | 2 | 12 |  |  |
| 17/06/2013 | 18 | 2 | 5 | 2 |  |  |  |
| 17/06/2013 | 18 | 2 | 2 | 3 | 37 | 9 |  |
| 17/06/2013 | 18 | 2 | 3 | 3 | 10 |  |  |
| 17/06/2013 | 18 | 2 | 6 | 3 | 80 |  |  |
| 17/06/2013 | 18 | 2 | 1 | 4 | 23 |  |  |
| 17/06/2013 | 18 | 1 | 12 | 1 |  |  |  |
| 17/06/2013 | 18 | 1 | 13 | 1 | 107 |  |  |
| 17/06/2013 | 18 | 1 | 15 | 2 | 7 | 10 |  |
| 17/06/2013 | 18 | 1 | 57 | 2 | 104 |  |  |
| 17/06/2013 | 18 | 1 | 18 | 3 | 12 | 25 | 12 |
| 17/06/2013 | 18 | 1 | 66 | 4 | 22 | 2 | 15 |
| 18/06/2013 | 19 | 2 | 0 | 4 |  |  |  |
| 18/06/2013 | 19 | 2 | 4 | 4 | 5 |  |  |
| 18/06/2013 | 19 | 2 | 7 | 4 |  |  |  |
| 18/06/2013 | 19 | 2 | 2 | 5 | 4 | 2 |  |
| 18/06/2013 | 19 | 2 | 5 | 5 | 30 |  |  |
| 18/06/2013 | 19 | 2 | 3 | 7 | 3 | 8 |  |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| 18/06/2013 | 19 | 2 | 1 | 8 | 5 | 3 |  |
| 18/06/2013 | 19 | 2 | 6 | 10 | 42 | 11 | 59 |
| 18/06/2013 | 19 | 1 | 15 | 1 | 8 |  |  |
| 18/06/2013 | 19 | 1 | 12 | 2 | 5 | 5 |  |
| 18/06/2013 | 19 | 1 | 18 | 2 |  |  |  |
| 18/06/2013 | 19 | 1 | 57 | 2 | 18 |  |  |
| 18/06/2013 | 19 | 1 | 66 | 2 |  |  |  |
| 20/06/2013 | 20 | 2 | 0 | 1 |  |  |  |
| 20/06/2013 | 20 | 2 | 2 | 1 |  |  |  |
| 20/06/2013 | 20 | 2 | 7 | 1 |  |  |  |
| 20/06/2013 | 20 | 1 | 18 | 1 |  |  |  |
| 20/06/2013 | 20 | 1 | 57 | 1 |  |  |  |
| 20/06/2013 | 20 | 1 | 66 | 1 |  |  |  |
| 21/06/2013 | 21 | 2 | 1 | 1 |  |  |  |
| 21/06/2013 | 21 | 2 | 4 | 1 |  |  |  |
| 21/06/2013 | 21 | 2 | 5 | 2 |  |  |  |
| 21/06/2013 | 21 | 2 | 0 | 3 | 6 |  |  |
| 21/06/2013 | 21 | 2 | 2 | 3 |  |  |  |
| 21/06/2013 | 21 | 2 | 3 | 3 | 6 |  |  |
| 21/06/2013 | 21 | 2 | 7 | 3 |  |  |  |
| 21/06/2013 | 21 | 2 | 6 | 4 | 67 |  |  |
| 21/06/2013 | 21 | 1 | 10 | 1 |  |  |  |

|  |  |  |  |  |
|---|---|---|---|---|
| 21/06/2013 | 21 | 1 | 12 | 1 |
| 21/06/2013 | 21 | 1 | 13 | 1 |
| 21/06/2013 | 21 | 1 | 15 | 1 |
| 21/06/2013 | 21 | 1 | 18 | 1 |
| 21/06/2013 | 21 | 1 | 57 | 1 |
| 21/06/2013 | 21 | 1 | 66 | 1 |
| 21/06/2013 | 21 | 1 | 33 | 1 |
| 22/06/2013 | 22 | 2 | 3 | 1 |
| 22/06/2013 | 22 | 2 | 5 | 1 |
| 22/06/2013 | 22 | 2 | 7 | 1 |
| 22/06/2013 | 22 | 2 | 0 | 2 |
| 22/06/2013 | 22 | 2 | 1 | 2 |
| 22/06/2013 | 22 | 2 | 2 | 2 |
| 22/06/2013 | 22 | 2 | 4 | 2 |
| 22/06/2013 | 22 | 2 | 6 | 2 |
| 22/06/2013 | 22 | 1 | 10 | 1 |
| 22/06/2013 | 22 | 1 | 12 | 1 |
| 22/06/2013 | 22 | 1 | 13 | 1 |
| 22/06/2013 | 22 | 1 | 15 | 1 |
| 22/06/2013 | 22 | 1 | 18 | 1 |
| 22/06/2013 | 22 | 1 | 66 | 1 |
| 22/06/2013 | 22 | 1 | 33 | 1 |

|  |  |  |  |  |
|---|---|---|---|---|
| 22/06/2013 | 22 | 1 | 57 | 2 |
| 23/06/2013 | 23 | 2 | 0 | 1 |
| 23/06/2013 | 23 | 2 | 1 | 1 |
| 23/06/2013 | 23 | 2 | 3 | 1 |
| 23/06/2013 | 23 | 2 | 6 | 1 |
| 23/06/2013 | 23 | 2 | 7 | 1 |
| 23/06/2013 | 23 | 2 | 2 | 2 |
| 23/06/2013 | 23 | 2 | 4 | 2 |
| 23/06/2013 | 23 | 2 | 5 | 2 |
| 23/06/2013 | 23 | 1 | 10 | 1 |
| 23/06/2013 | 23 | 1 | 13 | 1 |
| 23/06/2013 | 23 | 1 | 15 | 1 |
| 23/06/2013 | 23 | 1 | 12 | 2 |
| 23/06/2013 | 23 | 1 | 18 | 2 |
| 23/06/2013 | 23 | 1 | 66 | 2 |
| 23/06/2013 | 23 | 1 | 33 | 2 |
| 23/06/2013 | 23 | 1 | 57 | 3 |
| 24/06/2013 | 24 | 2 | 1 | 1 |
| 24/06/2013 | 24 | 2 | 2 | 2 |
| 24/06/2013 | 24 | 2 | 4 | 2 |
| 24/06/2013 | 24 | 2 | 6 | 6 |
| 24/06/2013 | 24 | 1 | 15 | 1 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| 24/06/2013 | 24 | 1 | 18 | 1 | 15 |
| 25/06/2013 | 25 | 2 | 5 | 1 |  |
| 25/06/2013 | 25 | 2 | 0 | 2 |  |
| 25/06/2013 | 25 | 2 | 1 | 2 |  |
| 25/06/2013 | 25 | 2 | 3 | 3 |  |
| 25/06/2013 | 25 | 2 | 4 | 3 |  |
| 25/06/2013 | 25 | 2 | 6 | 3 |  |
| 25/06/2013 | 25 | 2 | 2 | 4 |  |
| 25/06/2013 | 25 | 1 | 10 | 1 |  |
| 25/06/2013 | 25 | 1 | 12 | 1 |  |
| 25/06/2013 | 25 | 1 | 15 | 1 |  |
| 25/06/2013 | 25 | 1 | 57 | 1 |  |

# Chapter 7 General Discussion

Mothers discriminated their own offspring from the offspring of other mothers, and the odds of successfully allosuckling were greater for offspring arriving 2nd (i.e. arriving 2nd in order after a mother's own offspring, and while the mother is nursing her offspring) than for those arriving 1st (i.e. soliciting an allosuckling bout before the mother's own offspring and other offspring), 3rd, 4th, 5th or 6th. Therefore, my thesis supports the misdirected parental care hypothesis due to milk theft (see Table 7.1; Chapter 3). There was evidence of reciprocal allonursing at the group level and within dyads (see Table 7.1; Chapter 4). The majority of dyads were not reciprocal (i.e. unidirectional allonursing). However, a large subset of mothers reciprocally allonursed, and most mothers were members of at least one strongly reciprocal dyad. Mothers did not reciprocally allonurse with closely related mothers. Therefore, reciprocal allonursing in reindeer can be attributed to reciprocal altruism (Trivers, 1971). Biological market theory was useful for assessing reciprocal allonursing (Noë & Hammerstein, 1994, 1995; Noë, 2001). Allonursing may be a tradable commodity exchanged among chosen partners within biological markets. Mothers allonursed the calves of several mothers but allonursing was not distributed evenly among all potential partners. Mothers did not allonurse to evacuate milk (see Table 7.1; Chapter 3; see Chapter 7, sub-section 7.5 Milk Evacuation) There was evidence to support the improved nutrition hypothesis, because offspring who allosuckled more often had a higher percentage of mass gain and a higher mass at the end of the study than offspring that allosuckled less often (see Table 7.1; Chapter 5). The compensation hypothesis was not supported, since offspring did not allosuckle to compensate for low birth mass, insufficient maternal milk supply or inadequate growth, (see Table 7.1; Chapter 5). The odds of successfully allosuckling were not influenced by genetic relatedness, which did not support the kin-selection hypothesis (see Table 7.1; Chapter 3). However, allonursing contributions varied with genetic relatedness when two groups of mothers were experimentally manipulated based on the two extremes of genetic relatedness (see Table 7.1; Chapter 6). Given that the misdirected parental care (i.e. milk-theft), reciprocal allonursing and improved nutrition hypotheses were supported, kin-selection alone is not sufficient to explain allosuckling and allonursing in reindeer (Clutton-Brock, 2002; Cockburn, 1998). I now will discuss: 1) whether the indirect fitness benefits of allonursing may be overestimated (Clutton-Brock, 2002; Cockburn, 1998), 2) whether allosuckling and allonursing in reindeer are unselected consequences of group living (i.e. by-products of group living), 3) how trading-off indirect fitness for direct fitness may explain aggregating with closely and distantly related mothers and reciprocal allonursing, 4) whether reciprocal allonursing is a result of biological markets or reciprocal altruism, 5) potential misinterpretations of reciprocal allonursing, 6) a potential misinterpretation of the partial support for mismothering, 7) milk evacuation, and 8) inter-population differences. In addition, I provide several areas for future research.

**Table 7.1** Summary of allosuckling and allonursing hypotheses supported and not supported in reindeer. The asterisk refers the reader to the finding that allonursing contributions detected can depend upon the research design (see Chapters 3 and 6).

| Hypotheses supported | Hypotheses not supported |
|---|---|
| Misdirected parental care (i.e. milk-theft) | Misdirected parental care (i.e. mismothering due to a lack of efficient kin recognition mechanisms) |
| Kin-selection* | Kin-selection* |
| Reciprocity | |
| | Milk evacuation |
| Improved nutrition | |
| | Compensation |

### 7.1 Overestimation of Kin-selection?

Researchers have often attributed the evolution of cooperative breeding primarily to kin-selection (Brown, 1987; Emlen, 1997), but researchers have also questioned whether the indirect fitness benefits of alloparental care may be overestimated (Clutton-Brock, 2002; Cockburn, 1998). Firstly, if invertebrates are not considered, especially haplodiploid species, genetic relatedness in cooperative breeders may not be higher than in non-cooperative breeders (Clutton-Brock, 2002; Hatchwell & Komdeur, 2000). Secondly, alloparents can be distantly related to offspring and invest as much or more than closely related alloparents or parents (Clutton-Brock, 2002), such as raising others' offspring in fish (e.g. sperm, egg and zygote dumping, zygote stealing and nest take-overs, dumping of young, brood amalgamation, adoption and brood parasitism) (Wisenden, 1999), investing in the total number of offspring in house mice (Ferrari et al., 2015), reciprocal allonursing (Chapter 4; Ferrari et al., 2015), babysitting in meerkats (Clutton-Brock et al., 2000), and food provisioning in bell miners (Clarke, 1989) and paper wasps, *Polistes dominulus* (Leadbeater et al., 2011; Queller et al., 2000). Thirdly, researchers may have overestimated the indirect fitness benefits (Clutton-Brock, 2002; Cockburn, 1998) because of: 1) incorrect calculations due to a mistake in a definition or double accounting (e.g. indirect fitness benefits from providing alloparental care to kin and receiving alloparental care from kin) (Creel, 1990), 2) calculations that do not take into account the inclusive fitness costs of competition among close kin, such as when dispersal is limited (Griffin & West, 2002; West et al., 2002), 3) calculations that do not control for the effects of territory quality on offspring production, growth and survival (Woodroffe & Macdonald, 2000), and 4) including apparent alloparents (e.g. individuals that have reproduced and provide alloparental care) in calculations, such as in white-browed scrubwrens (Magrath and Whittingham, 1997; Whittingham et al., 1997; Gilchrist, 2007). Beta male white-browed scrubwrens with within-group paternity were referred to as helpers, instead parents providing parental care and alloparental care (Whittingham et al., 1997). Cockburn (1998) reports that within-group paternity was shared in several species, and yet many of these studies referred to parents providing parental care and alloparental care as helpers. Fourthly, in groups that associate and interact with close kin, the provisioning of alloparental care may not vary with genetic relatedness (Clutton-Brock, 2002). However, altruistic traits can be selected for if the benefits to the recipient multiplied by the degree of relatedness between the actor and the recipient are greater than the costs to the recipient, which can arise from kin discrimination or from unconditional altruism with limited dispersal (Hamilton, 1964a, 1964b). Cornwallis et al. (2009) demonstrated that kin discrimination, in comparison to unconditional altruism with limited dispersal, has a greater influence on alloparental care in cooperative breeding vertebrates when: 1) the average relatedness in groups is lower and more variable, 2) the effect of alloparents on the parents' reproductive success is greater, and 3) the probability of providing alloparental care was measured rather than the amount of alloparental care provided.

A meta-analysis of the incidence of allonursing in singular cooperative breeders, which have greater mean within-group relatedness than non-singular cooperative breeders, revealed that the incidence of allonursing was not associated with relatedness in these groups (MacLeod & Lukas, 2014). I suggest that kin-selection alone is not sufficient to explain allonursing in cooperative breeding social systems (Clutton-Brock, 2002; Cockburn, 1998). Researchers have proposed a number of hypotheses to explain the evolution and maintenance of allosuckling and allonursing (Hayes, 2000; Jamieson, 1989; Packer et al., 1992; Roulin & Heeb, 1999; Roulin, 2002, 2003; Víchová & Bartoš, 2005). I have introduced and discussed alternative hypotheses explaining allosuckling and allonursing in Chapters 1, 3, 4, 5 and 6. Future research should assess the relative importance of the allosuckling and allonursing hypotheses (see Chapter 7, section 7.7. Future Areas of Research).

### *7.1.1 Aggregation, Allonursing and Kin Discrimination*

Aggregating and interacting with close relatives is important for the evolution of social behaviour (Hamilton, 1964a, 1964b). In Chapter 6, I discussed allonursing in free-ranging wildlife that aggregate and allonurse with close kin (e.g. Creel et al., 1991; Eberle & Kappeler, 2006; Ekvall, 1998), without considering kin discrimination (see Table 7.2), and a few studies reported that allonursing contributions varied with relatedness (Creel et al., 1991; MacLeod et al., 2013; Pusey & Packer, 1994). Female dwarf mongooses can recognize individuals by vocal recognition of playbacks (Sharpe, Hill, & Cherry, 2013), and spontaneous lactators breed communally with close relatives (Creel et al., 1991). Subordinate females that allonurse are more closely related to the dominant female than to the dominant male, and there are male and female dispersers and non-dispersers in every group (Creel et al., 1991). Female dwarf mongooses that spontaneously lactate generally remain in their natal pack, and the dominant female is often succeeded by a related female (Creel et al., 1991). Female meerkats use phenotype matching to recognize the odour of kin (Leclaire, Nielsen, Thavarajah, Manser, & Clutton-Brock, 2013), and within-group female relatedness is high (MacLeod et al., 2013). Female lions can recognize individuals by vocal recognition of playbacks (Grinnell & McComb, 1996), and lion prides consist of closely related females (Pusey & Packer, 1994). The probability that all female lions in a crèche were first order relatives ranged from 0 to 1 (Pusey & Packer, 1994). In fallow deer, offspring recognize mothers, who have distinct individual vocalizations, but mothers do not recognize their own offspring from the offspring of other mothers, at least during the early life of offspring (Torriani, Vannoni, & Mcelligott, 2006). The vocalizations of individual male and female fallow deer are individually distinctive, which suggests that fallow deer may be able to discriminate individuals (Torriani et al., 2006; Vannoni & McElligott, 2007). In Sweden, closely related female fallow deer form small, stable matrilineal groups, and young mothers associate strongly with their own mother at calving (Ekvall, 1998). Prairie dogs discriminate familiar individuals from their coterie by associative learning from all other individuals (Hoogland, 1995). Three to four female prairie dogs live in each group, and they are nearly always close kin because of high female philopatry (Hoogland, 1982). To my knowledge, kin discrimination has not been tested in fat dormice. However, fat dormice rarely nest with more than one related individual (Marin & Pilastro, 1994), and they communally nurse (Pilastro, 1992). Female grey mouse lemurs form groups with closely related females, and by regularly transferring only their own offspring among roosting sites, they demonstrate the ability to discriminate their own offspring from the offspring of closely related females (Eberle & Kappeler, 2006). I suggest that the average relatedness values in lions (Pusey & Packer, 1994), dwarf mongooses (Creel et al., 1991) and meerkats (MacLeod et al., 2013) groups were more variable than the average relatedness values in fallow deer (Ekvall, 1998), prairie dogs (Hoogland et al., 1989), fat dormice (Pilastro, 1992) and grey mouse lemurs (Eberle & Kappeler, 2006) as an explanation for allonursing contributions varying with relatedness in lions, dwarf mongoose and fallow deer (Cornwallis et al., 2009).

In Chapter 6, I discussed allonursing in groups of females that do not associate more strongly with close kin than with distantly related females and do not preferentially allonurse offspring of close kin, without considering kin discrimination (see Table 7.2). There is indirect evidence that mother-offspring recognition occurs in wood mice (Gerlach & Bartmann, 2002).

When the litter of a wood mouse mother was killed, she no longer allonursed reciprocally and decreased her nursing time by 94% (Gerlach & Bartmann, 2002). Wood mice have high probabilities of encountering related and unrelated conspecifics in their groups, and females may communally nest and nurse with related or unrelated females (Gerlach & Bartmann, 2002). Wood mice mothers should communally nest and nurse only when ecological conditions prevent solitary breeding (Gerlach & Bartmann, 2002). Mexican free-tailed bat mothers can discriminate pups by vocal recognition (Balcombe, 1990), and pups can discriminate mothers by vocal recognition (Balcombe & McCracken, 1992). Mexican free-tailed bats form colonies composed of millions of individuals and lack stable roosting associations, and pups steal milk (McCracken & Gustin, 1991). Female evening bats return to their natal colony and form nursery colonies, but the average relatedness among females within a colony is 0.01 (Wilkinson, 1992). Evening bat mothers communally nursed rarely prior to the two weeks before weaning, but mothers communal nursed more often during the two weeks before weaning, which coincided with the period when pups began hunting (Wilkinson, 1992). Evening bats did not

**Table 7.2** Summary of studies that assessed the kin-selection allonursing hypothesis. The asterisk refers the reader to the text.

| Species | Supports kin-selection? | Aggegates with close kin? | Kin recognition? | Other hypotheses supported | Authors |
|---|---|---|---|---|---|
| Dwarf mongoose | Yes | Yes | Yes | | Creel et al. (1991) |
| Meerkat | Yes | Yes | Yes | | MacLeod et al. (2013) |
| Lion | Yes | Yes | Yes | | Pusey and Packer (1994) |
| Fallow deer | Yes | Yes | Unknown* | | Ekvall (1998) |
| Prairie dog | Yes | Yes | Yes | | Hoogland et al. (1989) |
| Fat dormouse | Yes | Yes | Unknown* | | Pilastro (1992) |
| Grey mouse lemur | Yes | Yes | Yes* | | Eberle and Kapperler (2006) |
| River buffalo | No | Yes | See text | Milk-theft, compensation | Murphey et al. (1995) |
| Reindeer | Yes/No | No | Yes | Milk-theft, reciprocity, improved nutrition | Engelhardt et al. (2014, 2016, 2015, in press) |
| Wood mouse | No | No | Yes* | Reciprocity | Gerlach and Bartmann (2002) |
| Mexican free-tailed bat | No | No | Yes | Milk-theft | McCracken (1984); McCracken and Gustin (1991) |
| Evening bat | No | No | Yes* | Milk evacuation | Wilkinson (1992) |
| House mouse | No | No | No* | Reciprocity, mismothering | König (2006) |
| Wedge-capped capuchin | No | No | Yes* | See text | O’Brien and Robinson (1991) |

| | | | | | |
|---|---|---|---|---|---|
| Grey seal | No | No | Yes/No | See text | McCulloch et al. (1999); Perry et al. (1998) |
| Polar bear | No | No | No | Mismothering | Lunn et al. (2000) |

allonurse indiscriminately (Wilkinson, 1992), which suggests that mother-offspring recognition occurs in evening bats. Wilkinson (1992) suggested that mothers allonursed to evacuate milk. Mother-offspring recognition may not be well developed in polar bears (Lunn et al., 2000). In polar bears, the only extended social groups are composed of a mother and cubs, and these family groups are cautious of or avoid other polar bears (Lunn et al., 2000). A study reported that four polar bear mothers adopted genetically unrelated cubs, and two of those mothers were lactating (Lunn et al., 2000), which I suggest is evidence that lactating females allonursed due to a lack of efficient kin recognition mechanisms (i.e. mismothering). Grey seal mothers-offspring vocal recognition was found on Sable Island, where mothers rarely allonurse, but not on the Isle of May, where allonursing is common and suggests mismothering (McCulloch & Boness, 2000). However, indirect evidence of the ability to recognize individual mothers by other mothers, based on long-term associations between individuals, was shown on North Rona, Scotland (Pomeroy, Redman, Ruddell, Duck, & Twiss, 2005). In addition, newly weaned pups recognized familiar newly weaned pups from unfamiliar ones (Robinson et al., 2015). Although grey seals are philopatric, show breeding site and mate fidelity, the relatedness of grey seals pups within and between beaches on Faray Island, Canada, and Ramsey Island, Canada, did not differ (Perry et al., 1998). Allonursing females were not related to pups they allonursed (Perry et al., 1998). On Faray Island, 3 (3.8%) females allonursed daily, while on Ramsey Island, 7 (28%) females allonursed daily (Perry et al., 1998). Researchers reported kin discrimination in female wedge-capped capuchins based on high rates of affiliation and low aggression rates between close kin (O'Brien & Robinson, 1991). Female wedge-capped capuchins live in groups that vary in average relatedness (O'Brien & Robinson, 1991). O'Brien (1988) suggests allonursing in wedge-capped capuchins is an exploitative interaction and parasitic, since lower-ranking females always allonursed offspring of higher-ranking females. House mouse mothers may have poorly developed mother-offspring recognition mechanisms, since they indiscriminately allonurse in an egalitarian reproductive relationship (König, 2006), and they invest in the number of offspring in the communal nest (Ferrari et al., 2015). House mouse mothers could not discriminate their own offspring from that of others when retrieving offspring (Manning et al., 1995). However, Yamazaki, Beauchamp, Curran, Bard and Boyse (2000) reported mother-offspring phenotype matching recognition of MHC odortype, and mothers preferentially retrieved their own offspring. Ferrari et al. (2015) and König (2006) reported that evidence of mother-offspring recognition in house mice was weak: Yamazaki et al. (2000) provide the only support out of many studies. The average kinship between communally nesting house mice mothers was 0.16 ± 0.03 and ranged from 0 to 0.54 (Auclair et al., 2014). The effects of familiarity override the effects of relatedness in the formation of an egalitarian reproductive relationship (König, 2006; Weidt et al., 2014). Thus, allonursing in house mice is reciprocal and due to mismothering (Ferrari et al., 2015; König, 2006). To my knowledge, kin discrimination has not been tested in river buffalo. Feral river buffalo form maternal groups (Shackleton & Harestad, 2003). However, domesticated river buffalo mothers did not direct their allonursing contributions to close kin, and their allonursing contributions did not vary with kinship (Murphey et al., 1995). River buffalo offspring steal milk and compensate for insufficient maternal milk supply and inadequate growth (Murphey et al., 1995). Mother-offspring vocal (Espmark, 1971b) and olfactory (Källquist & Mossing, 1982) recognition have been reported in reindeer. Reindeer mothers and yearling daughters tend to associate throughout the year, except during calving when their associations did not differ from a control sample of unrelated females (Hirotani, 1990), which likely influenced the detected results in our two previous studies (Chapters 3 and 4). In wood mice (Gerlach & Bartmann, 2002), Mexican free-tailed bats (McCracken & Gustin, 1991), evening bats (Wilkinson, 1992), polar bears (Lunn et al., 2000), grey seals (McCulloch & Boness, 2000; Perry et al., 1998), wedge-capped capuchins (O'Brien & Robinson, 1991), house mice (König, 2006), river buffalo (Murphey et al., 1995), reindeer (Engelhardt et al., 2014, 2015, in press; Hirotani, 1990), the average relatedness in groups is low, and there is a high variation in relatedness (Cornwallis et al., 2009). Researchers have proposed that allonursing supported hypotheses other than kin-selection (see Table 6.2).

### *7.1.2 Direct fitness benefits*

Clutton-Brock (2002) suggested that alloparental care could be caused by parasitism, by-product mutualism, coercion, intra-specific mutualism, reciprocity and group augmentation, instead of kin-selection. The assessment of the evolutionary history of allonursing should include direct fitness benefits added to phylogenetic analyses. Allonursing in reindeer may have evolved due to the direct fitness benefits for offspring stealing milk and improving their nutrition and mass gain, which could increase their lifetime reproductive success (Lindström, 1999), and due to the direct fitness for lactating females reciprocally sharing of nursing loads. We supported the offspring parasitism strategy of milk-theft, and offspring that stole milk exploited lactating females (Chapter 3). The fitness effects of milk-theft on the reindeer mothers whose milk was stolen and their offspring were not addressed by our research designs, but the effects could be neutral or negative (Clutton-Brock, 2002). The fitness effects of milk-theft on the mothers from which milk was stolen and their offspring in red deer was neutral (Landete-Castillejos, García, Garde, et al., 2000; Landete-Castillejos et al., 2005). There was no growth reduction in late-born red deer offspring (Landete-Castillejos et al., 2005) and the percentage of allonursing was not correlated with the mother's percentage of mass loss (Landete-Castillejos, García, Garde, et al., 2000). Under laboratory conditions and when the interval between the first mother's parturition and the second mother's parturition was greater than 14 days in communally nesting and nursing rodents, parasitic milk-theft can have negative effects on the offspring of the younger litter, since the reproductive success of the second mother was significantly reduced and surviving offspring grew less compared to the first mother's offspring (König, 1993; Mennella et al., 1990; Sayler & Salmon, 1969; Werboff et al., 1970). Clutton-Brock (2002) suggested that alloparental care in cooperative breeding social systems could be the result of by-product mutualism, without contributing to the selection pressures maintaining the behaviour. Taking into account Clutton-Brock's (2002) suggestion, I now consider whether allosuckling and allonursing may be apparently cooperative behaviours and examples of by-product mutualism. For example, offspring may be stealing milk and maximizing their own fitness (e.g. improved nutrition and mass gain, compensation, immunological function), and the direct fitness benefits of allonursing (e.g. reciprocity, milk evacuation, neuroendocrine function, learning to parent) for mothers may be coincidental, without contributing to the selection pressures maintaining allonursing. Alternatively, allosuckling and allonursing may be mutually beneficial. Allosuckling improved the nutrition and mass gain of reindeer calves (Chapter 5), and mothers may allonurse for neuroendocrine and immunological benefits (Roulin, 2002). In addition, early postnatal growth and mass gain from parturition to weaning is an important predictor of offspring survival and future fitness for birds and mammals (Lindström, 1999), which is mutually beneficial for allosuckling and allonursing reindeer. Reciprocity is an enforced form of cooperation (Gardner & Foster, 2008; West et al., 2007), and cheating can select against reciprocity. This thesis suggests that reindeer mothers may have directed agonistic interactions to the calves of other mothers (i.e. aggression and punishment) to decrease the risk of cheating and coerce mothers to reciprocally allonurse (Chapter 4). My thesis' data does not provide answers for the possibility that reindeer mothers allonurse for future group augmentation benefits, because the reindeer manager slaughters the vast majority of calves before, during and/or after rut.

#### *7.1.2.1 Did reindeer allonurse for the direct fitness benefits of alloparental care?*

I introduced the adaptive hypotheses of alloparental care based on direct fitness benefits in Chapter 2, section 2.7.1. To avoid potential allonursing effects because of primiparous mothers learning to parent (e.g. allonursing performed mainly by inexperienced mother) (Roulin, 2002), we did not select primiparous mothers for this study. We also did not observe spontaneous lactation. Therefore, mothers do not allonurse for the direct fitness benefits of acquiring maternal skills (Brown, 1987; Cockburn, 1998; Roulin, 2002). Reindeer mothers do not have to allonurse pay rent for access to group resources (Cockburn, 1998; Emlen et al., 1991), since reindeer mothers are plural breeders and do not delay dispersal or delay breeding. Female reindeer do not allonurse for the direct benefits of the social prestige hypothesis, which investigates male social prestige (Zahavi, 1990) or access to mating opportunities (Mumme, 1997). The sexes are segregated during the non-reproductive period. Therefore, allonursing does not influence mate choice or increase mating opportunities. My research does not provide answers for the possibility that reindeer mothers allonurse for future group augmentation benefits or recruitment of future alloparents (e.g. Ligon & Ligon, 1978), because the reindeer manager slaughters the vast majority of calves before, during and/or after rut.

## 7.2 Are Allosuckling and Allonursing By-products of Group Living?

Hayes (2000) suggested that the most plausible explanation for communal nursing in rodents was an unavoidable consequence of group living, such as communal defence against infanticide. If communal nursing is a by-product of group living, mothers should lack efficient kin recognition mechanisms and be unable to reject offspring of other mothers sharing a communal nest (Hayes, 2000). A lack of efficient kin recognition mechanisms (i.e. differential behaviour towards conspecifics based on the degree of genetic relatedness; Brown and Brown, 1996) implies that the costs of being vigilant to recognize and reject non-descendant kin and distantly related kin may be greater than the loss of milk and potential transmission of pathogens (Roulin, 2002). In addition, the costs of allonursing should be greater than the costs of solitary nursing (Hayes, 2000). However, reindeer mothers discriminated their own offspring from those of other mothers, since non-maternal rejection rates were greater than maternal rejection rates (Chapter 3). Further, reindeer mothers were more often agonistic towards the offspring of other mothers than they were towards their own offspring, both during solicitations for milk and when within one body length of a mother's udders (Chapters 3 and 4).

Infanticide is a selection pressure for group living, and females communally defend against infanticide (Ebensperger, 1998), which may explain allonursing in lions (Pusey & Packer, 1994) and in house mice (König, 2006; Manning et al., 1995) but not in reindeer. Lion mothers communally defend against infanticide by males (Pusey & Packer, 1994). House mouse mothers reduce infanticide by males and other conspecifics by communally defending against infanticide after having formed an egalitarian reproductive relationship (König, 2006). In contradiction to reports of females forming groups and establishing counter-strategies to defend against infanticide, Lukas and Huchard (2014) report that male infanticide does not promote counter-strategies. I did not observed infanticide by reindeer males or females, and the sexes segregate by sex during the non-rutting period (Hirotani, 1990). Infanticide may occur, and if so, it is likely to be rare. Thus, infanticide is not a selection pressure for group living by reindeer mothers during the calving season.

I cannot completely exclude the possibility that allosuckling and allonursing in reindeer are unavoidable consequences of the selection pressures for group living (Hayes, 2000). If allosuckling and allonursing are by-products of living in groups, the benefits of group living should outweigh the costs of group living (Krause & Ruxton, 2002), and these two behaviours should be maintained by the benefits outweighing the costs. The traditional cost/benefit approach to the study of group living assumes that group living evolved because it serves a function and that there is an optimal group size (Danchin, Giraldeau, & Wagner, 2008; Krause & Ruxton, 2002). Increasing the group size can improve foraging efficiency and decrease predation risk, but it can also increase pathogen transmission and competition for resources (Danchin, Giraldeau, et al., 2008; Krause & Ruxton, 2002). For reindeer during the calving season, predation and the distribution of food (i.e. clumped milk distribution for offspring, since milk is clumped within the mother's udders and the udders of other mothers) are selective pressures for group living, and the costs of dispersal are high because of these two selective pressures (Russell, 2004). The formation of reindeer nursery groups should provide benefits against predation (e.g. vigilance, dilution of risk and confusion of predator) (Krause & Ruxton, 2002), and allosuckling and allonursing may be by-products of predation as a selection pressure for group living. In addition, lactating females of most species reduce their physical activity to save energy (e.g. Dufour & Sauther, 2002; Tardif, 1997), which increases the risk of predation and increases the benefits of group living. At the Kutuharju Field Reindeer Research Station, predators, such as bears (*Ursus arctos*), wolverines (*Gulo gulo*) and golden eagles (*Aquila chrysaetos*), killed 3 adult females in 2012, and 1 adult and 1 offspring in 2013. The expression of allosuckling and allonursing in my research projects may be influenced by temporal variation in predation-risk (Lima and Bednekoff, 1999). The research station is fenced and can be described as a low predation risk area due to the fences. A brown bear approached the fenced calving paddock in 2013, and the two groups of mother-offspring pairs allosuckled and allonursed less often and appeared to walked more during the 24 hours following the high predation risk then compared to before the predation risk event. Reindeer in the fenced calving paddock (i.e. maintained in a low predation risk area) may have overestimated the intensity of predation-risk following the brief high predation risk, and they appeared to allocate more effort to antipredator behaviour (e.g. forming a dense group, vocalizing often, and walking for a few hours as a group) following the brief high predation risk than to consuming natural forage, supplemental feed, allosuckling and allonursing (Lima and Bednekoff, 1999). Since animals are more likely to feed in low predation risk situations than in high predation risk situations (Lima and Bednekoff, 1999), the maintenance of low predation risk (i.e. the area within the Kutuhurju Field Reindeer Reseasrch Station) likely increased the occurrence of allosuckling and allonursing compared to wild reindeer.

Reindeer mothers are not constrained by the distribution of vegetation in summer, but the distribution of milk is clumped. Calves must grow quickly and have fat deposits to survive winter, and mothers have to transmit a great deal of energy and protein before rut. Physiological and temporal variations in milk production can create individual and/or temporal high differences in milk availability. Therefore, reindeer mothers may live in groups during calving for the direct benefits of allonursing, instead of allonursing being a by-product of the selection pressures for group living. Allonursing may provide greater flexibility in the timing and frequency of milk production and provisioning. Reindeer mothers may gain direct fitness benefits from their offspring stealing milk from other mothers (i.e. milk parasitism) (Chapter 3; Packer et al., 1992) and improving their nutrition and mass gain (Chapter 5). Mothers may gain direct fitness by allonursing reciprocally, which may decrease nursing loads (Chapter 4).

#### *7.2.1 Epigenetic Hypothesis*

My thesis cannot reject the epigenetic hypothesis for allonursing in reindeer (Jamieson & Craig, 1987; Jamieson, 1989; see Chapter 7, section 7.7.2.1 Genes for Alloparental Care). The epigenetic hypothesis postulates that alloparental care is an expression of a heterochronic change in ontogeny brought about as an unselected consequence of group living, due to a shift in life-history pattern (e.g. delayed dispersal), and the neuroendocrine mechanisms and development responsible for the expression of parental care (Jamieson & Craig, 1987; Jamieson, 1989; see Chapter 2, section 2.7.3 Nonadaptive Hypotheses of Alloparental Care). My thesis does not assess the epigenetics of alloparental (Jamieson & Craig, 1987; Jamieson, 1989; West-Eberhard, 1987)), and behavioural plasticity may be epigenetically regulated in animals (Simola et al., 2016). Nonetheless, I provide arguments against the epigenetic hypothesis (Jamieson & Craig, 1987; Jamieson, 1989). I consider my results and compare them to 3 critiques of a priori assumptions that natural selection has influenced alloparental care have pointed out that (Jamieson & Craig, 1987; Jamieson, 1989; see Chapter 2, section 2.7.3 Nonadaptive Hypotheses of Alloparental Care for the 3 critiques). Firstly, reindeer mothers did not respond to the begging of calves by allonursing them. Calves allosuckled by soliciting after a mother had started to nurse her own offspring, and mothers rejected nearly all allosuckling solicitations by calves that arrived first (i.e. before the mother had started to nurse her own offspring). Secondly, mothers allonursed offspring of closely and distantly related mothers, and a large sub-group of mothers allonursed reciprocally (i.e. an adaptive hypothesis). Thirdly, lactation is the most energetically costly aspect of mammalian reproduction (Gittleman & Thompson, 1988; König et al., 1988), and mothers that allonurse incur both lactation and allonursing costs (see Chapter 1, section 1.5.1 Lactation and section 1.5.2 Allonursing Costs).

## 7.3 Reciprocal Allonursing

### *7.3.1 Trading-off Indirect Fitness Benefits for Direct Fitness Benefits?*

The nursing of offspring is dependent on the mother's milk production and availability, and the distribution of milk is clumped within the mother's udders. Resource (i.e. milk) availability for offspring can be low during lactation, since maternal milk availability for transfer to the offspring is temporally variable. Variation in resource (i.e. milk) availability for offspring and predation are selection pressures for group living. Aggregating with close kin and preferentially allonursing offspring of closely related mothers may be counteracted by the selection for direct fitness benefits (Wilson, 1975). Reindeer calves need to consume milk, grow quickly and have fat deposits to survive the winter, and mothers need to supply milk to their offspring, reduce predation risk and increase the probability of current reproductive success. There may come a point when the inclusive fitness gained by aggregating with and preferentially allonursing offspring of close kin are lower than the direct fitness benefits of aggregating with mothers ranging from distantly to closely related. Therefore, mothers may trade-off indirect fitness benefits for direct fitness benefits and aggregate with closely and distantly related mothers to reduce predation risk and provide their offspring with access to maternal milk and non-maternal milk. I would like to emphasize a point that I have already made: physiological and temporal variations in milk production can create individual and/or temporally high differences in milk availability. Additionally, the daily volume of milk produced decreases throughout lactation (Gjøstein, Holand, & Weladji, 2004; White & Luick, 1984). When a mother's milk is depleted, and her calf is hungry, having established reciprocal relationships with other mothers can provide access to milk for her offspring as she produces more milk. In addition, the availability of many mothers in the group, and therefore access to milk resources, increases the chances that a calf can attempt to steal milk to improve its nutrition and mass gain. Since allosuckling stimulates the neuroendocrine system (Roulin, 2003), and reciprocal allonursing can influence the neuroendocrine system by decreasing the occurrence of milk depletion through adjusting or maintaining optimal prolactin concentrations. Under these circumstances, reciprocal allonursing and improved nutrition by ingestion of maternal and non-maternal milk provide direct fitness benefits during the calving season, which could explain why reindeer mothers and yearling daughters tend to associate throughout the year, except during calving (Hirotani, 1990).

Female wood mice can breed solitarily or communally nest and nurse with closely or distantly related females (Gerlach & Bartmann, 2002). The individual fitness of solitary breeding wood mice is greater than the inclusive fitness of communally nesting and nursing mothers, except for a dominant mother communally nesting and nursing with a subordinate daughter (Gerlach & Bartmann, 2002). Genetic relatedness is lower between two sisters than between mother and daughter because of the high degree of multiple mating of female wood mice (Baker, Makova, & Chesser, 1999; Bartmann & Gerlach, 2001). Thus, a dominant female should reject communal nesting and nursing with a subordinate female that is not her daughter, since communal nesting and nursing reduces her fitness (Gerlach & Bartmann, 2002). When there are no nesting sites for solitary breeding, the inclusive fitness associated with communal nesting and nursing is greater than individual fitness, and subordinate females gain more inclusive fitness by communally nesting and nursing with their mother than with a familiar sister or unfamiliar, distantly related female (Gerlach & Bartmann, 2002). Therefore, when there are no nesting sites, female wood mice should trade-off individual fitness for inclusive fitness, which may explain communal nesting and reciprocal allonursing in wood mice (Gerlach & Bartmann, 2002).

Communally nesting and nursing female wood mice do not evenly share nursing loads (Gerlach & Bartmann, 2002). When there are no nesting sites for solitary breeding, a subordinate daughter that communally nests and nurses with its dominant mother invests more in nursing than it's mother (Gerlach & Bartmann, 2002). In contrast, breeding pairs of both familiar sisters and unfamiliar, distantly related females are less related to each other than mother-daughter breeding pairs, gain less inclusive fitness by forming a breeding pair, and significantly reduce their nursing investment, which may be a trade-off between current reproductive success and future reproductive success (Gerlach & Bartmann, 2002). Therefore, when there are no breeding sites for solitary breeding, female wood mice should first trade-off the loss of reproductive success for some direct fitness with or without indirect fitness benefits by forming a breeding pair (Gerlach & Bartmann, 2002). Secondly, if they do not form a breeding pair with their mother, they should trade-off current reproductive success, by reducing their energetic costs (i.e. reduced nursing investment), for future reproductive success (Gerlach & Bartmann, 2002).

### *7.3.2 Biological Market or Reciprocal Altruism?*

Allonursing interactions were modelled as a biological market place to test the suitability of the biological market theory to the behaviour of reciprocal allonursing (Noë & Hammerstein, 1994, 1995; Noë, 2001). There was evidence of reciprocal allonursing at the group level and at the dyadic level (Chapter 4). Allonursing was not distributed evenly among all potential reindeer partners, which was interpreted as evidence of partner choice (Chapter 4). Reciprocal allonursing was not influenced by genetic relatedness or social rank. We suggested that the number and duration of allonursing bouts could be traded for themselves among chosen partners. Although biological market theory was useful for assessing reciprocal allonursing, the argument in favour of the operation of market mechanisms would be more convincing if the results revealed clear effects of shifts in the supply-demand ratios and/or clear effects of partner choice or partner switching (Noë & Hammerstein, 1994, 1995; Noë, 2001). A limitation of allonursing in a monotocous species is that the nursing mother to offspring ratio is always 1:1 in the different classes of traders, which limits the effect that supply and demand ratios can have on the exchange rates for allonursing (Noë & Hammerstein, 1994, 1995; Noë, 2001). In addition, mothers could not monopolize resources, and that limits the effect of outbidding competition on the exchange rates for allonursing (Noë & Hammerstein, 1994, 1995; Noë, 2001).

I can also attribute our reciprocal allonursing results at the dyadic level to reciprocal altruism among unrelated individuals (Trivers, 1971). I made a claim that our results did not support reciprocal altruism. However, I should consider other aspects, such as the probability of further interactions, the outcome of previous allonursing solicitations, the outcome of previous agonistic interactions, and enforcement (Rand & Nowak, 2013). The probability of further interactions was high, since mothers were confined within an enclosure and formed a single group. In the future, researchers should assess whether the giving of an allonursing bout depends on the outcome of previous solicitations for allonursing bouts by a mother’s own calf (Rand & Nowak, 2013).

There are now 2 two allonursing studies that have reported standardized Shannon-Wiener diversity index values (Engelhardt et al., 2015; Gloneková et al., 2016). Allonursing was not distributed evenly among all potential reindeer partners, which was interpreted as evidence of partner choice (Chapter 4), but it was more evenly distributed than in giraffes (mean = 0.43 ± 0.31; range = 0-0.95) (Gloneková et al., 2016). Gloneková et al. (2016) do not report whether the 0.31 is standard deviation or standard error. The mean standardized Shannon-Wiener diversity index values for both the number (mean ± *SD* = 0.744 ± 0.085) and duration (mean ± *SD* = 0.722 ± 0.085) of allonursing bouts were higher in reindeer (Chapter 4) than in giraffes (Gloneková et al., 2016). Reindeer mothers did not focus their allonursing to a single mother's offspring, otherwise the diversity index values would near 0 (Chapter 4). There were very large inter-individuals differences in diversity index values in giraffes, and some giraffe mothers had low diversity index values, which reflect that these mothers focused their allonursing on a relatively small number of other females (Gloneková et al., 2016). It should be pointed out that there were limited opportunities for partner choice in the captive giraffe herds, since there were between 2 and 5 allonursing mothers per herd per year, between 1 and 5 allosuckling offspring per herd per year, and low allonursing bouts (i.e. 3-11) in some herds (Gloneková et al., 2016).

### *7.3.3 Misinterpretation of Reciprocal Allonursing?*

Allonursing is often believed to have evolved from reciprocity among unrelated individuals, even though nearly all studies report a lack of evidence to support reciprocal allonursing (Chapter 4; Roulin, 2002). In communally nesting and nursing Norway rats, house mice and prairie voles, allonursing tends to be reciprocal, when the interval between the first mother's parturition and the second mother's parturition was less than 15 days (Ferrari et al., 2015; Hayes & Solomon, 2004; König, 2006; Mennella et al., 1990). In Norway rats, 92% and 75% of first and second mothers allonurse in the communal nest, respectively, and daily observations demonstrated that the first and second mothers allonursed (mean ± *SE*) 43 ± 7 % and 40 ± 6 % of the other mother's pups, respectively (Mennella et al., 1990). Even though nursing loads are not shared equally, reciprocity maintains allonursing in Norway rats (Mennella et al., 1990) and prairie voles (Hayes & Solomon, 2004). When house mouse mothers form egalitarian reproductive relationships, they invest in the total number of offspring in the communal nest and reciprocally allonurse (Ferrari et al., 2015; König, 2006). Although investing in the total number of offspring in the nest results in uneven nursing loads, reciprocity, but not kin-selection, in egalitarian reproductive relationships maintains allonursing in house mice (Ferrari et al., 2015; König, 2006).

There was evidence that allonursing was unidirectional, and therefore not reciprocal, in 132 (56.14%) dyads (Chapter 4). Readers may interpret this result as evidence against reciprocal allonursing. I have been working on the time-frame and reciprocation of allonursing, and the results are not included in my thesis. Even though, most dyads were not reciprocal, the 102 dyads that allonursed bidirectionally (mean RAFI ± *SD* = 0.64 ± 0.21) performed most allonursing bouts. There were 200 reciprocated allonursing bouts, and that accounts for 400 (38.95%) allonursing bouts. These 400 allonursing bouts only represent the even exchanges (i.e. RAFI = 1.0), but the mean RAFI value for the 102 dyads was 0.64. There was an additional 255 allonursing bouts that were exchanged between the 102 dyads. This means that 655 of 1027 (63.78%) of allonursing bouts in 2012 can be accounted for by the 102 dyads and can be attributed to reciprocal allonursing. Therefore, the evolution of allonursing in reindeer may originate from inclusive fitness, but the results of my thesis demonstrate that the direct fitness benefits of milk-theft, reciprocal allonursing and improved nutrition and mass gain maintain allonursing in reindeer.

#### *7.3.3.1 Misinterpretation of Reciprocal Allonursing and Milk-theft in Giraffes?*

Gloneková et al.'s (2016) interpret their results as evidence to support milk-theft, and that mothers may tolerate this behaviour if reciprocal. However, there are other possible interpretations to their results, and these possible interpretations weaken the support for the milk-theft hypothesis and tolerance of milk-theft if reciprocal in giraffes, and potentially create confusion in the literature.

Ekvall (1998) measured a ratio of the duration female A allonursed female B's offspring divided by the duration female B allonursed female A's offspring as a measure of reciprocal allonursing in fallow deer. I used an index of reciprocity used by primatologists studying allogrooming (Chapter 4; Newton-Fisher & Lee, 2011). Gloneková et al. (2016) divided the number of nursing bouts by the number of solicitations within a dyad AB and within dyad BA (i.e. acceptance rates). In giraffes, acceptance rates in dyad AB were not associated with the acceptance rates in dyad BA, which did not support reciprocal allonursing (Gloneková et al., 2016). The probability of offspring A allonursing at least once from mother B was greater if offspring B allonursed from mother A at least once, which was interpreted as support for reciprocal allonursing in giraffes (Gloneková et al., 2016). However, Gloneková et al. (2016) stated that there were 56 possible reciprocal dyads out of a potential 138, but only 22 dyads allonursed bidirectionally, 18 were unidirectional and 16 did not allonurse.

Giraffe mothers allonursed 95 (i.e. 25% of allonursing bouts) times without nursing their own offspring (Gloneková et al., 2016), and Gloneková et al. (2016) do not state whether the mother's own offspring was soliciting an allosuckling bout or foraging, which is important information to collect for evidence to support or not support the milk evacuation hypothesis. In addition, F offspring arrived 2nd, 3rd, etc. after the NF offspring arrived 1st on 33 occasions (Gloneková et al., 2016). Therefore, 34% (128 out of 381, which is not negligible) of all successful NF solicitations were performed by NF offspring that arrived 1st (34% is not negligible). Could allonursing begin as milk evacuation 128 times, and, in 33 of those times, could the mother's own offspring arrive after the 1st NF offspring and be nursed? These 128 allonursing bouts can be interpreted as strong support for both the misdirected parental care due a lack of efficient kin recognition mechanisms (i.e. mismothering) and milk evacuation hypotheses (Roulin, 2002).

The probability of successfully suckling (i.e. suckling and allosuckling) was influenced by order of arrival (Gloneková et al., 2016). Giraffes are polytocous, and the costs of nursing an additional offspring are lower than in monotocous species, in which allonursing is often attributed to milk-theft (Packer et al., 1992). This explains why arriving later in the order of arrival increased the probability of successfully allosuckling in giraffes (Gloneková et al., 2016). However, when the probability of successfully suckling (F offspring only) was tested, it was not influenced by the order of arrival, which does not support one of Gloneková et al.'s (2016) milk-theft predictions. In addition, acceptance rates of F and NF offspring were similar (~0.3), which is evidence to support the misdirected parental care hypothesis due to a lack of efficient kin recognition mechanisms (i.e. mismothering) and supports one prediction for mismothering (Gloneková et al., 2016). Moreover, the success rate of NF offspring (38.1%) was greater than that of F offspring (32.3%) (Gloneková et al., 2016), which is evidence to support mismothering. Gloneková et al.'s (2016) even wrote the following: "This means that the female decides whether to allow or prevent suckling mostly when the first calf arrives and when she accepts a calf she does not differentiate that from other calves (allo)suckling from her."

Gloneková et al. (2016) neglect to give full weight to and thoroughly interpret the predictions that do not support the milk-theft and tolerance for milk-theft if reciprocal hypotheses, while thoroughly interpreting the results that support the milk-theft and reciprocity hypotheses, and this bias can cause confusion in the literature. Therefore, I argue beyond not being able to reject the milk evacuation hypothesis in giraffes (Gloneková et al., 2016), and I argue that there is support for mismothering and milk evacuation in giraffes. I also argue that Gloneková et al.'s (2016) interpretations of milk-theft and tolerance of milk-theft if reciprocal are not as strongly supported as stated in their study.

### 7.4 Misinterpretation of Partial Support for Mismothering?

My research reported partial support for the misdirected parental care hypothesis due to a lack of efficient kin-recognition mechanisms (i.e. mismothering) (Chapter 3). Researchers may misinterpret this statement as reindeer mothers being unable to discriminate kin from non-kin, and therefore supporting the mismothering hypothesis, and this is incorrect. The odds of successfully allosuckling were not influenced by the position adopted (Chapter 3). Therefore, reindeer offspring were as likely to successfully allosuckle by adopting the parallel, perpendicular or antiparallel positions, and this was the partial support for the mismothering hypothesis (i.e. misdirected parental care due to a lack of efficient kin-recognition mechanisms). However, the proportions of antiparallel positions adopted were significantly greater for the lactating female's own offspring than for alien offspring, for both successful and unsuccessful solicitations (Chapter 3). I provide a detailed explanation below, to help readers clarify the interpretation of the results.

Firstly, mother-offspring recognition was reported in reindeer (Espmark, 1971b). Secondly, the rejection rates of NF offspring were significantly greater than the rejection rates of maternal offspring (Chapter 3). This evidence supported the misdirected parental care hypothesis due to milk-theft. Thirdly, the odds of successfully allosuckling were lower for NF offspring arriving 1st, 3rd, or 4th (and consequently those arriving later, since none of the reindeer offspring arriving later successfully allosuckled) (Chapter 3). The odds of successfully allosuckling were very low for NF offspring arriving 1st, before the lactating female's own offspring, which did not support the misdirected parental care hypothesis due to a lack of efficient kin-recognition mechanisms. In addition, there were 2340 allosuckling solicitations and only 6 solicitations were successful when the NF offspring arrived 1st. There were 1389 allosuckling bouts, and 1142 allosuckling bouts were for NF offspring arriving 2nd. Thus, arriving 2nd was the best strategy (Chapter 3). These results did not support the misdirected parental care hypothesis due to a lack of efficient kin-recognition mechanisms. Fourthly, allosuckling bouts are short in reindeer (mean ± *SD* = 14.82 ± 0.29 s) compared to the duration of allosuckling bouts in most other mammals, which can be attributed to reindeer having smaller udders than most ungulates (White & Luick, 1984) and the prohibitive energetic costs of nursing additional offspring in monotocous species (Packer et al., 1992), offspring should arrive 2nd to steal milk (Chapter 3). Fifthly, based on the same data, the reciprocity hypothesis was supported (Chapter 4). For reciprocal allonursing to occur, lactating females would have to discriminate the offspring of reciprocal partners, and NF offspring of reciprocal partners may be allowed to adopt the parallel position, allowing reciprocal partners to identify offspring by olfaction of the ano-genital region. Therefore, the partial support for the misdirected parental care hypothesis due to a lack of efficient kin-recognition mechanisms is not strong evidence to support the hypothesis, and I suggest that it is misinterpretation to write that reindeer mothers could not discriminate kin from non-kin.

### 7.5 Milk Evacuation

The hypothesized causes and functions of allosuckling and allonursing are non-mutually exclusive (Roulin, 2002). Therefore, lactating females may allonurse on occasion to evacuate milk that their own offspring did not consume, and they may allonurse because of other causes and functions. The milk evacuation hypothesis does not apply when a mother's own offspring is hungry and attempting to suckle or allosuckle (Roulin, 2002). In 2012, there were 2430 NF solicitations, and 234 (9.6 %) NF solicitations where the NF offspring arrived first and without other offspring (Chapter 3): only 3 (0.1 %) solicitations by NF offspring alone were successful (Chapter 3). In addition, there were 3 (0.1 %) solicitations with NF offspring arriving first, successfully allosuckling and the F offspring was beside its mother and suckled second (Chapter 3). In 2013, there were 1650 solicitations (Chapter 6), and of the 65 (20.4 %) NF solicitations where the NF offspring arrived first and without other offspring: only 3 (0.9 %) solicitations by

NF offspring alone were successful. In 2013, there were no successful solicitations with the NF offspring arriving first and the F offspring arriving second. Reindeer mothers did not allonurse while their own offspring was attempting to allosuckle or consuming forage, which did not support the milk evacuation hypothesis (Roulin, 2002). Reindeer mothers rarely allonursed without nursing their own offspring, which also did not support the milk evacuation hypothesis (Roulin, 2002).

### 7.6 Inter-population Differences

My thesis does not assess allosuckling and allonursing differences between populations, and there can be significant differences between populations. Eighty-five successful allonursing bouts were recorded over 14 weeks in an experimental enclosure at the National Reindeer Research Station Kuolpavare in Sweden (Espmark, 1971c). Fourteen of 15 mothers allonursed and all calves solicited allosuckling bouts (Espmark, 1971c). In another study, 6 of 6 mothers allonursed and their calves allosuckled 290 times over 25 weeks in an experimental enclosure at the Norwegian University of Life Sciences (Marken, 2003). In yet another study, 5 mothers-calf pairs were observed over 160 days in 1988, and 5 mother-calf pairs were observed over 55 days in 1989 at the Jardin Zoologique du Québec, in Quebec City (Lavigueur & Barrette, 1992). Over two years, two mothers allonursed once and one calf allosuckled twice (Lavigueur & Barrette, 1992). Therefore, allonursing can vary greatly between populations of reindeer.

There are significant inter-population allonursing differences in grey seals (McCulloch & Boness, 2000; Perry et al., 1998). On Sable Island, grey seal mothers rarely allonursed (McCulloch & Boness, 2000; Perry et al., 1998). Based on daily observations throughout lactation, 3 of 78 grey seal mothers allonursed daily on Faray Island, while 7 of 25 mothers allonursed daily on Ramsey Island (Perry et al., 1998). Over 68 h of observation on the Isle of May, observers recorded 17 allosuckling bouts (McCulloch et al., 1999). In contrast to the large inter-population variations in reindeer (e.g. Engelhardt et al., 2014; Espmark, 1971c; Lavigueur & Barrette, 1992) and in grey seals (McCulloch & Boness, 2000; Perry et al., 1998), there were no significant differences between 4 fallow deer groups, based on the duration of allosuckling bouts, the cumulative number of allosuckling bouts performed by each offspring, the cumulative number of allonursing bouts performed by each mother and the frequency of allosuckling (Ekvall, 1998).

In vertebrates, obligate cooperative breeding is rare, and solitary breeding occurs at varying frequencies in most species (Pruett-Jones, 2004). Wolff (1994) states that, in general, small rodents nest solitarily, and communal nesting and nursing in white-footed mice occurred when densities ranged between 50-103 mice/ha, which caused a shortage of suitable habitats and delayed dispersal. Therefore, higher densities of white-footed mice, shortage of suitable habitats and delayed dispersal can cause inter-population differences in allonursing. Over 4 breeding seasons in the 3 groups, allonursing in meerkats was observed in 6 of 25 litters, of which 3 included a spontaneous lactator (Doolan & Macdonald, 1999). In one litter, there were two lactating meerkat females allonursing, while there was 1 lactating female in the other 5 litters (Doolan & Macdonald, 1999). Subordinate meerkat females that allonursed had lost their litter either to infanticide or predation (Doolan & Macdonald, 1999). Therefore, predation, infanticide and the proximate causes of spontaneous lactation can cause inter-population differences. For an avian example, in acorn woodpeckers, *Melanerpes formicivorus*, cooperative breeding occurred in 15% and 77% of groups at the Research Ranch in Arizona and at the Hastings Reservation in California, respectively (Koenig & Stacey, 1990). Therefore, cooperative breeding is often opportunistic and under selective pressures, which can account for inter-population differences in allonursing.

## 7.7 Future Areas of Research

### *7.7.1 Allosuckling and Allonursing*

#### *7.7.1.1 Relative Importance of Allonursing*

Although hypothesized causes and functions of allonursing have been proposed, the extent to which each hypothesis can account for inter- and intra-specific variation in the propensity to allonurse remains unclear (Roulin, 2002). Given that the hypotheses are non-mutually exclusive, observations may be consistent with more than one hypothesis. An assessment of the relative importance of allonursing hypotheses would provide insights into the proximate and ultimate causes of cooperative breeding and into the origins and maintenance of sociality in complex social systems. However no such assessment has been performed. Experimental designs are required to assess the relative importance of allonursing hypotheses misdirected parental care, kin-selection, reciprocity, compensation, milk evacuation and neuroendocrine hypotheses (Bartoš, Vaňková, Hyánek, et al., 2001; Roulin, 2002, 2003) within and between populations and across species.

#### *7.7.1.2 The time frame and symmetry of reciprocal allonursing*

The time frame and symmetry of reciprocal allonursing have not been assessed by researchers. This research project would elucidate the appropriate time frame to choose when studying allonursing reciprocation, which would avoid inaccurate measures of symmetry or mistaken interpretation of the absence of reciprocation (i.e. if the time frame chosen is too short and individuals have not yet reciprocated) (Gomes, Mundry, & Boesch, 2009). This research project would also assess whether lactating mothers reciprocate allonursing within an observation day or over longer periods of time.

#### *7.7.1.3 Social networking of allosuckling and allonursing*

Social networking theory should be applied to nursing, allosuckling, allonursing and agonistic data. This research project could assess the spread of allosuckling, allonursing and agonistic interactions across individuals over time, which individuals are central nodes, and be used as an analytical tool to assess reciprocal allonursing.

### *7.7.2 Alloparental Care*

#### *7.7.2.1 Genes for Alloparental Care*

Research investigating the genetics and epigenetics of alloparental care is needed. Researchers are currently investigating how variation in alloparental care is attributed to inherited genetic variation and environmentally induced variation in gene expression (Champagne & Curley, 2012; Simola et al., 2016). The model species include honeybees (Champagne & Curley, 2012) and carpenter ants (Simola et al., 2016). The honeybee genome was sequenced in 2006 (Champagne & Curley, 2012), and the carpenter ant genome was recently sequenced (Simola et al., 2016). Researchers use molecular techniques and bioinformatics to identify candidate genes and candidate epigenetic mechanisms that regulate the expression of alloparental care (Champagne & Curley, 2012; Simola et al., 2016). Variation in the alloparental care of honeybee workers (e.g. hygienic behaviour, food provision and brood care) is attributed to inherited genetic variation and environmentally induced variation in gene expression (Champagne & Curley, 2012). Behavioural castes of carpenter ants were regulated and reprogrammed by histone modification (Simola et al., 2016).

#### *7.7.2.2 Learning to parent*

To support the learning to parent hypothesis for alloparental care, alloparental experience prior to primiparity should enhance successful rearing of own offspring and lifetime reproductive success compared to inexperienced primiparous parents (Solomon & Hayes, 2012; Tardif, 1997). To assess the causal relationship between alloparental experience and future direct fitness, experiments should be designed to control for age-related effects (e.g. Salo & French, 1989), primiparity, and alloparental experience to assess survival of offspring, reproductive success and lifetime reproductive success.

#### *7.7.2.3 Influence of alloparental care on reproductive success*

The positive relationship between the number of alloparents and the number of offspring may not be causal, and it may be a spurious relationship generated by another factor (Woodroffe & Macdonald, 2000). Research projects that find a relationship between the number of alloparents and reproductive success should experimentally remove alloparents (Mumme, 1992) or control for confounding effects, such as the effect of territory quality (Doerr & Doerr, 2007; Woodroffe & Macdonald, 2000). In the mammalian literature, there is little evidence that alloparental care increases the number of offspring within a litter (Creel & Creel, 2002; Russell, Brotherton, et al., 2003). For example, African wild dogs packs containing ten or more adults produced larger litters (mean = 13.2) than packs containing nine or less adults (mean = 6.1) (Creel & Creel, 2002). In another study, the number of meerkat alloparents was positively associated with the mass of mothers, which is positively correlated with litter size (Russell, Brotherton, et al., 2003).

#### *7.7.2.4 Influence of alloparental care on increased mass gain and future indirect fitness*

The association between alloparental care and increased mass gain is correlative. Experimental designs that control for the level of alloparental care provided (Mitani & Watts, 1997; Ross & MacLarnon, 2000), the level of parental care (e.g. see Chapter 5 for allosuckling to compensate for deficiencies), the birth mass of offspring (Víchová & Bartoš, 2005), the sex of alloparents and recipient offspring (Brotherton et al., 2001) and the quality of the territory are needed to assess whether the relationship is causal (Solomon & Hayes, 2012).

Most studies investigated the short-term benefits of alloparental care on offspring, such as increased mass gain (Chapter 5; Mitani & Watts, 1997; Powell & Fried, 1992; Ross & MacLarnon, 2000), without investigating the long-term benefits of alloparental care on offspring, such as survival (Solomon, 1991) and lifetime reproductive success (Russell et al., 2007). Investigating the effects of variations in alloparental care on the mass gain (Hodge, 2005; Mitani & Watts, 1997; Ross & MacLarnon, 2000), survival and lifetime reproductive success of recipient offspring may improve our understanding of the short-term and long-term influences of alloparental care on recipient offspring (Solomon & Hayes, 2012).

The long-term effects of alloparental care on the future survival and reproductive success of recipient offspring are difficult to assess at the Kutuharju Field Reindeer Research Station. The livelihood of the manager is partially based on slaughtering offspring. The manager of the reindeer slaughters nearly all offspring before they can become yearlings. Only a few male offspring survive past 3 years of age. Adult females who do not produce an offspring are also slaughtered.

#### *7.7.2.5 Nonadaptive hypotheses of alloparental care*

Many studies of cooperative breeding social systems have focused on and suggested that alloparental care was an adaptive trait. The epigenetic hypotheses suggested, however, that alloparental care may not be an adaptive trait (Jamieson & Craig, 1987; Jamieson, 1989; West-Eberhard, 1987). Strong claims about the adaptive value of alloparental care should also consider and gather evidence to refute nonadaptive hypotheses (Jamieson & Craig, 1987). Evidence to argue against the nonadaptive hypotheses include demonstrations that: 1) alloparental care is a flexible response with its variation being related to the parents' need for alloparental care, 2) alloparental care is a costly behaviour for alloparents, and 3) identifying types of alloparental care only performed by alloparents (Heinsohn & Legge, 1999; Jamieson & Craig, 1987). Babysitting in meerkats is a good example of a type of alloparental care with evidence to argue against nonadaptive hypotheses. In meerkats, babysitting is a costly and flexible response related to the parents' need, and it is seldom performed by parents (Clutton-Brock et al., 1998; Russell, Sharpe, et al., 2003). However, demonstrating all three lines of evidence is rare because: 1) parents generally contribute more than alloparents to most types of cooperative behaviours, 2) few studies have measured the costs of alloparental care to alloparents, and 3) few studies have investigated whether the contributions of alloparents are adjusted to the needs of the parents (Clutton-Brock et al., 1998). The epigenetics of alloparental care should also be considered before making strong claims about the adaptive value of alloparental care. Behavioural castes of carpenter ants were regulated and reprogrammed by histone modification (Simola et al., 2016), which is evidence in support of the non-adaptive hypothesis (Jamieson & Craig, 1987; Jamieson, 1989). Moreover, behavioural plasticity may be epigenetically regulated in other animals (Simola et al., 2016).

#### *7.7.2.6 Costs of alloparental care*

Research investigating the fitness costs of alloparental care is needed. Many studies assume that the costs of providing alloparental care are included in the assessments of the apparent benefits. However, the costs of expressing alloparental care should be measured and removed from the apparent benefits (Heinsohn & Legge, 1999). Russell, Sharpe, et al. (2003) argues that an understanding of the costs and benefits of alloparental care is important in order to understand and quantify selection on cooperative breeding social systems.

Assessments of the long-term fitness costs of alloparenting and tactics to mitigate the costs due to alloparental investment may benefit by following the results and hypotheses generated by studies of parental care (Clutton-Brock, 1991; Heinsohn & Legge, 1999; Russell, Sharpe, et al., 2003). For example, parental investment is limited, and when parents invest heavily in parental care, they may: 1) increase their foraging efforts during the non-reproductive period, 2) invest based on their own condition, and 3) reduce their contribution to parental care during the next breeding event (Russell, Sharpe, et al., 2003). Researchers should investigate how alloparents mitigate alloparenting costs.

### 7.8 Conclusion

Allosuckling and allonursing in reindeer were better explained by the misdirected parental care due to milk-theft (i.e. offspring stole milk) (see Table 7.1; Chapter 3), reciprocal allonursing (i.e. a large subset of mothers allonursed reciprocally) (see Table 7.1; Chapter 4), and improved nutrition (i.e. allosuckling improved the nutrition and mass gain of offspring) (see Table 7.1; Chapter 5) hypotheses than by the misdirected parental care due to a lack of efficient kin recognition mechanisms (i.e. mismothering) (see Table 7.1; Chapter 3), kin-selection and milk evacuation (see Table 7.1; Chapters 3 and 4), and compensation (see Table 7.1; i.e. offspring did not allosuckle to compensate for low birth mass, insufficient maternal milk supply and/or inadequate growth; Chapter 5) hypotheses. However, allonursing contributions varied with genetic relatedness when two groups of mothers were experimentally manipulated based on the two extremes of genetic relatedness (see Table 7.1; Chapter 6). Therefore, kin-selection alone is not sufficient to explain allonursing in reindeer, and the indirect fitness benefits of allonursing may be overestimated (Clutton-Brock, 2002; Cockburn, 1998). The evolution of allonursing in reindeer may have originated from inclusive fitness, but the results of my thesis demonstrate that the direct fitness benefits of milk-theft, reciprocal allonursing, and improved nutrition and mass gain maintain allonursing in reindeer. Future research projects should assess the relative importance of alloparental care. My thesis cannot reject the hypothesis that allonursing is an unselected consequence of group living (i.e. by-product of group living) due to the selection pressure of predation, even though the frequency of high predation risk is low compared to wild reindeer. However my thesis' results do provide evidence against other predictions of the by-product of group living hypothesis: 1) that mothers should lack efficient kin recognition mechanisms and be unable to reject offspring of other mothers sharing a communal nest (Hayes, 2000), 2) the costs of allonursing should be greater than the costs of solitary nursing (Hayes, 2000), and 3) reduced infanticide (König, 2006; Manning et al., 1995; Pusey & Packer, 1994). My thesis cannot reject the nonadaptive epigenetic hypothesis (Jamieson & Craig, 1987; Jamieson, 1989), but some of the results do provide arguments against it. I provide several areas of future research in allosuckling and allonursing and more generally in the study of alloparental care.

## Chapter 8 References

Achenbach, G. G., & Snowdon, C. T. (2002). Costs of caregiving: weight loss in captive adult male cotton-top tamarins (*Saguinus oedipus*) following the birth of infants. *International Journal of Primatology*, *23*, 179–189.

Albon, S. D., Mitchell, B., & Staines, B. W. (1983). Fertility and body weight in female red deer: a density-dependent relationship. *Journal of Animal Ecology*, *52*, 969–980.

Angelier, F., Barbraud, C., Lormée, H., Prud'homme, F., & Chastel, O. (2006). Kidnapping of chicks in emperor penguins: a hormonal by-product? *Journal of Experimental Biology*, *209*, 1413–1420.

Angelier, F., & Chastel, O. (2009). Stress, prolactin and parental investment in birds: a review. *General and Comparative Endocrinology*, *163*, 142–148.

Arnold, K., & Whiten, A. (2003). Grooming interactions among the chimpanzees of the Budongo Forest, Uganda: tests of five explanatory models. *Behaviour*, *140*, 519–552.

Arnold, W. (1990). The evolution of marmot sociality. II. *Behavioral Ecology and Sociobiology*, *27*, 239–246.

Arvola, M., Gustafsson, E., & Mattsson, R. (2001). Neonatal ingestion of IgG-containing milk increases the survival of adoptively transferred B-lineage cells in B cell-deficient mice. *Journal of Reproductive Immunology*, *50*, 121–132.

Asa, C. S. (1997). Hormonal and experiential factors in the expression of social and parental behavior in canids. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 129–149). Cambridge, U.K.: Cambridge University Press.

Auclair, Y., König, B., Ferrari, M., Perony, N., & Lindholm, A. K. (2014). Nest attendance of lactating females in a wild house mouse population: benefits associated with communal nesting. *Animal Behaviour*, *92*, 143–149.

Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, *211*, 1390–1396.

Baker, A. J., Dietz, J. M., & Kleiman, D. G. (1993). Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Animal Behaviour*, *46*, 1091–1103.

Baker, R. J., Makova, K. D., & Chesser, R. K. (1999). Microsatellites indicate a high frequency of multiple paternity in *Apodemus* (Rodentia). *Molecular Ecology*, *8*, 107–111.

Balcombe, J. P. (1990). Vocal recognition of pups by mother Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. *Animal Behaviour*, *39*, 960–966.

Balcombe, J. P., & McCracken, G. F. (1992). Vocal recognition in Mexican free-tailed bats: do pups recognize mothers? *Animal Behaviour*, *43*, 79–87.

Baldovino, M. C., & Di Bitetti, M. S. (2008). Allonursing in tufted capuchin monkeys (*Cebus nigritus*): milk or pacifier? *Folia Primatologica*, *79*, 79–92.

Bales, K., Dietz, J., Baker, A., Miller, K., & Tardif, S. D. (2000). Effects of allocare-givers on fitness of infants and parents in callitrichid primates. *Folia Primatologica*, *71*, 27–38.

Bales, K. L., Pfeifer, L. A., & Carter, C. S. (2004). Sex differences and development effects of manipulations of oxytocin on alloparenting and anxiety in prairie voles. *Developmental Psychobiology*, *44*, 123–131.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London B: Biological Sciences*, *266*, 665–670.

Bartmann, S., & Gerlach, G. (2001). Multiple paternity and similar variance in reproductive success of male and female wood mice (*Apodemus sylvaticus*). *Ethology*, *107*, 889–899.

Barton, K. (2013). MuMIn: multi-model Inference. R Package Version 1.9.5. http://cran.r-project.org/package=MuMIn (accessed on 23.04.15).

Bartoš, L., Vaňková, D., Hyánek, J., & Šiler, J. (2001). Impact of allosucking on growth of farmed red deer calves (*Cervus elaphus*). *Animal Science*, *72*, 493–500.

Bartoš, L., Vaňková, D., Šiler, J., & Illmann, G. (2001). Adoption , allonursing and allosucking in farmed red deer (*Cervus elaphus*). *Animal Science*, 483–492.

Becker, M. I., De Ioannes, A. E., León, C., & Ebensperger, L. A. (2007). Females of the communally breeding rodent, *Octodon degus*, transfer antibodies to their offspring during pregnancy and lactation. *Journal of Reproductive Immunology*, *74*, 68–77.

Bender, N., Taborsky, M., & Power, D. (2008). The role of prolactin in the regulation of brood care in the cooperatively breeding fish *Neolamprologus pulcher*. *Journal of Experimental Zoology*, *309*, 515–524.

Bergmüller, R., Heg, D., & Taborsky, M. (2005). Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints. *Proceedings of the Royal Society of London B: Biological Sciences*, *272*, 325–331.

Bergmüller, R., Johnstone, R. A., Russell, A. F., & Bshary, R. (2007). Integrating cooperative breeding into theoretical concepts of cooperation. *Behavioural Processes*, *76*, 61–72.

Bilde, T., & Lubin, Y. (2011). Group living in spiders: cooperative breeding and coloniality. In M. E. Herberstein (Ed.), *Spider behaviour: flexibility and versatility* (pp. 275–306). Cambridge, U.K.: Cambridge University Press.

Birgersson, B., & Ekvall, K. (1994). Suckling time and fawn growth in fallow deer (*Dama dama*). *Journal of Zoology*, *232*, 641–650.

Birgersson, B., Ekvall, K., & Temrin, H. (1991). Allosuckling in fallow deer, *Dama dama*. *Animal Behaviour*, *42*, 326–327.

Bishop, M. D., Kappes, S. M., Keele, J. W., Stone, R. T., Sunden, S. L., & Hawkins, G. A. (1994). A genetic linkage map for cattle. *Genetics*, *136*, 619–639.

Blackmore, C. J., Peakall, R., & Heinsohn, R. (2011). The absence of sex-biased dispersal in the cooperatively breeding grey-crowned babbler. *Journal of Animal Ecology*, *80*, 69–78.

Blaustein, A. R. (1983). Kin recognition mechanisms: phenotypic matching or recognition alleles? *American Naturalist*, *121*, 749–754.

Body, G. (2014). *Importance of group dynamics on female mating behaviour in reindeer Rangifer tarandus* (Doctoral Thesis). Montreal, Canada: Concordia University.

Boness, D. J. (1990). Fostering behavior in Hawaiian monk seals: is there a reproductive cost? *Behavioral Ecology and Sociobiology*, *27*, 113–122.

Boomsma, J. J. (2007). Kin selection versus sexual selection: why the ends do not meet. *Current Biology*, *17*, R673–R683.

Boomsma, J. J. (2009). Lifetime monogamy and the evolution of eusociality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 3191–3207.

Bourke, A. F. G. (1999). Colony size, social complexity and reproductive conflict in social insects. *Journal of Evolutionary Biology*, *12*, 245–257.

Bourke, A. F. G., & Franks, N. R. (1995). *Social evolution in ants.* Princeton, NJ: Princeton University Press.

Bowen, W. D., Iverson, S. J., Boness, D. J., & Oftedal, O. T. (2001). Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. *Functional Ecology*, *15*, 325–334.

Brandlová, K., Bartoš, L., & Haberová, T. (2013). Camel calves as opportunistic milk thefts? The first description of allosuckling in domestic bactrian camel (*Camelus bactrianus*). *PloS One*, *8*, e53052.

Brotherton, P. N. M., Clutton-Brock, T. H., O'Riain, M. J., Gaynor, D., L., S., R., K., & M., M. G. (2001). Offspring food allocation by parents and helpers in a cooperative mammal. *Behavioral Ecology*, *12*, 590–599.

Brown, G. E., & Brown, J. A. (1996). Kin discrimination in salmonids. *Reviews in Fish Biology and Fisheries*, *6*, 201–219.

Brown, J. L. (1987). *Helping and communal breeding in birds.* Princeton, NJ: Princeton University Press.

Brown, J. L., Brown, E. R., Brown, S. D., & Dow, D. D. (1982). Helpers: effects of experimental removal on reproductive success. *Science*, *215*, 421–2.

Brown, J. L., & Vleck, C. M. (1998). Prolactin and helping in birds: has natural selection strengthened helping behavior? *Behavioral Ecology*, *9*, 541–545.

Bshary, R., & Grutter, A. S. (2002). Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: the cleaner fish case. *Ecology Letters*, *5*, 130–136.

Buchanan, F. C., & Crawford, A. M. (1993). Ovine microsatellites at the OarFCB11, OarFCB128, OarFCB193, OarFCB266 and OarFCB304 loci. *Animal Genetics*, *24*, 145

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach* (2nd ed.). New York, NY: Springer.

Cameron, E. Z. (1998). Is suckling behaviour a useful predictor of milk intake? A review. *Animal Behaviour*, *56*, 521–532.

Cant, M. A. (2012). Cooperative breeding systems. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care.* (pp. 206–225). Oxford, U.K.: Oxford University Press.

Carlier, Y., & Truyens, C. (1995). Influence of maternal infection on offspring resistance towards parasites. *Parasitology Today*, *11*, 94–99.

Carlisle, T. R., & Zahavi, A. (1986). Helping at the nest, allofeeding and social status in immature arabian babblers. *Behavioral Ecology and Sociobiology*, *18*, 339–351.

Carlson, A. A., Manser, M. B., Young, A. J., Russell, A. F., Jordan, N. R., McNeilly, A. S., & Clutton-Brock, T. H. (2006). Cortisol levels are positively associated with pup-feeding rates in male meerkats. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*, 571–577.

Carlson, A. A., Russell, A. F., Young, A. J., Jordan, N. R., McNeilly, A. S., Parlow, A. F., & Clutton-Brock, T. H. (2006). Elevated prolactin levels immediately precede decisions to babysit by male meerkat helpers. *Hormones and Behavior*, *50*, 94–100.

Carlson, A. A., Young, A. J., Russell, A. F., Bennett, N. C., McNeilly, A. S., & Clutton-Brock, T. H. (2004). Hormonal correlates of dominance in meerkats (*Suricata suricatta*). *Hormones and Behavior*, *46*, 141–150.

Carter, C. S., & Roberts, R. L. (1997). The psychobiological basis of cooperative breeding in rodents. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 231–266). Cambridge, U.K.: Cambridge University Press.

Cassinello, J. (1999). Allosuckling behaviour in *Ammotragus*. *Zeitschrift für Säugetierkunde*, *64*, 363–370.

Champagne, F. A., & Curley, J. P. (2012). Genetics and epigenetics of parental care. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The Evolution of Parental Care* (pp. 304–325). Oxford, U.K.: Oxford University Press.

Cheeseman, C. L., Mallinson, P. J., Ryan, J., & Wilesmith, J. W. (1993). Recolonisation by badgers in Gloucestershire. In T. J. Hayden (Ed.), *The badger* (pp. 78–93). Dublin, Ireland: Royal Irish Academy.

Cheney, D. L. (1992). Intragroup cohesion and intergroup hostility: the relation between grooming distributions and intergroup competition among female primates. *Behavioral Ecology*, *3*, 334–345.

Clarke, M. F. (1989). The pattern of helping in the bell miner (*Manorina melanophrys*). *Ethology*, *80*, 292–306.

Clobert, J., de Fraipont, M., & Danchin, É. (2008). Evolution of dispersal. In É. Danchin, F. Cézilly, & L.-A. Giraldeau (Eds.), *Behavioural ecology* (pp. 323–359). Oxford, U.K.: Oxford University Press.

Clutton-Brock, T. H. (1991). *The evolution of parental care.* Princeton, NJ: Princeton University Press.

Clutton-Brock, T. H. (1998). Reproductive skew, concessions and limited control. *Trends in Ecology & Evolution*, *13*, 288–292.

Clutton-Brock, T. H. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, *296*, 69–72.

Clutton-Brock, T. H. (2006). Cooperative breeding in mammals. In P. M. Kappeler & C. P. van Shaik (Eds.), *Cooperation in primates and humans: mechanisms and evolution* (pp. 173–190). Berlin, Germany: Springer-Verlag.

Clutton-Brock, T. H. (2009). Cooperation between non-kin in animal societies. *Nature*, *462*, 51–57.

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature*, *337*, 260–262.

Clutton-Brock, T. H., Brotherton, P. N., O'Riain, M. J., Griffin, A. S., Gaynor, D., Sharpe, L., et al. (2000). Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. *Proceedings of the Royal Society of London B: Biological Sciences*, *267*, 301–305.

Clutton-Brock, T. H., Gaynor, D., Kansky, R., MacColl, A. D., McIlrath, G., Chadwick, P., et al. (1998). Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proceedings of the Royal Society of London B: Biological Sciences*, *265*, 185–90.

Clutton-Brock, T. H., & Parker, G. A. (1995). Punishment in animal societies. *Nature*, *373*, 209–216.

Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Young, A. J., Balmforth, Z., & McIlrath, G. M. (2002). Evolution and development of sex differences in cooperative behavior in meerkats. *Science*, *297*, 253–256.

Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology, Evolution, and Systematics*, *29*, 141–177.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*, 1375–1383.

Connor, R. C. (1995). Altruism among non-relatives: alternatives to the "Prisoner"s Dilemma'. *Trends in Ecology & Evolution*, *10*, 84–86.

Cooper, M. A., Berntein, I. S., & Hemelrijk, C. K. (2005). Reconciliation and relationship quality in Assamese macaques (*Macaca assamensis*). *American Journal of Primatology*, *65*, 269–282.

Cornwallis, C. K., West, S. A., Davis, K. E., & Griffin, A. S. (2010). Promiscuity and the evolutionary transition to complex societies. *Nature*, *466*, 969–972.

Cornwallis, C. K., West, S. A., & Griffin, A. S. (2009). Routes to indirect fitness in cooperatively breeding vertebrates: kin discrimination and limited dispersal. *Journal of Evolutionary Biology*, *22*, 2445–2457.

Courchamp, F., & Macdonald, D. W. (2001). Crucial importance of pack size in the African wild dog *Lycaon pictus*. *Animal Conservation*, *4*, 169–174.

Creel, S. (1990). How to measure inclusive fitness. *Proceedings of the Royal Society of London B: Biological Sciences*, *241*, 229–231.

Creel, S. (2001). Social dominance and stress hormones. *Trends in Ecology & Evolution*, *16*, 491–497.

Creel, S., & Macdonald, D. (1995). Sociality, group size, and reproductive suppression among carnivores. *Advances in the Study of Behavior*, *24*, 203–257.

Creel, S. R., & Creel, N. M. (2002). *The African wild dog: behavior, ecology and conservation.* Princeton, NJ: Princeton University Press.

Creel, S. R., Monfort, S. L., Wildt, D. E., & Waser, P. M. (1991). Spontaneous lactation is an adaptive result of pseudopregnancy. *Nature*, *351*, 660–662.

Creel, S. R., & Waser, P. M. (1991). Failures of reproductive suppression in dwarf mongooses (*Helogale parvula*): accident or adaptation? *Behavioral Ecology*, *2*, 7–15.

Creel, S. R., & Waser, P. M. (1997). Variation in reproductive suppression among dwarf mongooses: interplay between mechanisms and evaluation. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 150–170). Cambridge, U.K.: Cambridge University Press.

Curry, R. L., & Grant, P. R. (1990). Galapagos mockingbirds: territorial cooperative breeding in a climatically variable environment. In P. B. Stacey & W. D. Koenig (Eds.), *Cooperative breeding in birds: long term studies of ecology and behaviour* (pp. 291–331). Cambridge, U.K.: Cambridge University Press.

D'Ettorre, P., & Lenoir, A. (2009). Nestmate Recognition. In L. Lach, C. Parr, & K. Abbott (Eds.), *Ant ecology* (pp. 194–209). Oxford, U.K.: Oxford University Press.

da Silva Mota, M. T., & de Sousa, M. B. C. (2000). Prolactin levels of fathers and helpers related to alloparental care in common marmosets, *Callithrix jacchus*. *Folia Primatologica; International Journal of Primatology*, *71*, 22–6.

da Silva Mota, M. T., Franci, C. R., & de Sousa, M. B. C. (2006). Hormonal changes related to paternal and alloparental care in common marmosets (*Callithrix jacchus*). *Hormones and*

*Behavior*, *49*, 293–302.

Danchin, É., Cézilly, F., & Giraldeau, L.-A. (2008). Fundamental concepts in behavioural ecology. In É. Danchin, F. Cézilly, & L.-A. Giraldeau (Eds.), *Behavioural ecology* (pp. 29–53). Oxford, U.K.: Oxford University Press.

Danchin, É., Giraldeau, L.-A., & Wagner, R. H. (2008). Animal aggregations: hypotheses and controversies. In É. Danchin, F. Cézilly, & L.-A. Giraldeau (Eds.), *Behavioural ecology.* (pp. 503–545). Oxford, U.K.: Oxford University Press.

Darwin, C. (1859). *The origin of species by means of natural selection.* London, U.K.: John Murray.

Darwin, C. (1871). *The descent of man, and selection in relation to sex.* London, U.K.: John Murray.

Das, S., Redbo, I., & Wiktorsson, H. (2000). Effect of age of calf on suckling behaviour and other behavioural activities of Zebu and crossbred calves during restricted suckling periods. *Applied Animal Behaviour Science*, *67*, 47–57.

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioural ecology.* (4th ed.). Oxford, U.K.: Wiley-Blackwell.

Dawkins, R. (1979). Twelve misunderstandings of kin selection. *Zeitschrift für Tierpsychologie*, *51*, 184–200.

de Vries, H. (1998). Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour*, *55*, 827–843.

Dengler-Crish, C. M., & Catania, K. C. (2007). Phenotypic plasticity in female naked mole-rats after removal from reproductive suppression. *The Journal of Experimental Biology*, *210*, 4351–4358.

Dickinson, J., & Hatchwell, B. J. (2004). Fitness consequences of helping. In W. D. Koenig & J. L. Dickinson (Eds.), *Ecology and evolution of cooperative breeding in birds* (pp. 48–66). Cambridge, U.K.: Cambridge University Press.

Dixson, A. F., & George, L. (1982). Prolactin and parental behaviour in a male New World primate. *Nature*, *299*, 551–553.

Djaković, N. (2012). *Female mating strategy in reindeer (Rangifer tarandus): the importance of male age structure and availability in the social organisation, behaviour and mate choice* (Doctoral Thesis). Ås, Norway: Norwegian University of Life Sciences.

Djaković, N., Holand, Ø., Hovland, A. L., Røed, K. H., Weladji, R. B., Fjeldstad, E., et al. (2012). Association patterns and kinship in female reindeer (*Rangifer tarandus*) during rut. *Acta Ethologica*, *15*, 165–171.

Doerr, E. D., & Doerr, V. A. J. (2007). Positive effects of helpers on reproductive success in the brown treecreeper and the general importance of future benefits. *Journal of Animal Ecology*, *76*, 966–976.

Doerr, E. D., Doerr, V. A. J., & Safran, R. J. (2007). Integrating delayed dispersal into broader concepts of social group formation. *Behavioural Processes*, *76*, 114–117.

Doncaster, C. P., & Woodroffe, R. (1993). Den site can determine shape and size of badger territories: implications for group-living. *Oikos*, *66*, 88–93.

Doolan, S. P., & Macdonald, D. W. (1999). Co-operative rearing by slender-tailed meerkats (*Suricata suricata*) in the Southern Kalahari. *Ethology*, *105*, 851–866.

Drábková, J., Bartošová, J., Bartoš, L., Kotrba, R., Pluháček, J., Švecová, L., et al. (2008). Sucking and allosucking duration in farmed red deer (*Cervus elaphus*). *Applied Animal Behaviour Science*, *113*, 215–223.

Duffy, J. E. (1996). Eusociality in a coral-reef shrimp. *Nature*, *381*, 512–514.

Duffy, J. E. (2003). The ecology and evolution of eusociality in sponge-dwelling shrimp. In T. Kikuchi, S. Higashi, & N. Azuma (Eds.), *Genes, behaviors, and evolution in social insects* (pp. 217–252). Sapporo, Japan: University of Hokkaido Press.

Duffy, J. E., & Macdonald, K. S. (2010). Kin structure, ecology and the evolution of social organization in shrimp: a comparative analysis. *Proceedings of the Royal Society of London B: Biological Sciences*, *277*, 575–584.

Dufour, D. L., & Sauther, M. L. (2002). Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. *American Journal of Human Biology*, *14*, 584–602.

Dugdale, H. L., Ellwood, S. A., & Macdonald, D. W. (2010). Alloparental behaviour and long-term costs of mothers tolerating other members of the group in a plurally breeding mammal. *Animal Behaviour*, *80*, 721–735.

Ebensperger, L. A. (1998). Strategies and counterstrategies to infanticide in mammals. *Biological Reviews*, *73*, 321–346.

Eberle, M., & Kappeler, P. M. (2006). Family insurance: kin selection and cooperative breeding in a solitary primate (*Microcebus murinus*). *Behavioral Ecology and Sociobiology*, *60*, 582–588.

Ekman, J., Dickinson, J. L., Hatchwell, B. J., & Griesser, M. (2004). Delayed dispersal. In W. D. Koenig & J. L. Dickinson (Eds.), *Ecology and evolution of cooperative breeding in birds* (pp. 35–47). Cambridge, U.K.: Cambridge University Press.

Ekvall, K. (1998). Effects of social organization, age and aggressive behaviour on allosuckling in wild fallow deer. *Animal Behaviour*, *56*, 695–703.

Eloranta, E., & Nieminen, M. (1986). Calving of the experimental reindeer herd in Kaamanen during 1970 - 85. *Rangifer*, *Special Issue 1, 6*, 115–121.

Eloranta, E., Nieminen, M., & Soppela, P. (1990). Reindeer milk. *Rangifer*, *Special Issue 4*, *10*, 47–48.

Emlen, S. T. (1991). The evolution of cooperative breeding in birds and mammals. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology* (3rd ed., pp. 301–337). Oxford, U.K.: Blackwell Scientific Publications.

Emlen, S. T. (1997). Predicting family dynamics in social vertebrates. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: an evolutionary approach* (4th ed., pp. 228–253). Oxford, U.K.: Blackwell.

Emlen, S. T., Reeve, H. K., Sherman, P. W., & Wrege, P. H. (1991). Adaptive versus nonadaptive explanations of behavior: the case of alloparental helping. *American Naturalist*, *138*, 259–270.

Engelhardt, S. C., Weladji, R. B., Holand, Ø., de Rioja, C. M., Ehmann, R. K., & Nieminen, M. (2014). Allosuckling in reindeer (*Rangifer tarandus*): milk-theft, mismothering or kin selection? *Behavioural Processes*, *107*, 133–141.

Engelhardt, S. C., Weladji, R. B., Holand, Ø., & Nieminen, M. (*2016*). Allosuckling in reindeer (*Rangifer tarandus*): a test of the improved nutrition and compensation hypotheses. *Mammalian Biology*, *81*, 146–152.

Engelhardt, S. C., Weladji, R. B., Holand, Ø., Røed, K. H., & Nieminen, M. (2015). Evidence of reciprocal allonursing in reindeer, *Rangifer tarandus*. *Ethology*, *121*, 245–259.

Engelhardt, S. C., Weladji, R. B., Holand, Ø., Røed, K. H., & Nieminen, M. (First published online on March 10th 2016. DOI: 10.1093/jmammal/gyw027). Allonursing in reindeer, *Rangifer tarandus*: a test of the kin-selection hypothesis. *Journal of Mammalogy*.

Espmark, Y. (1971a). Antler shedding in relation to parturition in female reindeer. *The Journal of Wildlife Management*, *35*, 175–177.

Espmark, Y. (1971b). Individual recognition by voice in reindeer mother-young relationship. Field observations and playback experiments. *Behaviour*, *40*, 295–301.

Espmark, Y. (1971c). Mother-young relationship and ontogeny of behaviour in reindeer (*Rangifer tarandus* L.). *Zeitschrift für Tierpsychologie*, *29*, 42–81.

Farmer, M. B., & Alonzo, S. H. (2008). Competition for territories does not explain allopaternal care in the tessellated darter. *Environmental Biology of Fishes*, *83*, 391–395.

Faulkes, C. G., & Abbott, D. H. (1997). The physiology of a reproductive dictatorship: regulation of male and female reproduction by a single breeding female in colonies of naked mole-rats. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 302–334). Cambridge, U.K.: Cambridge University Press.

Faulkes, C. G., Bennett, N. C., Bruford, M. W., O'Brien, H. P., Aguilar, G. H., & Jarvis, J. U. (1997). Ecological constraints drive social evolution in the African mole-rats. *Proceedings of the Royal Society of London B: Biological Sciences*, *264*, 1619–1627.

Feldhamer, G. A., Drickamer, L. C., Vessey, S. H., Merritt, J. F., & Krajewski, C. (2007). *Mammalogy: adaptation, diversity, ecology* (3rd ed.). Baltimore, MD: Johns Hopkins University Press.

Ferrari, M., Lindholm, A. K., & König, B. (2015). The risk of exploitation during communal nursing in house mice, *Mus musculus domesticus*. *Animal Behaviour*, *110*, 133–143.

Field, J., & Brace, S. (2004). Pre-social benefits of extended parental care. *Nature*, *428*, 650–652.

Field, J., Paxton, R. J., Soro, A., & Bridge, C. (2010). Cryptic plasticity underlies a major evolutionary transition. *Current Biology*, *20*, 2028–2031.

Field, J., Shreeves, G., Sumner, S., & Casiraghi, M. (2000). Insurance-based advantage to helpers in a tropical hover wasp. *Nature*, *404*, 869–71.

Fischer, S., Zöttl, M., Groenewoud, F., & Taborsky, B. (2014). Group-size-dependent punishment of idle subordinates in a cooperative breeder where helpers pay to stay. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*, 20140184.

Fisher, M. W., Fennessy, P. F., & Davis, G. H. (1989). A note on the induction of ovulation in lactating red deer hinds prior to the breeding season. *Animal Production*, *4967*, 134–138.

Fisher, R. A. (1930). *The genetical theory of natural selection.* Oxford, U.K.: Clarendon Press.

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression* (2nd ed.). Thousand Oaks, CA: Sage.

Freeman, M. E., Kanyicska, B., Lerant, A., & Nagy, G. (2000). Prolactin: structure, function, and regulation of secretion. *Physiological Reviews*, *80*, 1523–1631.

French, J. A. (1997). Proximate regulation of singular breeding in callitrichid primates. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 34–75). Cambridge, U.K.: Cambridge University Press.

Gardner, A., & Foster, K. (2008). The evolution and ecology of cooperation—history and concepts. In J. Korb & J. Heinze (Eds.), *Ecology of social evolution* (pp. 1–36). Berlin, Germany: Springer-Verlag.

Gaston, A. J. (1978). The evolution of group territorial behavior and cooperative breeding. *American Naturalist*, *112*, 1091–1100.

Gauthier, D., & Barrette, C. (1985). Suckling and weaning in captive white-tailed and fallow deer. *Behaviour*, *94*, 128–149.

Geist, V. (1999). *Deer of the world: their evolution, behaviour and ecology*. Shrewsbury, U.K.: Swan Hill Press.

Geist, V., & Bayer, M. (1988). Sexual dimorphism in the Cervidae and its relation to habitat. *Journal of Zoology*, *214*, 45–53.

Gerlach, G., & Bartmann, S. (2002). Reproductive skew, costs, and benefits of cooperative breeding in female wood mice (*Apodemus sylvaticus*). *Behavioral Ecology*, *13*, 408–418.

Gilchrist, J. S. (2006a). Female eviction, abortion, and infanticide in banded mongooses (*Mungos mungo*): implications for social control of reproduction and synchronized parturition. *Behavioral Ecology*, *17*, 664–669.

Gilchrist, J. S. (2006b). Reproductive success in a low skew, communal breeding mammal: the banded mongoose, *Mungos mungo*. *Behavioral Ecology and Sociobiology*, *60*, 854–863.

Gilchrist, J. S. (2007). Cooperative behaviour in cooperative breeders: costs, benefits, and communal breeding. *Behavioural Processes*, *76*, 100–105.

Gittleman, J. L., & Thompson, S. D. (1988). Energy allocation in mammalian reproduction. *American Zoologist*, *28*, 863–875.

Gjøstein, H., Holand, Ø., Bolstad, T., Hove, K., & Weladji, R. B. (2004). Effect of calf stimulation on milk ejection in reindeer (*Rangifer tarandus*). *Rangifer*, *24*, 3–6.

Gjøstein, H., Holand, Ø., & Weladji, R. B. (2004). Milk production and composition in reindeer (*Rangifer tarandus*): Effect of lactational stage. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, *137*, 649–656.

Gloneková, M., Brandlová, K., & Pluháček, J. (2016). Stealing milk by young and reciprocal mothers: high incidence of allonursing in giraffes, *Giraffa camelopardalis*. *Animal Behaviour*, *113*, 113–123.

Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*, 699–706.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, *28*, 1140–1162.

Griesser, M. (2003). Nepotistic vigilance behavior in Siberian jay parents. *Behavioral Ecology*, *14*, 246–250.

Griesser, M., & Ekman, J. (2004). Nepotistic alarm calling in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, *67*, 933–939.

Griffin, A. S., & West, S. A. (2002). Kin selection: fact and fiction. *Trends in Ecology & Evolution*, *17*, 15–21.

Griffin, A. S., & West, S. A. (2003). Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science*, *302*, 634–636.

Grinnell, J., & McComb, K. (1996). Maternal grouping as a defense against infanticide by males: evidence from field playback experiments on African lions. *Behavioral Ecology*, *7*, 55–59.

Grinsted, L., Breuker, C. J., & Bilde, T. (2014). Cooperative breeding favors maternal investment in size over number of eggs in spiders. *Evolution*, *68*, 1961–1973.

Guinness, F. E., Hall, M. J., & Cockerill, R. A. (1979). Mother-offspring association in red deer (*Cervus elaphus* L.) on Rhum. *Animal Behaviour*, *27*, 536–544.

Gustafsson, E., Mattsson, A., Holmdahl, R., & Mattsson, R. (1994). Pregnancy in B-cell-deficient mice: postpartum transfer of immunoglobulins prevents neonatal runting and death. *Biology of Reproduction*, *51*, 1173–1180.

Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*, 1–16.

Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, *7*, 17–52.

Hass, C. C. (1990). Alternative maternal-care patterns in two herds of bighorn sheep. *Journal of Mammalogy*, *71*, 24–35.

Hatchwell, B. J. (1999). Investment strategies of breeders in avian cooperative breeding systems. *American Naturalist*, *154*, 205–219.

Hatchwell, B. J. (2010). Cryptic kin selection: kin structure in vertebrate populations and opportunities for kin-directed cooperation. *Ethology*, *116*, 203–216.

Hatchwell, B. J., & Komdeur, J. (2000). Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour*, *59*, 1079–1086.

Hayes, L. D. (2000). To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Animal Behaviour*, *59*, 677–688.

Hayes, L. D., & Solomon, N. G. (2004). Costs and benefits of communal rearing to female prairie voles (*Microtus ochrogaster*). *Behavioral Ecology and Sociobiology*, *56*, 585–593.

Heg, D., Bachar, Z., Brouwer, L., & Taborsky, M. (2004). Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proceedings of the Royal Society of London B: Biological Sciences*, *271*, 2367–2374.

Heinsohn, R., & Cockburn, A. (1994). Helping is costly to young birds in cooperatively breeding white-winged choughs. *Proceedings of the Royal Society of London B: Biological Sciences*, *256*, 293–298.

Heinsohn, R. G., Cockburn, A., & Cunningham, R. B. (1988). Foraging, delayed maturity and cooperative breeding in white-winged choughs (*Corcorax melanorhamphos*). *Ethology*, *77*, 177–186.

Heinsohn, R. G., & Legge, S. (1999). The costs of helping. *Trends in Ecology & Evolution*, *14*, 53–57.

Hemelrijk, C. K. (1990a). A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. *Journal of Theoretical Biology*, *143*, 405–420.

Hemelrijk, C. K. (1990b). Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Animal Behaviour*, *39*, 1013–1029.

Hemelrijk, C. K. (1994). Support for being groomed in long-tailed macaques, *Macaca* *fascicularis*. *Animal Behaviour*, *48*, 479–481.

Hirotani, A. (1989). Social relationships of reindeer *Rangifer tarandus* during rut: implications for female choice. *Applied Animal Behaviour Science*, *24*, 183–202.

Hirotani, A. (1990). Social organization of reindeer (*Rangifer tarandus*), with special reference to relationships among females. *Canadian Journal of Zoology*, *68*, 743–749.

Hodge, S. J. (2005). Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose. *Proceedings of the Royal Society of London B: Biological Sciences*, *272*, 2479–2484.

Hodge, S. J., Bell, V., & Cant, M. A. (2011). Reproductive competition and the evolution of extreme birth synchrony in a cooperative mammal. *Biology Letters*, *7*, 54–56.

Holand, Ø., Askim, K. R., Røed, K. H., Weladji, R. B., Gjøstein, H., & Nieminen, M. (2007). No evidence of inbreeding avoidance in a polygynous ungulate: the reindeer (*Rangifer tarandus*). *Biology Letters*, *3*, 36–39.

Holand, Ø., Gjøstein, H., Losvar, A., Kumpula, J., Smith, M. E., Røed, K. H., et al. (2004). Social rank in female reindeer (*Rangifer tarandus*): effects of body mass, antler size and age. *Journal of Zoology*, *263*, 365–372.

Hoogland, J. L. (1982). Prairie dogs avoid extreme inbreeding. *Science*, *215*, 1639–1641.

Hoogland, J. L. (1995). *The black-tailed prairie dog: social life of a burrowing mammal*. Chicago, IL: University of Chicago Press.

Hoogland, J. L., Tamarin, R. H., & Levy, C. K. (1989). Communal nursing in prairie dogs. *Behavioral Ecology and Sociobiology*, *24*, 91–95.

Høymork, A., & Reimers, E. (2002). Antler development in reindeer in relation to age and sex. *Rangifer*, *22*, 75–82.

Hrdy, S. B. (1976). Care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Advances in the Study of Behavior*, *6*, 101–158.

Huber, S., Millesi, E., Walzl, M., Dittami, J., & Arnold, W. (1999). Reproductive effort and costs of reproduction in female European ground squirrels. *Oecologia*, *121*, 19–24.

Hughes, W. O. H., Oldroyd, B. P., Beekman, M., & Francis, L. W. (2008). Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science*, *320*, 1213–1216.

Jain, P., & Sharma, V. K. (2015). Cooperative breeding increases reproductive success in the social spider *Stegodyphus sarasinorum* (Araneae, Eresidae). *Journal of Entomology and*

*Zoology Studies*, *495*, 495–500.

Jamieson, I. G. (1989). Behavioral heterochrony and the evolution of birds' helping at the nest: an unselected consequences of communal breeding? *American Naturalist*, *133*, 394–406.

Jamieson, I. G., & Craig, J. L. (1987). Critique of helping behavior in birds: a departure from functional explanations. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Perspectives in ethology* (pp. 79–98). New York, NY: Plenum Press.

Jennions, M. D., & Macdonald, D. W. (1994). Cooperative breeding in mammals. *Trends in Ecology & Evolution*, *9*, 89–93.

Johannesen, J., Lubin, Y., Smith, D. R., Bilde, T., & Schneider, J. M. (2007). The age and evolution of sociality in *Stegodyphus* spiders: a molecular phylogenetic perspective. *Proceedings of the Royal Society of London B: Biological Sciences*, *274*, 231–237.

Johnstone, R. A., Cant, M. A., & Field, J. (2012). Sex-biased dispersal, haplodiploidy and the evolution of helping in social insects. *Proceedings of the Royal Society of London B: Biological Sciences*, *279*, 787–793.

Jones, T. C., & Parker, P. G. (2002). Delayed juvenile dispersal benefits both mother and offspring in the cooperative spider *Anelosimus studiosus* (Araneae: Theridiidae). *Behavioral Ecology*, *13*, 142–148.

Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, *16*, 1099–1106.

Källquist, L., & Mossing, T. (1982). Olfactory recognition between mother and calf in reindeer (*Rangifer t. tarandus* L.). *Applied Animal Ethology*, *8*, 561–565.

Keller, L., & Ross, K. G. (1998). Selfish genes: a green beard in the red fire ant. *Nature*, *394*, 573–575.

Kerth, G. (2008). Causes and consequences of sociality in bats. *BioScience*, *58*, 737–746.

Khan, M. Z., McNabb, F. M., Walters, J. R., & Sharp, P. J. (2001). Patterns of testosterone and prolactin concentrations and reproductive behavior of helpers and breeders in the cooperatively breeding red-cockaded woodpecker (*Picoides borealis*). *Hormones and Behavior*, *40*, 1–13.

Khan, M. Z., & Walters, J. R. (2002). Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*). *Behavioral Ecology and Sociobiology*, *51*, 336–344.

Kleiman, D. G. (1977). Monogamy in mammals. *The Quarterly Review of Biology*, *52*, 39–69.

Kline, R. (2009). *Becoming a behavioural science researcher: a guide to producing research that matters*. New York, NY: Guilford Press.

Koenig, W. D., & Haydock, J. (2004). Incest and incest avoidance. In W. D. Koenig & J. L. Dickinson (Eds.), *Ecology and evolution of cooperative breeding in birds* (pp. 142–156). Cambridge, U.K.: Cambridge University Press.

Koenig, W. D., Hooge, P. N., Stanback, M. T., & Haydock, J. (2000). Natal dispersal in the cooperatively breeding acorn woodpecker. *The Condor*, *102*, 492–502.

Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L., & Stanback, M. T. (1992). The evolution of delayed dispersal in cooperative breeders. *The Quarterly Review of Biology*, *67*, 111–150.

Koenig, W. D., & Stacey, P. B. (1990). Acorn woodpeckers: group living and food storage under contrasting ecological conditions. In P. B. Stacey & W. D. Koenig (Eds.), *Cooperative breeding in birds: long term studies of ecology and behaviour* (pp. 413–454). Cambridge, U.K.: Cambridge University Press.

Komdeur, J. (1992). Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature*, *358*, 493–495.

Komdeur, J. (1996). Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. *Behavioral Ecology*, *7*, 326–333.

Komdeur, J., Huffstadt, A., Prast, W., Castle, G., Mileto, R., & Wattel, J. (1995). Transfer experiments of Seychelles warblers to new islands: changes in dispersal and helping behaviour. *Animal Behaviour*, *49*, 695–708.

Komdeur, J., Richardson, D. S., & Hatchwell, B. J. (2008). Kin recognition mechanisms in cooperative breeding systems: ecological causes and behavioural consequences of variation. In J. Korb & J. Heinze (Eds.), *Ecology of social evolution* (pp. 175–194). Berlin, Germany: Springer-Verlag.

König, B. (1993). Maternal investment of communally nursing female house mice (*Mus musculus domesticus*). *Behavioural Processes*, *30*, 61–73.

König, B. (1994a). Components of lifetime reproductive success in communally and solitarily nursing house mice – a laboratory study. *Behavioral Ecology and Sociobiology*, *34*, 275–283.

König, B. (1994b). Fitness effects of communal rearing in house mice: the role of relatedness versus familiarity. *Animal Behaviour*, *48*, 1449–1457.

König, B. (2006). Non-offspring nursing in mammals: general implications from a case study on house mice. In P. M. Kappeler & C. P. van Shaik (Eds.), *Cooperation in primates and humans: mechanisms and evolution* (pp. 191–205). Berlin, Germany: Springer-Verlag.

König, B., Riester, J., & Markl, H. (1988). Maternal care in house mice (*Mus musculus*): II. The energy cost of lactation as a function of litter size. *Journal of Zoology*, *216*, 195–210.

Korb, J., Weil, T., Hoffmann, K., Foster, K. R., & Rehli, M. (2009). A gene necessary for reproductive suppression in termites. *Science*, *324*, 758.

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford, U.K.: Oxford University Press.

Krebs, C. J. (1989). *Ecological Methodology.* New York, NY: Harper and Row.

Kreeger, T. J., Seal, U. S., Cohen, Y., Plotka, E. D., & Asa, C. S. (1991). Characterization of prolactin secretion in gray wolves (*Canis lupus*). *Canadian Journal of Zoology*, *69*, 1366–1374.

Lancaster, J. B. (1971). Play-mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatologica*, *15*, 163–182.

Landete-Castillejos, T., García, A., & Gallego, L. (2001). Calf growth in captive Iberian red deer (*Cervus elaphus hispanicus*): effects of birth date and hind milk production and composition. *Journal of Animal Science*, *79*, 1085–1092.

Landete-Castillejos, T., García, A., Garde, J., & Gallego, L. (2000). Milk intake and production curves and allosuckling in captive Iberian red deer, *Cervus elaphus hispanicus*. *Animal Behaviour*, *60*, 679–687.

Landete-Castillejos, T., García, A., Gomez, J. A., Berruga, M. I., & Gallego, L. (2005). Effects of birth date and order in lactation performance of Iberian red deer (*Cervus elaphus hispanicus*). *Journal of Dairy Science*, *88*, 154–158.

Landete-Castillejos, T., García, A., Molina, P., Vergara, H., Garde, J., & Gallego, L. (2000). Milk production and composition in captive Iberian red deer (*Cervus elaphus hispanicus*): effect of birth date 1. *Journal of Animal Science*, *78*, 2771–2777.

Lavigueur, L., & Barrette, C. (1992). Suckling, weaning, and growth in captive woodland caribou. *Canadian Journal of Zoology*, *70*, 1753–1766.

Lawson Handley, L. J., & Perrin, N. (2007). Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology*, *16*, 1559–1578.

Le Galliard, J.-F., & Ferrière, R. (2008). The adaptive evolution of social traits. In É. Danchin, F. Cézilly, & L.-A. Giraldeau (Eds.), *Behavioural ecology* (pp. 547–575). Oxford, U.K.: Oxford University Press.

Leadbeater, E., Carruthers, J. M., Green, J. P., Rosser, N. S., & Field, J. (2011). Nest inheritance is the missing source of direct fitness in a primitively eusocial insect. *Science*, *333*, 874–876.

Leclaire, S., Nielsen, J. F., Thavarajah, N. K., Manser, M., & Clutton-Brock, T. H. (2013). Odour-based kin discrimination in the cooperatively breeding meerkat. *Biology Letters*, *9*, 20121054.

Legge, S. (2000). The effect of helpers on reproductive success in the laughing kookaburra. *Journal of Animal Ecology*, *69*, 714–724.

Leinfelder, I., de Vries, H., Deleu, R., & Nelissen, M. (2001). Rank and grooming reciprocity among females in a mixed-sex group of captive hamadryas baboons. *American Journal of Primatology*, *55*, 25–42.

Leonard, M. L., Horn, A. G., & Eden, S. F. (1989). Does juvenile helping enhance breeder reproductive success? *Behavioral Ecology and Sociobiology*, *25*, 357–361.

Leung, E. S., Vergara, V., & Barrett-Lennard, L. G. (2010). Allonursing in captive belugas (*Delphinapterus leucas*). *Zoo Biology*, *29*, 633–637.

Lewis, S. E., & Pusey, A. E. (1997). Factors influencing the occurrence of communal care in plural breeding mammals. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals.* (pp. 335–363). Cambridge, U.K.: Cambridge University Press.

Ligon, J. D., & Ligon, S. H. (1978). Communal breeding in green woodhoopoes as a case for reciprocity. *Nature*, *276*, 496–498.

Ligon, J. D., & Ligon, S. H. (1983). Reciprocity in the green woodhoopoe (*Phoeniculus purpureus*). *Animal Behaviour*, *31*, 480–489.

Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behaviour: the predation risk allocation hypothesis. *American Naturalist*, *153*, 649–659.

Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, *14*, 343–348.

Littell, R. C., Miliken, G. A., Stroup, W. W., Wolfinger, R. D., & Schabenberger, O. (2006). *SAS for Mixed Models* (2nd ed.). Carey, NC: SAS Institute Inc.

Lubin, M., Leon, M., Moltz, H., & Numan, M. (1972). Hormones and maternal behavior in the male rat. *Hormones and Behavior*, *3*, 369–374.

Lucas, E. R., & Field, J. (2011). Assured fitness returns in a social wasp with no worker caste. *Proceedings of the Royal Society of London B: Biological Sciences*, *278*, 2991–2995.

Lucas, J. R., Creel, S. R., & Waser, P. M. (1997). Dynamic optimization and cooperative breeding: an evaluation of future fitness effects. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 171–198). Cambridge, U.K.: Cambridge University Press.

Lucia, K. E., Keane, B., Hayes, L. D., Lin, Y. K., Schaefer, R. L., & Solomon, N. G. (2008). Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis. *Behavioral Ecology*, *19*, 774–783.

Luick, J. R., White, R. G., Gau, A. M., & Jenness, R. (1974). Compositional changes in the milk secreted by grazing reindeer I. Gross composition and ash. *Journal of Dairy Science*, *57*, 1325–1333.

Lukas, D., & Clutton-Brock, T. H. (2012). Cooperative breeding and monogamy in mammalian societies. *Proceedings of the Royal Society of London B: Biological Sciences*, *279*, 2151–2156.

Lukas, D., & Huchard, E. (2014). Sexual conflict. The evolution of infanticide by males in mammalian societies. *Science*, *346*, 841–844.

Lunn, N. J., Paetkau, D., Calvert, W., Atkinson, S., Taylor, M., & Strobeck, C. (2000). Cub adoption by polar bears (*Ursus maritimus*): determining relatedness with microsatellite markers. *Journal of Zoology*, *251*, 23–30.

Lynch, M., & Ritland, K. (1999). Estimation of pairwise relatedness with molecular markers. *Genetics*, *152*, 1753–1766.

MacLeod, K. J., & Clutton-Brock, T. H. (2014). Low costs of allonursing in meerkats: mitigation by behavioral change? *Behavioral Ecology*, *26*, 697–705.

MacLeod, K. J., & Lukas, D. (2014). Revisiting non-offspring nursing: allonursing evolves when the costs are low. *Biology Letters*, *10*, 20140378–20140378.

MacLeod, K. J., McGhee, K. E., & Clutton-Brock, T. H. (2015). No apparent benefits of allonursing for recipient offspring and mothers in the cooperatively breeding meerkat. *Journal of Animal Ecology*, *84*, 1050–1058.

MacLeod, K. J., Nielsen, J. F., & Clutton-Brock, T. H. (2013). Factors predicting the frequency, likelihood and duration of allonursing in the cooperatively breeding meerkat. *Animal Behaviour*, *86*, 1059–1067.

Magrath, R. D., Heinsohn, R. G., & Johnstone, R. A. (2004). Reproductive skew. In W. D. Koenig & J. L. Dickinson (Eds.), *Ecology and evolution of cooperative breeding in birds* (pp. 157–176). Cambridge, U.K.: Cambridge University Press.

Magrath, R. D., & Whittingham, L. A. (1997). Subordinate males are more likely to help if unrelated to the breeding female in cooperatively breeding white-browed scrubwrens. *Behavioural Ecology and Sociobiology*, *41*, 185–192.

Majer, M., Svenning, J.-C., & Bilde, T. (2013). Habitat productivity constrains the distribution of social spiders across continents - case study of the genus *Stegodyphus*. *Frontiers in Zoology*, *10*, 9.

Maniscalco, J. M., Harris, K. R., Atkinson, S., & Parker, P. (2007). Alloparenting in Steller sea lions (*Eumetopias jubatus*): correlations with misdirected care and other observations. *Journal of Ethology*, *25*, 125–131.

Manning, C. J., Dewsbury, D. A., Wakeland, E. K., & Potts, W. K. (1995). Communal nesting and communal nursing in house mice, *Mus musculus domesticus*. *Animal Behaviour*, *50*, 741–751.

Marin, G., & Pilastro, A. (1994). Communally breeding dormice, *Glis glis*, are close kin. *Animal Behaviour*, *47*, 1485–1487.

Marken, J. M. (2003). *Suckling behaviour in semi domesticated reindeer (Rangifer tarandus tarandus)* (Master's Thesis). Ås, Norway: Norwegian University of Life Sciences.

Martin, P., & Bateson, P. (2007). *Measuring behaviour: an introductory guide* (3rd ed.). Cambridge, U.K.: Cambridge University Press.

Maurel, D., Lacroix, A., & Boissin, J. (1984). Seasonal reproductive endocrine profiles in two wild mammals: the red fox (*Vulpes vulpes* L.) and the European badger (*Meles meles* L.) considered as short-day mammals. *Acta Endocrinologica*, *105*, 130–138.

McCracken, G. F. (1984). Communal nursing in mexican free-tailed bat maternity colonies. *Science*, *223*, 1090–1091.

McCracken, G. F., & Gustin, M. K. (1991). Nursing behavior in Mexican free-tailed bat maternity colonies. *Ethology*, *89*, 305–321.

McCulloch, S., & Boness, D. J. (2000). Mother-pup vocal recognition in the grey seal (*Halichoerus grypus*) of Sable Island, Nova Scotia, Canada. *Journal of Zoology*, *251*, 449–455.

McCulloch, S., Pomeroy, P. P., & Slater, P. J. (1999). Individually distinctive pup vocalizations fail to prevent allo-suckling in grey seals. *Canadian Journal of Zoology*, *77*, 716–723.

McDonald, P. G. (2014). Cooperative breeding beyond kinship: why else do helpers help? *Emu*, *114*, 91–96.

McDonald, P. G., te Marvelde, L., Kazem, A. J. N., & Wright, J. (2008). Helping as a signal and the effect of a potential audience during provisioning visits in a cooperative bird. *Animal Behaviour*, *75*, 1318–1330.

Meade, J., Nam, K. B., Beckerman, A. P., & Hatchwell, B. J. (2010). Consequences of "load-lightening" for future indirect fitness gains by helpers in a cooperatively breeding bird. *Journal of Animal Ecology*, *79*, 529–537.

Melnycky, N. A., Weladji, R. B., Holand, Ø., & Nieminen, M. (2013). Scaling of antler size in reindeer (*Rangifer tarandus*): sexual dimorphism and variability in resource allocation. *Journal of Mammalogy*, *94*, 1371–1379.

Mennella, J. A., Blumberg, M. S., McClintock, M. K., & Moltz, H. (1990). Inter-litter competition and communal nursing among Norway rats: advantages of birth synchrony. *Behavioral Ecology and Sociobiology*, *27*, 183–190.

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*, 633–640.

Mitani, J. C., & Watts, D. (1997). The evolution of non-maternal caretaking among anthropoid primates: do helpers help? *Behavioral Ecology and Sociobiology*, *40*, 213–220.

Moltz, H., Lubin, M., Leon, M., & Numan, M. (1970). Hormonal induction of maternal behavior in the ovariectomized nulliparous rat. *Physiology & Behavior*, *5*, 1373–1377.

Mondain-Monval, M., Møller, O. M., Smith, A. J., McNeilly, A. S., & Scholler, R. (1985). Seasonal variations of plasma prolactin and LH concentrations in the female blue fox (*Alopex lagopus*). *Journal of Reproduction and Fertility*, *74*, 439–448.

Montgomery, D. C., & Peck, E. A. (1992). *Introduction to linear regression analysis*. New York, NY: Wiley.

Mulder, R. A., & Langmore, N. E. (1993). Dominant males punish helpers for temporary defection in superb fairy-wrens. *Animal Behaviour*, *45*, 830–833.

Mumme, R. L. (1992). Do helpers increase reproductive success? *Behavioral Ecology and Sociobiology*, *31*, 319–328.

Mumme, R. L. (1997). A bird's-eye view of mammalian cooperative breeding. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals.* (pp. 364–388). Cambridge, U.K.: Cambridge University Press.

Murphey, R. M., Paranhos da Costa, M. J. R., Da Silva, R. G., & de Souza, R. C. (1995). Allonursing in river buffalo, *Bubalus bubalis*: nepotism, incompetence, or thievery? *Animal Behaviour*, *49*, 1611–1616.

Mysterud, A., Røed, K. H., Holand, Ø., Yoccoz, N. G., & Nieminen, M. (2009). Age-related gestation length adjustment in a large iteroparous mammal at northern latitude. *Journal of Animal Ecology*, *78*, 1002–1006.

Newman, J. (1995). How breast milk protects newborns. *Scientific American*, *273*, 76–79.

Newton-Fisher, N. E., & Lee, P. C. (2011). Grooming reciprocity in wild male chimpanzees. *Animal Behaviour*, *81*, 439–446.

Nicoll, G. B. (1982a). Effects of double suckling at pasture 1. Cow performance. *Animal Production*, *35236*, 385–393.

Nicoll, G. B. (1982b). Effects of double suckling at pasture 2. Calf performance. *Animal Production*, *35236*, 395–400.

Noë, R. (2001). Biological markets: partner choice as the driving force behind the evolution of cooperation. In R. Noë, J. A. R. A. M. van Hooff, & P. Hammerstein (Eds.), *Economics in nature. social dilemmas, mate choice and biological markets* (pp. 93–118). Cambridge, U.K.: Cambridge University Press.

Noë, R., & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, *35*, 1–11.

Noë, R., & Hammerstein, P. (1995). Biological markets. *Trends in Ecology & Evolution*, *10*, 336–339.

O'Brien, T. G. (1988). Parasitic nursing behavior in the wedge-capped capuchin monkey (*Cebus* *olivaceus*). *American Journal of Primatology*, *16*, 341–344.

O'Brien, T. G., & Robinson, J. G. (1991). Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank and relatedness. *Behaviour*, *119*, 30–50.

Ochi, H., & Yanagisawa, Y. (2005). Farming-out of offspring is a predominantly male tactics in a biparental mouthbrooding cichlid *Perrisodus mircolepis*. *Environmental Biology of Fishes*, *73*, 335–340.

Oftedal, O. T. (1984). Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symposia of the Zoological Society of London*, *51*, 33–85.

Oftedal, O. T. (1985). Pregnancy and lactation. In R. J. Hudson & R. G. White (Eds.), *Bioenergetics of wild herbivores* (pp. 215–238). Boca Raton, FL: CRC Press.

Olléová, M., Pluháček, J., & King, S. R. B. (2012). Effect of social system on allosuckling and adoption in zebras. *Journal of Zoology*, *288*, 127–134.

Oswald, C., & Mcclure, P. A. (1990). Energetics of concurrent pregnancy and lactation in cotton rats and woodrats. *Journal of Mammalogy*, *71*, 500–509.

Ota, K., & Kohda, M. (2005). Nest use by territorial males in a shell-brooding cichlid: the effect of reproductive parasitism. *Journal of Ethology*, *24*, 91–95.

Owens, D. D., & Owens, M. J. (1984). Helping behaviour in brown hyenas. *Nature*, *308*, 843–845.

Packer, C., Lewis, S. ., & Pusey, A. (1992). A comparative analysis of non-offspring nursing. *Animal Behaviour*, *43*, 265–281.

Paranhos da Costa, M. J. R., Andriolo, A., Simplício de Oliveira, J. F., & Schmidek, W. R. (2000). Suckling and allosuckling in river buffalo calves and its relation with weight gain. *Applied Animal Behaviour Science*, *66*, 1–10.

Parker, K. L., White, R. G., Gillingham, M. P., & Holleman, D. F. (1990). Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. *Canadian Journal of Zoology*, *68*, 106–114.

Peakall, R., & Smouse, P. E. (2006). Genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, *6*, 288–295.

Pélabon, C., Yoccoz, N. G., Ropert-Coudert, Y., Caron, M., & Peirera, V. (1998). Suckling and allosuckling in captive fallow deer (*Dama dama*, Cervidae). *Ethology*, *104*, 75–86.

Penn, D. J. (2002). The scent of genetic compatibility: sexual selection and the major histocompatibility complex. *Ethology*, *108*, 1–21.

Perry, E. A., Boness, D. J., & Fleischer, R. C. (1998). DNA fingerprinting evidence of nonfilial nursing in grey seals. *Molecular Ecology*, *7*, 81–85.

Pilastro, A. (1992). Communal nesting between breeding females in a free-living population of fat dormouse (*Glis glis* L.). *Bollettino di zoologica*, *59*, 63–68.

Pintus, E., Uccheddu, S., Røed, K. H., Perez Gonzalez, J., Carranza, J., Nieminen, M., et al. (2015). Flexible mating tactics and associated reproductive effort during the rutting season in male reindeer (*Rangifer tarandus*, L. 1758). *Current Zoology*, *61*, 802–810.

Plesner Jensen, S., Siefert, L., Okori, J. J. L., & Clutton-Brock, T. H. (1999). Age-related participation in allosuckling by nursing warthogs (*Phacochoerus africanus*). *Journal of Zoology*, *248*, 443–449.

Pomeroy, P. P., Redman, P. R., Ruddell, S. J. S., Duck, C. D., & Twiss, S. D. (2005). Breeding site choice fails to explain interannual associations of female grey seals. *Behavioral Ecology and Sociobiology*, *57*, 546–556.

Pottinger, T. G. (1999). The impact of stress on animal reproductive activities. In P. H. M. Balm (Ed.), *Stress physiology in animals* (pp. 130–177). Sheffield, U.K.: Sheffield Academic Press.

Powell, R. A., & Fried, J. J. (1992). Helping by juvenile pine voles (*Microtus pinetorum*), growth and survival of younger siblings, and the evolution of pine vole sociality. *Behavioral Ecology*, *3*, 325–333.

Price, E. C. (1990). Infant carrying as a courtship strategy of breeding male cotton-top tamarins. *Animal Behaviour*, *40*, 784–786.

Pruett-Jones, S. (2004). Summary. In W. D. Koenig & J. L. Dickinson (Eds.), *Ecology and evolution of cooperative breeding in birds* (pp. 228–238). Cambridge, U.K.: Cambridge University Press.

Pruett-Jones, S. G., & Lewis, M. J. (1990). Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature*, *348*, 541–542.

Pusey, A. E., & Packer, C. (1994). Non-offspring nursing in social carnivores: minimizing the costs. *Behavioral Ecology*, *5*, 362–374.

Queller, D. C., & Goodnight, K. F. (1989). Estimating relatedness using genetic markers evolution. *Evolution*, *43*, 258–275.

Queller, D. C., Zacchi, F., Cervo, R., Turillazzi, S., Henshaw, M. T., Santorelli, L. A., et al. (2000). Unrelated helpers in a social insect. *Nature*, *405*, 784–787.

R Core Team. (2013). *R: a language and environment for statistical computing*. Vienna, Austria: R foundation for statistical computing. http://www.R-project.org/.

R Development Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria.: R Foundation for Statistical Computing. http://www.R-project.org/.

Rabenold, K. N. (1990). *Campylorhynchus* wrens: the ecology of delayed dispersal and cooperation in the Venezuelan savanna. In P. B. Stacey & W. D. Koenig (Eds.), *Cooperative breeding in birds: long-term studies of ecology and behavior* (pp. 159–196). Cambridge, U.K.: Cambridge University Press.

Radisky, D. C., & Hartmann, L. C. (2009). Mammary involution and breast cancer risk: transgenic models and clinical studies. *Journal of Mammary Gland Biology and Neoplasia*, *14*, 181–191.

Rand, D. G., & Nowak, M. A. (2013). Human cooperation. *Trends in Cognitive Sciences*, *17*, 413–425.

Ratnieks, F. L. W., Foster, K. R., & Wenseleers, T. (2006). Conflict resolution in insect societies. *Annual Review of Entomology*, *51*, 581–608.

Réale, D., Boussès, P., & Chapuis, J. L. (1999). Nursing behaviour and mother-lamb relationships in mouflon under fluctuating population densities. *Behavioural Processes*, *47*, 81–94.

Reeve, H. K., Emlen, S. T., & Keller, L. (1998). Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behavioral Ecology*, *9*, 267–278.

Reimers, E. (1983). Reproduction in wild reindeer in Norway. *Canadian Journal of Zoology*, *61*, 211–217.

Reiter, J., Stinson, N. L., & Le Boeuf, B. J. (1978). Northern elephant seal development: the transition from weaning to nutritional independence. *Behavioral Ecology and Sociobiology*, *3*, 337–367.

Reyer, H.-U. (1984). Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Animal Behaviour*, *32*, 1163–1178.

Richardson, B. D. (1975). Lactation in grandmothers. *South African Medicine Journal*, *49*, 2028.

Ridgway, S., Kamolnick, T., Reddy, M., Curry, C., & Tarpley, R. J. (1995). Orphan-induced lactation in *Tursiops* and analysis of collected milk. *Marine Mammal Science*, *11*, 172–182.

Riedman, M. L. (1982). The evolution of alloparental care and adoption in mammals and birds. *The Quarterly Review of Biology*, *57*, 405–435.

Roberts, R. L., Jenkins, K. T., Lawler, T., Wegner, F. H., & Newman, J. D. (2001). Bromocriptine administration lowers serum prolactin and disrupts parental responsiveness in common marmosets (*Callithrix j. jacchus*). *Hormones and Behavior*, *39*, 106–112.

Robinson, K. J., Twiss, S. D., Hazon, N., Moss, S., Lonergan, M., & Pomeroy, P. P. (2015). Conspecific recognition and aggression reduction to familiars in newly weaned, socially plastic mammals. *Behavioral Ecology and Sociobiology*, *69*, 1383–1394.

Røed, K. H. (2005). Refugial origin and postglacial colonization of holarctic reindeer and caribou. *Rangifer*, *25*, 19–30.

Røed, K. H., Holand, Ø., Gjøstein, H., & Hansen, H. (2005). Variation in male reproductive success in a wild population of reindeer. *The Journal of Wildlife Management*, *69*, 1163–1170.

Røed, K. H., Holand, Ø., Smith, M. E., Gjøstein, H., Kumpula, J., & Nieminen, M. (2002). Reproductive success in reindeer males in a herd with varying sex ratio. *Molecular Ecology*, *11*, 1239–1243.

Røed, K. H., & Midthjell, L. (1998). Microsatellites in reindeer, *Rangifer tarandus*, and their use in other cervids. *Molecular Ecology*, *7*, 1773–1776.

Rosenblatt, J. S. (1967). Nonhormonal basis of maternal behavior in the rat. *Science*, *156*, 1512–1514.

Ross, C., & MacLarnon, A. (2000). The evolution of non-maternal care in anthropoid primates: a test of the hypotheses. *Folia Primatologica*, *71*, 93–113.

Roulin, A. (2002). Why do lactating females nurse alien offspring? A review of hypotheses and empirical evidence. *Animal Behaviour*, *63*, 201–208.

Roulin, A. (2003). The neuroendocrine function of allosuckling. *Ethology*, *109*, 185–195.

Roulin, A., & Heeb, P. (1999). The immunological function of allosuckling. *Ecology Letters*, *2*, 319–324.

Rubenstein, D. R., & Lovette, I. J. (2007). Temporal environmental variability drives the evolution of cooperative breeding in birds. *Current Biology*, *17*, 1414–1419.

Russell, A. F. (2004). Mammals: comparisons and contrasts. In W. D. Koenig & J. L. Dickinson (Eds.), *Ecology and evolution of cooperative breeding in birds* (pp. 210–227). Cambridge, U.K.: Cambridge University Press.

Russell, A. F., Brotherton, P. N. M., McIlrath, G. M., Sharpe, L. L., & Clutton-Brock, T. H. (2003). Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behavioral Ecology*, *14*, 486–492.

Russell, A. F., Sharpe, L. L., Brotherton, P. N. M., & Clutton-Brock, T. H. (2003). Cost minimization by helpers in cooperative vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 3333–3338.

Russell, A. F., Young, A. J., Spong, G., Jordan, N. R., & Clutton-Brock, T. H. (2007). Helpers increase the reproductive potential of offspring in cooperative meerkats. *Proceedings of the Royal Society of London B: Biological Sciences*, *274*, 513–520.

Ryba, K. A., & Ryba, A. E. (1984). Induced lactation in nulliparous adoptive mothers. *The New Zealand Medical Journal*, *97*, 822–823.

Salo, A. L., & French, J. A. (1989). Early experience, reproductive success, and development of parental behaviour in Mongolian gerbils. *Animal Behaviour*, *38*, 693–702.

Salomon, M., & Lubin, Y. (2007). Cooperative breeding increases reproductive success in the social spider *Stegodyphus dumicola* (Araneae, Eresidae). *Behavioral Ecology and Sociobiology*, *61*, 1743–1750.

Sánchez, S., Peláez, F., Gil-Bürmann, C., & Kaumanns, W. (1999). Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, *48*, 99–111.

SAS. (2012). The SAS system for windows. Carey, NC: SAS Institute Inc.

Sato, T. (1986). A brood parasitic catfish of mouthbrooding cichlid fishes in Lake Tanganyika. *Nature*, *323*, 58–59.

Sayler, A., & Salmon, M. (1969). Communal nursing in mice: influence of multiple mothers on the growth of the young. *Science*, *164*, 1309–1310.

Scantlebury, M., Russell, A. F., McIlrath, G. M., Speakman, J. R., & Clutton-Brock, T. H. (2002). The energetics of lactation in cooperatively breeding meerkats *Suricata suricatta*. *Proceedings of the Royal Society of London B: Biological Sciences*, *269*, 2147–2153.

Schino, G., & Aureli, F. (2009). Reciprocal altruism in primates: partner choice, cognition, and emotions. *Advances in the Study of Behavior*, *39*, 45–69.

Schino, G., & Aureli, F. (2010). A few misunderstandings about reciprocal altruism. *Communicative & Inegrative Biology*, *3*, 561–563.

Schino, G., Ventura, R., & Troisi, A. (2003). Grooming among female Japanese macaques: distinguishing between reciprocation and interchange. *Behavioral Ecology*, *14*, 887–891.

Schoech, S. J., Mumme, R. L., & Wingfield, J. C. (1996). Prolactin and helping behaviour in the cooperatively breeding Florida scrub-jay, *Aphelocoma coerulescens*. *Animal Behaviour*, *52*, 445–456.

Schoech, S. J., Reynolds, S. J., & Boughton, R. K. (2004). Endocrinology. In W. D. Koenig & J. L. Dickinson (Eds.), *Ecology and evolution of cooperative breeding in birds* (pp. 128–141). Cambridge, U.K.: Cambridge University Press.

Scott-Phillips, T. C., Dickins, T. E., & West, S. A. (2011). Evolutionary theory and the ultimate-proximate distinction in the human behavioral sciences. *Perspectives on Psychological Science*, *6*, 38–47.

Sefc, K. M. (2011). Mating and parental care in Lake Tanganyika's cichlids. *International Journal of Evolutionary Biology*, 470875.

Selander, R. K. (1964). Speciation in wrens of the genus *Campylorynchus*. *University of California Publications in Zoology*, *74*, 1–305.

Shackleton, D., & Harestad, A. (2003). Bovids I – kudus, buffaloes, and bison. In M. Hutchins, V. Geist, & M. McDade (Eds.), *Grzimek's animal life encyclopedia, Vol. 16* (2nd ed., pp. 11–25). Farmington Hills, MI: The Gale Group.

Sharpe, L. L., Hill, A., & Cherry, M. I. (2013). Individual recognition in a wild cooperative mammal using contact calls. *Animal Behaviour*, *86*, 893–900.

Sherley, G. H. (1990). Co-operative breeding in rifleman (*Acanthisitta chloris*): benefits to parents, offspring and helpers. *Behaviour*, *112*, 1–22.

Shreeves, G., Cant, M. A., Bolton, A., & Field, J. (2003). Insurance-based advantages for subordinate co-foundresses in a temperate paper wasp. *Nature*, *404*, 869–871.

Sikes, R. S., Gannon, W. L., & the Animal Care and Use Committee of the American Society of Mammalogists. (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, *92*, 235–253.

Silk, J. B., Robert, M. S., & Cheney, D. L. (1999). The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. *Behaviour*, *136*, 679–703.

Simola, D. F., Graham, R. J., Brady, C. M., Enzmann, B. L., Desplan, C., Ray, A., et al. (2016). Epigenetic (re)programming of caste-specific behavior in the ant *Camponotus floridanus*. *Science*, *351*, aac6633.

Skogland, T. (1989). Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. *Advances in Ethology*, *29*, 1–74.

Skutch, A. F. (1935). Helpers at the nest. *Auk*, *52*, 257–273.

Smiseth, P. T., Kölliker, M., & Royle, N. J. (2012). What is parental care? In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 1–17). Oxford, U.K.: Oxford University Press.

Smith, A. C., Herrera, E. R. T., Buchanan-Smith, H. M., & Heymann, E. W. (2001). Multiple breeding females and allo-nursing in a wild group of moustached tamarins (*Saguinus mystax*). *Neotropical Primates*, *9*, 67–69.

Solomon, N. G. (1991). Current indirect fitness benefits associated with philopatry in juvenile prairie voles. *Behavioral Ecology and Sociobiology*, *29*, 277–282.

Solomon, N. G., & French, J. A. (1997). The study of mammalian cooperative breeding. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 1–10). Cambridge, U.K.: Cambridge University Press.

Solomon, N. G., & Getz, L. L. (1997). Examination of alternative hypotheses for cooperative breeding in rodents. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 199–230). Cambridge, U.K.: Cambridge University Press.

Solomon, N. G., & Hayes, L. D. (2012). The biological basis of alloparental behaviour in mammals. In G. Bentley & R. Mace (Eds.), *Substitue parents. Biological and social perspectives on alloparenting in human societies* (pp. 13–49). New York, NY: Berghahn Books.

Sorenson, M. D., & Payne, R. B. (2005). Molecular systematics: cuckoo phylogeny inferred from mitochondrial DNA sequences. In R. B. Payne (Ed.), *Bird families of the world: cuckoos* (pp. 68–94). Oxford, U.K.: Oxford University Press.

Špinka, M., & Illmann, G. (1992). Suckling behaviour of young dairy calves with their own and alien mothers. *Applied Animal Behaviour Science*, *33*, 165–173.

Spinks, A. C., Jarvis, J. U. M., & Bennett, N. C. (2000). Comparative patterns of philopatry and dispersal in two common mole-rat populations: implications for the evolution of mole-rat sociality. *Journal of Animal Ecology*, *69*, 224–234.

Staaland, H., & Nieminen, M. (1993). World reindeer herding: origin, history, distribution, economy. In *Proceedings VII World Conference on Animal Production, June 28–July 2, Edmonton, Alberta, Vol. 1* (pp. 161–203).

Stacey, P. B. K., & Koenig, W. D. (1990). *Cooperative breeding in birds: long-term studies of ecology and behavior.* Cambridge, U.K.: Cambridge University Press.

Stephens, P. A., Buskirk, S. W., Hayward, G. D., & Martínez Del Rio, C. (2005). Information theory and hypothesis testing: a call for pluralism. *Journal of Applied Ecology*, *42*, 4–12.

Stiver, K. A., & Alonzo, S. H. (2010). Alloparental care increases mating success. *Behavioral Ecology*, *22*, 206–211.

Strassmann, J. E. (1981). Parasitoids, predators, and group size in the paper wasp, *Polistes exclamans*. *Ecology*, *62*, 1225–1233.

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*.

Szumilas, M. (2010). Explaining odds ratios. *Journal of the Canadian Academy of Child and Adolescent Psychiatry*, *19*, 227–229.

Taborsky, M. (1984). Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior*, *23*, 1–100.

Taborsky, M. (1985). Breeder-helper conflict in a cichlid fish with broodcare helpers: an experimental analysis. *Behaviour*, *95*, 45–75.

Taborsky, M. (2009). Reproductive skew in cooperative fish groups: virtue and limitations of alternative modeling approaches. In R. Hager & C. B. Jones (Eds.), *Reproductive skew in vertebrates: proximate and ultimate causes* (pp. 265–304). Cambridge, U.K.: Cambridge University Press.

Tallamy, D. W. (2005). Egg dumping in insects. *Annual Review of Entomology*, *50*, 347–370.

Tardif, S. (1997). The bioenergetics of parental behavior and the evolution of alloparental care marmosets and tamarins. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 11–33). Cambridge, U.K.: Cambridge University Press.

Thomas, J. A., & Settele, J. (2004). Evolutionary biology: butterfly mimics of ants. *Nature*, *432*, 283–284.

Thomson, B. R. (1977). *The behaviour of wild reindeer in Norway* (Doctoral Thesis). Edinburgh, U.K.: Univeristy of Edinburgh.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, *20*, 410–433.

Torriani, M. V. G., Vannoni, E., & Mcelligott, A. G. (2006). Mother-young recognition in an ungulate hider species: a unidirectional process. *American Naturalist*, *168*, 412–420.

Tóth, E., & Duffy, J. E. (2005). Coordinated group response to nest intruders in social shrimp. *Biology Letters*, *1*, 49–52.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, *46*, 35–57.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871-1971* (pp. 136–179). Chicago, IL: Aldine.

van den Berghe, E. P. (1988). Piracy as an alternative reproductive tactic for males. *Nature*, *334*, 697–698.

van Zweden, J. S. (2010). The evolution of honest queen pheromones in insect societies. *Communicative & Integrative Biology*, *3*, 50–52.

van Zweden, J. S., & D'Ettorre, P. (2010). Nestmate recognition in social insects and the role of hydrocarbons. In G. J. Blomquist & A.-G. Bagnères (Eds.), *Insect hydrocarbons: biology, biochemistry, and chemical ecology* (pp. 222–243). Cambridge, U.K.: Cambridge University Press.

Vaňková, D., Bartos, L., Cízová-Schröffelová, D., Nespor, F., & Jandurová, O. (2001). Mother-offspring bonding in farmed red deer: accuracy of visual observation verified by DNA analysis. *Applied Animal Behaviour Science*, *73*, 157–165.

Vannoni, E., & McElligott, A. G. (2007). Individual acoustic variation in fallow deer (*Dama dama*) common and harsh groans: a source-filter theory perspective. *Ethology*, *113*, 223–234.

Vaughan, T. A., Ryan, J. M., & Czaplewski, N. J. (2011). *Mammalogy* (5th ed.). Sudbury, MA: Jones and Bartlett Publishers.

Vehrencamp, S. L. (1983). A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour*, *31*, 667–682.

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). New York, NY: Springer.

Víchová, J., & Bartoš, L. (2005). Allosuckling in cattle: gain or compensation? *Applied Animal Behaviour Science*, *94*, 223–235.

Vleck, C. M., & Goldsmith, A. R. (1991). Hormonal correlates of parental and helping behavior in cooperatively breeding Harris' hawks (*Parabuteo unicinctus*). *Auk*, *108*, 638–648.

Waltl, B., Appleby, M. C., & Sölkner, J. (1995). Effects of relatedness on the suckling behaviour of calves in a herd of beef cattle rearing twins. *Applied Animal Behaviour Science*, *45*, 1–9.

Watts, D. P. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, *139*, 343–370.

Weidt, A., Lindholm, A. K., & König, B. (2014). Communal nursing in wild house mice is not a by-product of group living: females choose. *Naturwissenschaften*, *101*, 73–76.

Weladji, R. B., Gaillard, J.-M., Yoccoz, N. G., Holand, Ø., Mysterud, A., Loison, A., et al. (2006). Good reindeer mothers live longer and become better in raising offspring. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*, 1239–1244.

Weladji, R. B., Holand, Ø., Gaillard, J.-M., Yoccoz, N. G., Mysterud, A., Nieminen, M., et al. (2010). Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? *Oecologia*, *162*, 261–271.

Welch, R. A. S., & Kilgour, R. (1970). Mis-mothering among Romneys. *New Zealand Journal of Agriculture*, *121*, 26–27.

Werboff, J., Steg, M., & Barnes, L. (1970). Communal nursing in mice: strain-specific effects of multiple mothers on growth and behavior. *Psychonomic Science*, *19*, 269–271.

West, S. A., Griffin, A. S., & Gardner, A. (2007). Evolutionary explanations for cooperation. *Current Biology*, *17*, R661–R672.

West, S. A., Pen, I., & Griffin, A. S. (2002). Cooperation and competition between relatives. *Science*, *296*, 72–75.

West-Eberhard, M. J. (1987). The epigenetical origins of insect sociality. In J. Eder & H. Rembold (Eds.), *Chemistry and biology of social insects* (pp. 362–372). Munich, Germany: Proceedings of the X International Congress of the IUSSI.

White, R. G., & Luick, J. R. (1984). Plasticity and constraints in the lactational strategy of reindeer and caribou. In R. G. Vernon, C. H. Knight, & M. P. Peaker (Eds.), *Physiological strategies in lactation* (pp. 215–232). London, U.K.: Zoological Society of London.

Whittingham, L. A., Dunn, P. O., & Magrath, R. D. (1997). Relatedness, polyandry and extra-group paternity in the cooperatively-breeding white-browed scrubwren (Sericornis frontalis). *Behavioral Ecology and Sociobiology*, 40, 261–270.

Wilkinson, G. S. (1992). Communal nursing in the evening bat, *Nycticeius humeralis*. *Behavioral Ecology and Sociobiology*, *31*, 225–235.

Wilkinson, G. S., & Baker, A. E. M. (1988). Communal nesting among genetically similar house mice. *Ethology*, *77*, 103–114.

Wilson, D. S. (1975). A theory of group selection. *Proceedings of the National Academy of Sciences of the United States of America*, *72*, 143–146.

Wilson, E. O. (1971). *The insect societies.* Cambridge, MA: Belknap Press of Harvard University Press.

Wilson, E. O. (1975). *Sociobiology.* Cambridge, MA: Harvard University Press.

Wilson, G. A., Strobeck, C., Wu, L., & Coffin, J. W. (1997). Characterization of microsatellite loci in caribou *Rangifer tarandus*, and their use in other artiodactyls. *Molecular Ecology*, *6*, 697–699.

Wisenden, B. D. (1999). Alloparental care in fishes. *Reviews in Fish Biology and Fisheries*, *9*, 45–70.

Wolff, J. O. (1994). Reproductive success of solitarily and communally nesting white-footed mice and deer mice. *Behav Ecol*, *5*, 206–209.

Woodroffe, R., & Macdonald, D. W. (2000). Helpers provide no detectable benefits in the European badger (*Meles meles*). *Journal of Zoology*, *250*, 113–119.

Wright, J. (1999). Altruism as a signal: Zahavi’s alternative to kin selection and reciprocity. *Journal of Avian Biology*, *30*, 108–115.

Wyatt, T. D. (2014). *Pheromones and animal behavior* (2nd ed.). Cambridge, U.K.: Cambridge University Press.

Yamazaki, K., Beauchamp, G. K., Curran, M., Bard, J., & Boyse, E. A. (2000). Parent-progeny recognition as a function of MHC odortype identity. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 10500–10502.

Yanagisawa, Y. (1985). Parental strategy of the cichlid fish *Perissodus microlepis*, with particular reference to intraspecific brood “farming out.” *Environmental Biology of Fishes*, *12*, 241–249.

Zahavi, A. (1990). Arabian babblers: the quest for social status in a cooperative breeder. In P. B. Stacey & W. D. Koenig (Eds.), *Cooperative breeding in birds: long term studies of ecology and behaviour* (pp. 103–130). Cambridge, U.K.: Cambridge University Press.

Zapata, B., Correa, L., Soto-Gamboa, M., Latorre, E., González, B. A., & Ebensperger, L. A. (2010). Allosuckling allows growing offspring to compensate for insufficient maternal milk in farmed guanacos (*Lama guanicoe*). *Applied Animal Behaviour Science*, *122*, 119–126.

Zapata, B., Gaete, G., Correa, L. A., González, B. A., & Ebensperger, L. A. (2009). A case of allosuckling in wild guanacos (*Lama guanicoe*). *Journal of Ethology*, *27*, 295–297.

Zapata, B., González, B. A., & Ebensperger, L. A. (2009). Allonursing in captive guanacos, *Lama guanicoe*: milk theft or misdirected parental care? *Ethology*, *115*, 731–737.