Investigation of personality in subdominant male reindeer (*Rangifer tarandus*) and its relation to somatic cost and reproductive success

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ABSTRACT

Investigation of personality in subdominant male reindeer (*Rangifer tarandus*) and its relation to somatic cost and reproductive success

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Animal personalities are individual behavioural tendencies that are consistent across time and context. The presence of personality has yet to be assessed in reindeer (*Rangifer tarandus*), a species where subdominant males may attempt to gain access to females within a harem while risking physical confrontation with a dominant male. I investigated bold-shy personality in subdominant male reindeer based on individual subdominant male propensity to penetrate into a mating group and flight initiation distance. I also investigated how boldness related to somatic cost and reproductive success, respectively. Data was collected at the Kutuharju Reindeer Research Station in Kaamanen, Finland, where measures of personality were generated using field observation data based on the relative frequency of dominant male-subdominant male agonistic interactions over four years and subdominant male flight initiation distance measured over one year. Individual propensity to penetrate a mating group was not significantly repeatable and therefore not a personality trait, but instead decreased with subdominant male weight and group sex ratio, and was best described by a quadratic relationship with day of the mating season. There was no relationship between propensity and relative weight loss or reproductive success. Subject to no discernable fitness consequences related to propensity to penetrate a mating group, individuals do not adopt personalities and may instead base decisions on proximate factors. Flight initiation distance increased with starting distance and was negatively related to trial number.

Individual flight initiation distance was significantly repeatable and therefore indicated personality differences along the bold-shy axis.

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INTRODUCTION

Animal personality

Individual behavioural tendencies that are consistent across time and context are referred to as animal personality (Dingemanse et al. 2004). Personality traits are not dichotomous, but rather should be classified along a continuum; an individual phenotype is not expressed as either “bold” or “shy”, it lies between these two extremes and describes the individual’s degree of boldness (Réale et al. 2007). Animal personalities are commonly categorized on the basis of one of five axes: shyness-boldness, exploration-avoidance, activity, aggressiveness, and sociability (Réale et al. 2007). However, animal personality research is evolving as researchers broaden their scope of potential personality traits, expanding upon these main axes to consider a variety of prospective behaviours within the personality paradigm, specifically those of ecological relevance to the species (Koski 2014). Consistently correlated yet functionally different suites of behaviours are known as behavioural syndromes, where individual expression of a specific behavioural trait appears to be accompanied by the consistent expression of another behavioural trait (Sih et al. 2004).

Included in an integrative view of animal personality is the understanding that a given personality trait may be complemented by individual differences in plasticity in that trait, and effectively illustrated using behavioural reaction norms (Dingemanse et al. 2010). This implies that individual expression of a behavioural trait does not stay fixed relative to other individuals across contexts, but rather may vary, linearly or non-linearly, across an environmental gradient and still constitute personality and personality differences between individuals (Dingemanse et al. 2010). The mechanisms maintaining animal personality are yet to be clearly substantiated (Réale et al. 2010). From traditional theory homogenizing selection should work to erode individual behavioural differences within a population, yet distinct and consistent individual differences exist in a wide variety of behaviours. Researchers have proposed numerous potential processes by which such personality differences may be maintained, the most common being a state-dependent explanation (Réale et al. 2010) which posits that personality traits are linked to a state condition (i.e. body weight, reproductive value etc.), ultimately relating consistent differences in behaviour to differences in decision-making in order to maximize fitness based on an individual's current state (Dingemanse and Wolf 2010, Wolf and Weissing 2010). However, this assumes the perpetuation of consistent individual differences in state, and does not elucidate the mechanisms maintaining these state differences nor why they would be consistent across an environmental gradient (Dingemanse and Wolf 2010). Relatedly, personality differences have been linked to consistent differences in life history between individuals, with some researchers positing that personality differences are maintained due to trade-offs in associated life history characteristics. For example, Biro and Stamps (2008) elucidate the mechanisms by which personality differences could be maintained through differences in life history productivity, such as boldness, activity, and aggressiveness appear to be positively related to food intake, growth rate, and fecundity in numerous species.

Réale et al. (2007) recommend that studies of animal personality be performed in an experimental and controlled setting to avoid the inclusion of non-target behaviours. However, field-based studies of personality may generate a more applied understanding of the associations between personality and life history and fitness, by observing ecologically relevant behaviour in a more natural setting. Powell and Gartner (2011) attest that studies of personality based on recorded behavior in natural environments (i.e. natural with regard to habitat and social setting) may provide the most thorough and accurate examination of individual behavioural tendencies. Experimental tests may not be applicable to personality traits stemming from the interaction of two of more individuals, and the actual personality traits measured by an experimental behavioural test and how to interpret the behaviours displayed may be difficult to ascertain (Powell and Gartner 2011).

The term "boldness" represents an individual's propensity for risky behaviour including its affinity for exploration in a novel environment (Wilson et al.1994). There exists a considerably large body of research on a variety of taxa exploring individual variation along the boldness-shyness continuum, including fish (Biro et al. 2010, Brown et al. 2014), birds (Barnett et al. 2012, Patrick et al. 2013), reptiles (Carter et al. 2012, Bajer et al. 2015), amphibians (Brodin et al. 2013, González-Bernal et al. 2014), invertebrates (Tremmel and Müller 2012, Shearer and Pruitt 2014), and mammals (Michelena et al. 2009). Within the latter, numerous researchers have examined boldness and its association to life history and fitness in ungulates. In their study of fallow deer (*Dama dama*), Bergvall et al. (2011) observed that boldness was related to foraging decisions; boldness had a positive effect on the consumption of both novel food in non-novel situations and non-novel food in novel situations. In addition, Ciuti et al. (2012) concluded that harvested male elk (*Cervus elaphus*) were more likely to display risky behaviour during life than non-harvested elk, which were typically shyer. Réale et al. (2009) found that boldness was highly heritable in bighorn sheep rams (*Ovis canadensis*) and was positively related to survivorship, as well as having a strong positive effect on reproductive success later in life. In their comprehensive review of the fitness consequences of personality traits, Smith and Blumstein (2008) show that across multiple species in captivity, boldness is positively related to reproductive success.

Flight initiation distance

Researchers have also measured flight initiation distance to investigate how individuals behave in risky situations. Flight initiation distance is the distance between an individual animal and an approaching observer or other source of perceived risk upon which the animal chooses to flee, and is an indication of the animal's tolerance of risk (Ydenberg and Dill 1986). The distance between the observer and animal at the start of the approach is called the starting distance, and has been shown to influence flight initiation distance (Blumstein 2003). Flight initiation distance has been used as a tool to investigate boldness of individuals and groups of individuals in numerous taxa, including ungulates (reviewed by Stankowich 2008), as well as life history characteristics that are associated with such differences (Blumstein 2006). However, a relatively small amount of research has been dedicated to elucidating consistent individual differences in flight initiation distance applicable within the personality paradigm. As such, literature on the subject is divided; Carrete and Tella (2009) observed considerable individual consistency in flight initiation distance, while Runyan and Blumstein (2009) did not. Petelle et al. (2013) observed that repeatability of flight initiation distance, and therefore the emergence of personality, was linked to individual age class in that boldness was significantly repeatable only in the youngest individuals.

Alternative mating strategies and tactics

In some species males display discrete variation in mating behaviour based on the use of alternative mating strategies and tactics (Isvaran 2005). A mating strategy is a set of rules, genetically based, by which an organism allocates its reproductive effort, displaying one of numerous possible behavioural phenotypes called alternative tactics (Gross 1996). Numerous mechanisms have been proposed to explain the maintenance of such variation. Alternative strategies may be maintained by frequency-dependent selection whereby the average fitnesses of all potential mating strategies are assumed equal (Gross 1996). Additionally, it has been proposed that the existence of alternative tactics is maintained by condition-dependence (Andersson 1994), whereby the adoption of a specific mating tactic is dependent upon internal and external cues received by the individual and functions to maximize individual fitness (reviewed by Dominey 1984). Individual males, driven by internal cues based on phenotypic quality (e.g. body size), may choose to adopt different mating tactics. Consequently variation in mating tactics will exist so long as there exists variation in male quality in a population (Isvaran 2005).

Mating competition in ungulates

Polygynous mating systems often produce intense male-male competition for access to mates, with females acting as a limited resource (Darwin 1871, Trivers 1972). Variation in mating opportunity amongst males can be attributed to phenotypic variation within a population. Phenotypic variation includes variation in mating behaviour which, when consistent, may be responsible for consistent differences in mating success between individuals. The ability of male ungulates to attain mates is highly variable, and accordingly males may use alternative mating tactics in order to maximize their access to potential mates (Clutton-Brock and Parker 1992). A hierarchal system is typically established in ungulate species during the mating season (Gosling 1986, Miller et al. 1987), in which rank therein is closely related to age and phenotypic quality on the basis of body size, body weight, and the size and complexity of horns and antlers (Epsmark 1964, Rutberg 1986, Lott and Galland 1987). Mating opportunity is determined in part by social rank (Clutton-Brock 1982, Komers et al. 1997, Wolff 1998); the oldest and most dominant individuals are typically able to secure more copulations than those subordinate, creating an unequal distribution of mates and reproductive success amongst males (Squibb 1985, Hirotani 1994, Røed et al. 2002, Willisch et al. 2012).

Study species

Reindeer (*Rangifer tarandus*) are a highly polygynous ungulate where both males and females assume a stratified social system during the mating season in a period known as the "rut" (Reimers 1972). Dominant males drastically decrease time spent foraging and invest heavily in reproductive effort during the rut as part of a capital breeding strategy, unlike young male reindeer (Kojola 1991), who in the presence of intense male-male competition may invest more in time spent foraging to minimize mass loss during the mating season (Greenwood 1980).

Dominant males attempt to monopolize access to estrous females in a polygynous mating system based on female-defense, in which they try to maintain cohesion within temporary harems by herding and tending females whilst inhibiting subdominant male access to mates by chasing and displacing encroaching males (Epsmark 1964, Holand et al. 2013, Body et al. 2014). This dominant male tactic is usually the most successful and typically produces the greatest reproductive output (Hirotani 1994, Røed et al. 2002) given that females typically mate with only one male each season (Epsmark 1964). However, subdominant males do contribute reproductively (Røed et al. 2002, Røed et al. 2005) through the use of alternative tactics (Røed et al. 2002, Holand et al. 2013). Subdominant males may attempt to gain copulations either by waiting to attain dominance and control over part or all of a mating group, or through intermittent, transient attempts on estrous females within a group. Consistent differences in the propensity of subdominant males to attempt to gain transient access to sexually receptive females that are centralized within the mating group, while receiving agonistic pressure from the dominant male may reveal individual personality differences along the bold-shy continuum (Wilson et al. 1994). Subdominant male boldness-shyness may also be interpreted using measures of flight initiation distance to assess consistencies in risk tolerance and aversion between individuals (Petelle et al. 2013). Differences in subdominant male personality may translate into differences in mating effort and ultimately somatic costs and reproductive success during the mating season (Smith and Blumstein 2008, Biro and Stamps 2010)

Objectives

I am aware of no studies that examine personality in reindeer, nor variation in subdominant male mating behaviour in this species. Past research has incorporated measurements of flight initiation distance in reindeer, however an investigation of consistent differences in flight initiation distances amongst individuals is a novel approach for this species and is under-examined in antecedent studies of flight initiation distance as a whole (Stankowich 2008, Reimers et al. 2012). Moreover, this study aims to elucidate potential fitness consequences of animal personality by means of relating boldness to somatic cost and reproductive success, building upon previous literature in order to develop a more comprehensive understanding of the adaptive value of personality, its maintenance, and its evolutionary implications (Réale et al. 2010). Relatedly, there is a demand for studies relating boldness to reproductive success in free-ranging males (Smith and Blumstein 2008).

Using a semi-domesticated reindeer herd, the objectives of this study were to:

1) Develop methods to investigate individual boldness in subdominant male reindeer, based on relative individual propensity to encroach within a mating group using direct observation of subdominant males during the mating season, as well as measurements of subdominant male flight initiation distance.

2) Examine energetic costs related to differences along the boldness-shyness axis. Somatic costs of male mating behaviour have been previously examined in this population using relative changes in body weight throughout the mating season (Holand et al. 2006, Holand et al. 2013, Tennenhouse et al. 2011, Tennenhouse et al. 2012).

3) Investigate the relationship between boldness and reproductive success in subdominant male reindeer.

Predictions

I predicted that:

1) Based on field observation, subdominant male propensity to encroach upon a defended harem, as well as flight initiation distance, will be consistently different amongst individuals; boldness indices will be significantly repeatable and constitute personality differences between males.

2) Individuals that are bolder based on their propensity to penetrate into a mating group will incur greater somatic costs during the mating season. Such individuals would likely make use of energetically costly behaviour (i.e. being chased and displaced by a dominant male) at a higher frequency than shyer individuals, which will translate into differences in relative weight loss during the mating season.

3) Individuals that are bolder based on their propensity to penetrate into a mating group will have higher reproductive success while shyer males, occupying the periphery of the group, will have a lower chance of reproducing. In studies of domestic and captive populations, bolder individuals were associated with higher reproductive success than shyer individuals (Smith and Blumstein 2008).

METHODS

Study area and population

Data was collected at the Kutuharju Reindeer Research Station in Kaamanen, Finland using a semi-domesticated herd of approximately 100 reindeer during the 2009, 2010, 2013, and 2014 mating seasons. This herd is free ranging for most of the year and has been monitored during the rut since 1996. Reindeer were housed in one of two enclosures (Lauluvaara = 13.8 km^2, Sinioivi = 13.4 km^2) during the mating season allowing for manual division of the herd and manipulation of the age structure and sex ratio. All individuals were fitted with VHF radio collars and assigned specific number-color combinations on each collar for individual identification in the field.

Data collection

Mating groups were located each day using ground tracking by radio telemetry. Group composition (i.e. the identity of all males and females within the group, as well as the number of calves) was recorded upon arrival at a group, and following the addition or departure of individuals to or from the group. As described in previous studies on this herd (Body et al. 2014), mating group structure is highly dynamic and adult sex ratio (ASR; the ratio of sexually mature males to sexually mature females) is variable across relatively short time periods. Such variation in social and environmental context allows me to assess personality differences between individuals based on consistency of behaviour across a contextual gradient.

Subdominant male behaviour was recorded using the focal-animal technique (Altmann 1974). This consisted of 15 minutes of continuous observation, during which activity was classified into one of the following categories at the end of each 15 second interval: rest, stand, walk, eat, fight, chase male, chase female, chased by male, chased by female, herd, spar, displace male, displace female, displaced by male, displaced by female, court, follow, flehmen, attempt copulation, or successful copulation, along with the individual identity of all individuals involved in each interaction. Data collection formed part of a long-term study (since 1996) on this herd, and as such, all behaviours were recorded, including behaviours that were not used in this study. During the mating season, a dominant male will chase or displace a subdominant male when the subdominant male encroaches upon his harem or dashes into the group in an attempt to access females within the interior of the group, who may be farthest along in their estrous cycles and therefore more sexually receptive than those occupying the periphery (Ø. Holand pers. comm. 2013). The frequency in which a subdominant male is chased or displaced by a dominant male therefore can be used as a proxy for its propensity to risk transient attempts for access to potentially estrous females that are guarded by the dominant male. For each subdominant male, I combined the frequency in which they were chased or displaced by each dominant male in each group each day and used this sum as its risk frequency score.

I recorded flight initiation distances for all males during the 2014 mating season. To measure flight initiation distance I approached individual subdominant males from a position anterior to them that appeared to be within their line of sight and walked at a constant speed in a straight line towards each individual. My proximity to the focal individual at the moment of flight was recorded to the nearest centimeter using a measuring tape. Starting distance (the distance from the focal individual at which I began my approach), total trial order for each individual male, the order of trials in a group each day, date, and time were recorded for each trial. Between 5 and 17 trials were performed opportunistically on each subdominant male over a period of 23 days.

To estimate somatic costs, all males were weighed to the nearest kilogram before and after each mating season. Relative weight loss for each individual was calculated as body weight in kilograms at the start of the mating season minus body weight after the mating season divided by body weight in kilograms at the start of the mating season.

As per previous research on this herd, paternity of calves was inferred using blood samples obtained from all individuals and analyzed for 16 DNA microsatellite loci as part of an ongoing progeny testing within this experimental herd (Røed et al. 2002). Parenthood assignments were analyzed with the simulation program software CERVUS 3.0 (Kalinowski et al. 2007), which is based on likelihood ratios between candidate parents. Paternity of calves is resolved based on the mismatch of a minimum of two microsatellite loci for exclusion (Røed et al., 2002), used to determine the number calves sired by each subdominant male each year.

Statistical analyses

Variation in dominant male aggressiveness was likely to affect differences in the frequency in which subdominant males were chased or displaced in each group irrespective of subdominant male propensity to enter a mating group, and therefore was quantified and controlled for in order to accurately assess subdominant male boldness using this proxy behaviour. To assign each dominant male an aggressiveness score, I created a generalized linear mixed model (GLMM) using a negative binomial distribution (to account for overdispersion in the data) and a log link function with subdominant male risk frequency score as the response variable, plus observation length, year, ASR, age, day number (day of mating season beginning with first day of data collection each year), day number^2, and body weight as fixed effects, and dominant male identity as a random effect (N = 683). I extracted the Best Linear Unbiased Predictor (BLUP), or conditional mean, for the effect of dominant male identity on subdominant male risk frequency score controlling for all other explanatory variables in the model and assigned these values as the aggressiveness score for each dominant male. These values represent the individual tendencies of each dominant male to instigate a chase event irrespective of subdominant male identity. To assess consistency of risk-taking behaviour and the emergence of personality in subdominant males during the mating season, I constructed a GLMM using a negative binomial distribution (to account for overdispersion in the data) and a log link function, with risk frequency score as the response variable, plus observation length, year, ASR, age, day number, day number^2, body weight, and dominant male aggressiveness as fixed effects and subdominant male identity as a random effect (N = 683). The BLUP values for the effect of subdominant male identity on risk frequency were extracted, and assigned to each subdominant male as a boldness score to be used in subsequent analyses. Day number was included as a power term in both models to investigate any potential parabolic relationships between male activity and day of the mating season, based on previous evidence within this herd that male mating effort and competition is at a maximum mid-way through the mating season, following and preceding, respectfully, periods of lower activity (Holand et al. 2013). Observation time was included to control for variation in time spent observing each subdominant male. In all models body weight was scaled such that values were in hundreds of kilograms and day number values was scaled and centered in order to facilitate model conversion. All models were created and analyzed using SAS software v. 9.3 (SAS 2010) with a significance level of 0.05.

Using an information-theoretical approach (Burnham and Anderson 2002), I compared the Akaike's Information Criterion (AIC) values of linear models with and without subdominant identity as a random effect to assess if subdominant male identity contributed significant predictive power in explaining risk-taking behaviour, therefore potentially suggesting the presence of personality differences in this trait. If the difference in AIC values between the two models is less than or equal to 2 then the difference in predictive power between the two models, and therefore the effect of the inclusion or exclusion of the random effect term, is negligible (Burnham and Anderson 2004). I quantified the consistency of risk-taking behaviour by calculating the repeatability of the risk frequency score for subdominant males within and across years, where repeatability is calculated as $\frac{V_{ind}}{V_{ind}+V_e}$ (V_{ind} = between-individual variation, V_e = within-individual variation; Boake 1989). If the inclusion of the individual random effect significantly increases predictive power of the model and repeatability is relatively high, this indicates that this trait is considerably consistent within and distinct amongst subdominant males, indicating that it forms a personality trait for this species (Boon et al. 2007).

To assess the consistency of flight initiation distance in subdominant males I constructed a GLMM with flight initiation distance in meters as the response variable, plus age, body weight, starting distance, trial order for each individual male, and trial order in each group each day as fixed effects and subdominant male identity as a random effect (N = 109). Observation number was included to account for any habituation that may have occurred in subdominant male response to the observer as a perceived threat when performing flight initiation distance measurements, as unavoidably I spent time within the group and was perceived by other subdominant males whilst collecting this data. Similarly, trial number was included to account for any individual habituation that may have happened due to repeated measures using the same threat stimulus over an extended period of time. As with the previous model, I compared AIC values of linear models with and without subdominant identity as a random effect and calculated the repeatability of flight initiation distance across individuals to infer any distinction and consistency of flight initiation responses between and amongst subdominant males.

To investigate the relationship between boldness and somatic costs I constructed a GLMM using a Gaussian distribution with relative weight loss as the response variable, boldness (see previous model of risk frequency for calculation of this parameter), boldness^2, and age as fixed effects, and subdominant male identity as a random effect to account for repeated measures of individuals (N = 50). Relative weight loss was log-transformed to account for non-normality of data.

To investigate the relationship between boldness and reproductive success I constructed a GLMM using a negative binomial distribution (to account for overdispersion) and a log link function with number of calves sired each year as the response variable and boldness (see previous model of risk frequency for calculation of this parameter), boldness^2, and age as fixed effects. Subdominant male identity was included as a random effect to account for repeated measures of individuals (N = 40). Note that for the results of all models, mean estimates are reported with their standard deviations and parameter estimates with their standard errors.

RESULTS

In total there were 45 individual subdominant males included in this study (Table 1), with a total of 1150 chases over four years (Table 1) in 683 mating groups (Table 1). ASR of mating groups ranged from 0.1 to 2.0, with a mean ASR of 0.39 ± SD 0.17 (Table 1). Subdominant males had a mean age of 2.39 ± 1.23 years (Table 1) and a mean weight of 105.12 ± 21.92 kg (Table 1).

Including individual subdominant male identity as a random effect (AIC = 1879.2) did not significantly increase the predictive power of the model compared to when it was excluded (AIC=1877. 2; ΔAIC =2), therefore risk frequency score for individual subdominant males was not significantly repeatable (repeatability = 0.225) across years.

Risk frequency score significantly decreased with subdominant male weight (β = -1.95 ± 0.91, p = 0.046; Figure 1) and the group's ASR (β = -2.50 ± 0.43, p < 0.001), where the presence of more males relative to females (higher ASR) in the mating group resulted in individual subdominant males being chased less often (Figure 2). The effect of "day number" on risk frequency was quadratic (Figure 3), with risk frequency increasing initially (β = 0.10 ± 0.05, p = 0.048) and decreasing afterward (β = -0.01 ± 0.003, p < 0.001) in the latter part of the mating season. Expectedly, the number of chases increased with observation time (β = 0.22 ± 0.02, p <0.001) and dominant male aggressiveness (β =1.59 ± 0.22, p < 0.001). The age of subdominant males was not related to risk frequency (β = 0.11 ± 0.16, p = 0.487).

Flight initiation distance data was recorded for 8 subdominant males in the mating season of 2014. The number of trials per male varied from 5 to 17, for a total of 109 trials. Mean flight initiation distance was 12.54 ± 6.47 m, with mean starting distance of 29.52 ± 8.03 m. Mean age of subdominant males for all trials was 2.26 ± 1.24 years, with a mean weight of 108.61 ± 27.80 kg. Flight initiation distance was significantly repeatable (repeatability = 0.231) as subdominant ma le identity added significant predictive power when included as a random effect in the model (AIC = 647.0) compared to when it was excluded (AIC = 655.6; ΔAIC = 8.6).

Flight initiation distance increased with starting distance (β = 0.29 ± 0.07, $p < 0.001$; Figure 4), and decreased with the number of trials performed on each male (β = -9.78 ± 3.30, p = 0.004; Figure 5) as well as the order of trials in each group each day (β = -4.53 ± 1.40, p = 0.002; Figure 6), yielding smaller flight initiation distances with each trial.

Relative weight loss during the mating season for subdominant males ranged from -0.0588 kg to 0.314 kg, with a mean of 0.0935 ± 0.099 kg over all four years (2009: 0.111 ± 0.098 kg, 2010: 0.105 ± 0.094 kg, 2013: 0.129 ± 0.133 kg, and 2014: 0.008 ± 0.043 kg). There was no discernable relationship between relative weight loss and boldness (p = 0.653), although relative weight loss increased with subdominant male age (β = 0.005 ± 0.002, p = 0.018; Figure 7).

The number of calves sired by each subdominant male was calculated for 35 of the 45 subdominant males included in this study where blood samples were available, with some males siring calves in multiple years for a total sample size of N = 40. The number of calves sired by each male ranged from 0 to 15 across all years, with 17 of 40 (42.5%) cases resulting in males siring no calves. The mean number of calves sired was 2.18 ± 3.37 across all years (2009: 2.13 ± 4.15 calves, 2010: 2.15 ± 2.96 calves, and

2013:2.50 ± 2.38). Older subdominant males sired more calves ($\beta = 0.81 \pm 0.19$, $p < 0.001$; Figure 8), but there was no discernable relationship between the number of calves sired by a subdominant male and boldness ($p = 0.462$).

DISCUSSION

Assessment of personality

To my knowledge this is the first study examining personality and repeatability of behaviour in reindeer. My prediction, that individual propensity to penetrate into a mating group would be consistent enough to constitute a personality trait, was not supported as this behaviour was not significantly repeatable across years. The repeatability of this behaviour was slightly lower than average relative to other studies of behavioural repeatability (Bell et al. 2009). Rather the frequency of this behaviour, what I have deemed an indication of boldness in this species, appears to be best predicted by phenotypic and environmental factors and not individual identity. However, individual flight initiation distance was significantly repeatable and suggests the existence of personality differences along the boldness-shyness axis. In one of the few published examinations of individual consistency in flight initiation distance, Carrete and Tella (2009) yielded similar results with burrowing owls (*Athene cunicularia*) in which individuals varied consistently in flight initiation distance, albeit at considerably higher repeatabilities than in this study. My results therefore present a discord in elucidating subdominant male personality; one measure represents bold and shy behaviour as distinct between and consistent within individuals, while the other does not.

Boldness as related to encroachment in a mating group

Risk frequency score decreased as mating group ASR increased (Figure 2), thus the addition of subdominant males in a mating group resulted in each male making less transient attempts into the group for access to females. However, previous researchers have shown that individual male reproductive effort, including the number of mating attempts, increases with the number of males in a group (Evans et al. 2003). Resource defense theory suggests that competition and aggression between males should increase as the operational sex ratio (OSR; the ratio of sexually active males to fertilizable females) increases but only up until a certain point, in which male-male aggression peaks before decreasing in groups with many males compared to females as male-male aggression becomes too costly to maintain (Brown 1964, Clutton-Brock et al. 2008). In a previous study on this herd, Tennenhouse et al. (2011) found that mature dominant males increased the frequency of agonistic interaction with subdominant males as the number of females in the group increased (and thus ASR decreased), a trend that complies with the results of my study. In groups with higher ASR (thus fewer females relative to males), dominant males appear to chase and displace encroaching subdominant males less frequently than in groups with a lower ASR. This may also be evidence for the "dilution effect" on harassment, where the presence of more individuals requires the dominant male to partition harassment between more recipients, necessitating fewer agonistic interactions for each individual (Clutton-Brock et al. 1992).

In this study, lighter males encroached upon a defended mating group more frequently than heavier subdominant males, subjecting themselves to more agonistic pressure from the dominant male (Figure 1). Previous research on this herd has shown that male reindeer of different ages and weights may show discretely different mating behaviour (Tennenhouse et al. 2012). Lighter, subdominant males have been shown to use mating tactics specialized towards "sneaky" copulations (Røed et al. 2002) in which they maintain subdominant rank and attempt to gain copulations while appearing to try and remain inconspicuous within the group. Higher-ranking males of higher phenotypic quality may be more likely to confront and overtake the dominant male, and may experience more receptiveness from females. Therefore, heavier males may invest more in attaining dominance over a group and thus access to a harem of females and less in transient attempts upon females that are guarded by a dominant male (Holand et al. 2013). As such, lighter males may need to rely more heavily on “sneaky” copulations, and therefore resort to brief transient attempts on females within a defended harem, ultimately presenting themselves as bolder.

Mating season in this herd generally occurs between mid-September and late October, lasting approximately 3 weeks (Tennenhouse et al. 2012). In this study, the number of transient attempts on females by subdominant males was at a maximum about one week into a three-week observational period (Figure 3). Male-male competition, including dominant male intolerance for subdominant males, and mating activity in this herd have been shown to be at a maximum in a period known as “peak rut”, which may coincide roughly with this point (Holand et al. 2013, Body et al. 2014). It is in this period when females are generally later in their estrus cycle and most sexually receptive (Kojola 1986), and as such males likely increase mating effort to maximize their chances of fertilization.

Boldness as related to flight initiation distance

Flight initiation distance decreased with both the number of previous trials on an individual in a season (Figure 5) and the number of previous trials in a group in a single day (Figure 6), indicating habituation in subdominant male flight initiation response with repeated exposure. The prevalence and effects of habituation in previous studies of flight initiation distance in ungulates is inconsistent; in some studies flight initiation distance shortened with repeated exposure to human observers, while others showed an increased flight initiation distance with repeated exposure and others showed no effect of human exposure on flight initiation distance (reviewed by Stankowich 2008). Additionally trials with larger starting distances yielded larger flight initiation distances (Figure 4), a pattern mirrored in previous literature (e.g. Blumstein 2003). As such, this emphasizes the need to account for habituation and starting distance, either manually or by statistical inclusion of appropriate covariates, to maximize the accuracy and reliability of flight initiation distance analyses.

Flight initiation distance was strongly positively correlated with boldness as measured by propensity to penetrate a harem (r= 0.757), such that individuals that were more likely to risk transient attempts on females (and therefore bolder based on this measure) chose to flee earlier when confronted by a human observer (shyer based on this measure). This apparent contradiction may be explained by an increased exposure to risk from the dominant male; subdominant males that are more willing to penetrate a harem may need to be more vigilant and sensitive to an approaching threat, such as a dominant male, in order to ensure their safety and avoid physical harm whilst attempting transient copulations on guarded females. These males may therefore be more reactionary to potential threats such as a human observer, proactively avoiding potential harm by maintaining larger flight initiation distances.

Somatic cost and boldness

Boldness did not explain variation in subdominant male relative weight loss during the mating season. Kojola (1991) indicated that young males who are heavier at the beginning of the mating season display greater relative weight loss than males that are lighter, and that time spent eating is inversely related to male initial weight. To complement this, my results reveal that boldness decreases as subdominant male weight increases (Figure 1). In consequence, lighter bolder subdominant males may also be eating more than heavier, shyer males (Kojola 1991), compensating for potential costs related to being more bold and ultimately masking any discernable relationship between boldness and somatic cost using relative weight loss during the mating season. Akin to findings by Kojola (1991), my results indicate that older subdominant males experienced greater relative weight loss than younger subdominant males (Figure 8). In the presence of intense male-male competition, as exists in reindeer mating systems, young males may compensate for lower phenotypic quality by investing more in somatic growth to maximize competitive ability, compared to older males that would possess greater energy reserves and be able to invest more in reproduction, ultimately incurring greater somatic costs (Greenwood 1980). Older, prime-aged male reindeer typically lose more weight than younger males during the mating season (Mysterud et al. 2003), a pattern also evident in red deer (Mysterud et al. 2008) and other ungulate species (reviewed by Mysterud et al. 2004).

Reproductive success and boldness

Reproductive success based on the number of calves sired was not related to boldness in subdominant male reindeer. Réale et al. (2009) have presented contrary results in another ungulate species, bighorn sheep, where bolder males sired more calves, albeit this relationship being stronger for older rams compared to younger rams. Boldness appears to be positively related to reproductive success in other taxa as well (e.g. zebrafish, *Danio rerio*; Ariyomo and Watt 2012) and in some species there is even evidence of female choice for bolder males compared to shyer ones (e.g. guppy, *Poecilia reticulata*; Godin and Dugatkin 1996). In this study, 27 of 39 (69.2%) subdominant males sired only one calf or less. Therefore there may be insufficient variation in reproductive success to reveal any causal relationship between boldness and success in this herd. What variation there was in reproductive success was explained in part by subdominant male age; older males sired more calves than younger males (Figure 9). Reproductive success has been found to increase with age in most iteroparous species (Pärt 1995), including reindeer (Røed et al. 2005).

Conclusion and future research

Subdominant male reindeer propensity to penetrate into a guarded mating group does not manifest itself as a personality trait in this species, and the modest variation that exists in such tendencies is not related to fitness differences in the form of somatic cost and reproductive success. Variation in this propensity appears to be better explained by male weight as well as social and temporal factors. Without any discernable fitness consequences, a lack of selection pressure on individual propensity to risk confrontation with a dominant male could explain why individuals do not display an affinity towards any consistency in transient attempts upon guarded females, but instead may base such decisions on proximate factors. Individual consistency in flight initiation distance however does manifest personality in this species. Consistent differences in individual susceptibility to human disturbance may arise from differences in exposure to and experience with human handlers as part of reindeer husbandry efforts using this herd. As such, individuals may differ in both perceived risk and reaction to such a disturbance when confronted by a human observer. Personality differences may have consequences for the ability and efficiency of reindeer herders in handling these individuals, and should be considered in husbandry efforts.

Future research should examine personality in this species in a more controlled setting, using a similar framework as previous animal personality research based on experiment set-ups implemented to reduce environmental variance (Both et al. 2005, Réale et al. 2007). Greater environmental variance in a relatively uncontrolled field setting may contribute to greater inter-individual variation in behaviour, masking personality differences that may otherwise present themselves if personality were examined in a more controlled and concise way. Such an experiment may be made more feasible if researchers examined personality based on a behaviour or a combination of behaviours involving only the focal individual (for example see Réale et al. 2009), as opposed to incorporating as markers of personality behaviours that require two or more individuals, as was implemented in this study. Relatedly, future research on this species should aim to disentangle any relationships between personality and relevant components of this species' ecology if they exist, including but not limited to life history and reproductive success as examined in this study. Expanding our knowledge of male reindeer rutting behaviour and reproductive success can benefit our understanding of reindeer population dynamics (Mysterud et al., 2003). As such, future research of this kind may have economic implications for reindeer husbandry in northern Europe and elsewhere. Powell and Gartner (2011) suggest that husbandry programs should consider the structure and compatibility of personalities within domestic populations. Insight from this study pertaining to the reproductive potential of certain personality types in male reindeer may be used to organize the composition of mating groups in ways that will maximize reproduction; and therefore economic output for reindeer herders.

REFERENCES

Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour*, *49*, 227–267.

Andersson, M. B. (1994). *Sexual Selection*. Princeton University Press.

Ariyomo, T. O., & Watt, P. J. (2012). The effect of variation in boldness and aggressiveness on the reproductive success of zebrafish. *Animal Behaviour*, *83*, 41–46. doi:10.1016/j.anbehav.2011.10.004

Bajer, K., Horváth, G., Molnár, O., Tötök, J., Garamszegi, L. Z., & Herczeg, G. (2015). European green lizard (Lacerta viridis) personalities: linking behavioural types to ecologically relevant traits at different ontogenetic stages. *Behavioural Processes*, *111*, 67-74.

Barnett, C. A., Thompson, C. F., & Sakaluk, S. K. (2012). Aggressiveness, boldness and parental food provisioning in male house wrens (Troglodytes aedon). *Ethology*, *118*, 984–993. doi: 10.1111/j.1439-0310.2012.02092.x

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, *77*, 771–783. doi:10.1016/j.anbehav.2008.12.022

Bergvall, U. A., Schäpers, A., Kjellander, P., & Weiss, A. (2011). Personality and foraging decisions in fallow deer, Dama dama. *Animal Behaviour*, *81*, 101–112. doi:10.1016/j.anbehav.2010.09.018

Biro, P. A., Beckmann, C., & Stamps, J. A. (2009). Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 71-77. doi: 10.1098/rspb.2009.1346.

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, *23*, 361–368. doi:10.1016/j.tree.2008.04.003

Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology and Evolution*, *25*, 653–659. doi:10.1016/j.tree.2010.08.003

Blumstein, D. T. (2003). Flight initiation distance in birds is dependent on intruder starting distance. *Journal of Wildlife Management*, *67,* 852-857.

Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*, *71*, 389-399.

Boake, C. R. B. (1989). Repeatability : its role in evolutionary studies of mating behavior. *Evolutionary Ecology*, *3*, 173–182.

Body, G., Weladji, R. B., Holand, Ø., & Nieminen, M. (2014). Highly competitive reindeer males control female behavior during the rut. *PLoS ONE*, *9*, 1–9. doi:10.1371/journal.pone.0095618

Boon, A. K., Réale, D., & Boutin, S. (2007). The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters*, *10*, 1094–1104. doi:10.1111/j.1461-0248.2007.01106.x

Both, C., Dingemanse, N. J., Drent, P. J., & Tinbergen, J. M. (2005). Pairs of extreme avian personalities have highest reproductive success. *Journal of Animal Ecology*, *74*, 667–674. doi:10.1111/j.1365-2656.2005.00962.x

Brodin, T., Lind, M. I., Wiberg, M. L., & Johansson, F. (2013). Personality trait differences between mainland and island populations in the common frog (Rana temporaria). *Behavioural Ecology and Sociobiology*, *67*, 135-143.

Brown, G. E., Elvidge, C. K., Ramnarine, I., Chivers, D. P., & Ferrari, M. C. O. (2014). Personality and the response to predation risk: effects of information quantity and quality. *Animal Cognition, 17*, 1063-1069. doi: 10.1007/s10071-014-0738-z.

Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *The Wilson Bulletin, 76*, 160-169.

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

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*, 261–304. doi:10.1177/0049124104268644

Carrete, M., & Tella, J. L. (2009). Individual consistency in flight initiation distances in burrowing owls : a new hypothesis on disturbance-induced habitat selection. *Biology Letters*, *6*, 167-170.

Carter, A. J., Heinsohn, R., Goldizen, A. W., & Biro, P. A. (2012). Boldness, trappability and sampling bias in wild lizards. *Animal Behaviour*, *83*, 1051-1058.

Ciuti, S., Muhly, T. B., Paton, D. G., McDevitt, A. D., Musiani, M., & Boyce, M. S. (2012). Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 4407–4416. doi:10.1098/rspb.2012.1483

Clutton-Brock, T. H., & Guinness, F. E. (1982). *Red Deer: Behavior and Ecology of Two Sexes* (Vol. 1982). University of Chicago Press.

Clutton-Brock, T. H., Hodge, S. J., & Flower, T. P. (2008). Group size and the suppression of subordinate reproduction in Kalahari meerkats. *Animal Behaviour*, *76,* 689-700.

Clutton-Brock, T. H., & Parker, G. A. (1992). Potential reproductive rates and the operation of sexual selection. *The Quarterly Review of Biology*, *67*, 437–456.

Clutton-Brock, T. H., Price, O. F., & Maccoll, A. D. C. (1992). Mate retention, harassment, and the evolution of ungulate leks. *Behavioural Ecology*, *3*, 234-242.

Darwin, C. R. (1871). *The descent of man, and selection in relation to sex*. London: John Murray. Volume 1. 1st edition.

Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society B: Biological Sciences*, *271*, 847–852. doi:10.1098/rspb.2004.2680

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*, *25*, 81–89. doi:10.1016/j.tree.2009.07.013

Dingemanse, N. J., & Wolf, M. (2010). Recent models for adaptive personality differences: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 3947–3958. doi:10.1098/rstb.2010.0221

Dominey, W. J. (1984). Alternative mating tactics and evolutionarily stable strategies. *American Zoologist*, *24*, 385–396. doi:10.1093/icb/24.2.385

Espmark, Y. (1964). Rutting behaviour in reindeer (Rangifer tarandus L.). *Animal Behaviour*, *12*, 159–160.

Espmark, Y. (1964). Studies in dominance-subordination relationship in a group of semi-domestic reindeer (Rangifer tarandus L.). *Animal Behaviour*, *12*, 420–426.

Evans, J. P., Pierotti, M., & Pilastro, A. (2003). Male mating behaviour and ejaculate expenditure under sperm competition risk in the eastern mosquitofish. *Behavioural Ecology*, *14*, 268-273.

Godin, J-G. J., & Dugatkin, L. A. (1996). Female mating preference for bold males in the guppy, Poecilia reticulata. *Proceedings of the National Academy of Sciences of the United States of America, 93*, 10262-10267.

González-Bernal, E., Brown, G. P., & Shine, R. (2014). Invasive cane toads: social facilitation depends upon an individual's personality. *PLoS ONE*, *9*, e102880. doi:10.1371/journal.pone.0102880

Gosling, L. M. (1986). The evolution of mating strategies in male antelopes. In D. I. Rubenstein & R. W. Wrangham (Eds.), *Ecological Aspects of Social Evolution* (pp. 244–281). Princeton, NJ: Princeton University Press.

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

Gross, M. R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology & Evolution*, *11*, 92–98. doi:10.1016/0169-5347(96)81050-0

Hirotani, A. (1994). Dominance rank, copulatory behaviour and estimated reproductive success in male reindeer. *Animal Behaviour*, *48*, 929–936. doi:10.1006/anbe.1994.1318

Holand, Ø., L'Italien, L., Weladji, R. B., Djaković, N., Røed, K., Hovland, A. L., & Nieminen, M. (2013). Shit happens - a glimpse into males' mating tactics in a polygynous ungulate - the reindeer. *Rangifer*, *32*, 65–72. doi:10.7557/2.32.1.2378

Holand, Ø., Weladji, R. B., Røed, K. H., Gjøstein, H., Kumpula, J., Gaillard, J.-M., Smith, M. E., & Nieminen, M. (2006). Male age structure influences females' mass change during rut in a polygynous ungulate: the reindeer (Rangifer tarandus). *Behavioral Ecology and Sociobiology*, *59*, 682–688.

Isvaran, K. (2005). Variation in male mating behaviour within ungulate populations: patterns and processes. *Current Science*, *89*, 1192–1199.

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.

Kojola, I. (1986). Rutting behaviour in an enclosured group of wild forest reindeer (Rangifer tarandus fennicus Lönnb.). *Rangifer*, *6*, 173–179. doi:10.7557/2.6.2.643

Kojola, I. (1991). Influence of age on the reproductive effort of male reindeer. *Journal of Mammalogy*, *72*, 208–210. doi:10.2307/1382001

Komers, P. E., Pélabon, C., & Stenström, D. (1997). Age at first reproduction in male fallow deer: age-specific versus dominance-specific behaviors. *Behavioral Ecology*, *8*, 456–462. doi:10.1093/beheco/8.4.456

Koski, S. E. (2014). Broader horizons for animal personality research. *Frontiers in Ecology and Evolution*, *2*, 1-6. doi:10.3389/fevo.2014.00070

Lott, D. F., & Galland, J. C. (1987). Body mass as a factor influencing dominance status in American bison cows. *Journal of Mammalogy*, *68*, 683-685.

Michelena, P., Sibbald, A. M., Erhard, H. W., & McLeod, J. E. (2009). Effects of group size and personality on social foraging: the distribution of sheep across patches. *Behavioural Ecology*, *20*, 145-152.

Miller, K. V., Marchinton, R. L., & Forand, K. J. (1987). Dominance, testerone levels, and scraping activity in a captive herd of white-tailed deer. *Journal of Mammalogy*, *68*, 812–817.

Mysterud, A., Bonenfant, C., Loe, L., Langvatn, R., Yoccoz, N., & Stenseth, N. (2008). Age-specific feeding cessation in male red deer during rut. *Journal of Zoology*, *275*, 407–412. doi:10.1111/j.1469-7998.2008.00453.x

Mysterud, A., Holand, Ø., Røed, K. H., Gjøstein, H., Kumpula, J., & Nieminen, M. (2003). Effects of age, density and sex ratio on reproductive effort in male reindeer (Rangifer tarandus). *Journal of Zoology*, *261*(4), 341–344. doi:10.1017/S0952836903004114

Mysterud, A., Langvatn, R., & Stenseth, N. C. (2004). Patterns of reproductive effort in male ungulates. *Journal of Zoology*, *264*, 209–215. doi:10.1017/S0952836904005618

Pärt, T. (1995). Does breeding experience explain increased reproductive success with age? An experiment. *Proceedings of the Royal Society B: Biological Sciences*, *260*, 113-117.

Patrick, S. C., Charmantier, A., & Weimerskirch, H. (2013). Differences in boldness are repeatable and heritable in a long-lived marine predator. *Ecology and Evolution*, *3*, 4291-4299.

Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. a, & Blumstein, D. T. (2013). Development of boldness and docility in yellow-bellied marmots. *Animal Behaviour*, *86*, 1147–1154. doi:10.1016/j.anbehav.2013.09.016

Powell, D. M., & Gartner, M. C. (2011). Applications of personality to the management and conservation of Nonhuman animals. In M. Inoue-Murayama, S. Kawamura, & A. Weiss (Eds.), *From Genes to Animal Behaviour* (pp. 185–199). Tokyo: Springer Japan. doi:10.1007/978-4-431-53892-9

Réale, D., Dingemanse, N. J., Kazem, A. J. N., & Wright, J. (2010). Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*, 3937–3946. doi:10.1098/rstb.2010.0222

Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology*, *22*, 1599–1607. doi:10.1111/j.1420-9101.2009.01781.x

Réale, D., Reader, S. M., Sol, D., MacDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*, 291–318.

Reimers, E. (1972). Growth in domestic and wild reindeer in Norway. *Journal of Wildlife Management*, *36*, 612-661.

Reimers, E., Røed, K. H., & Colman, J. E. (2012). Persistence of vigilance and flight response behaviour in wild reindeer with varying domestic ancestry. *Journal of Evolutionary Biology*, *25*, 1543–1554. doi:10.1111/j.1420-9101.2012.02538.x

Røed, K. H., Holand, Ø., Gjøstein, H., & Hansen, H. (2005). Variation in male reproductive success in a wild population of reindeer. *Journal of Wildlife Management*, *69*, 1163–1170. doi:10.2193/0022-541X(2005)069[1163:VIMRSI]2.0.CO;2

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. doi:10.1046/j.1365-294X.2002.01509.x

Runyan, A. M., & Blumstein, D. T. (2009). Do individual differences influence flight initiation distance? *Journal of Wildlife Management*, *68*, 1124–1129.

Rutberg, A. T. (1986). Dominance and its fitness consequences in American bison cows. *Behaviour, 96*, 62-91.

SAS. (2010). The SAS system for Windows, version 9.3. SAS Institute Inc., Cary, North Carolina, USA.

Shearer, T. A., & Pruitt, J. N. (2014). Individual differences in boldness positively correlate with heart rate in orb-weaving spiders of genus Larinioides. *Current Zoology*, *60*, 387-391.

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioural syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution*, *19*, 372-378.

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, *19*, 448–455. doi:10.1093/beheco/arm144

Squibb, R. C. (1985). Mating success of yearling and older bull elk. *The Journal of Wildlife Management*, *49*, 744–750.

Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation*, *141*, 2159–2173. doi:10.1016/j.biocon.2008.06.026

Tennenhouse, E. M., Weladji, R. B., Holand, Ø., & Nieminen, M. (2012). Timing of reproductive effort differs between young and old dominant male reindeer. *Annales Zoologici Fennici*, *49*, 152–160. doi:10.5735/086.049.0303

Tennenhouse, E. M., Weladji, R. B., Holand, Ø., Røed, K. H., & Nieminen, M. (2011). Mating group composition influences somatic costs and activity in rutting dominant male reindeer (Rangifer tarandus). *Behavioral Ecology and Sociobiology*, *65*, 287–295. doi:10.1007/s00265-010-1043-8

Tremmel, M., & Müller, C. (2013). Insect personality depends on environmental conditions. *Behavioural Ecology*, *24*, 386-392.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual Selection and the Descent of Man*. Chicago, IL: Aldine.

Willisch, C. S., Biebach, I., Koller, U., Bucher, T., Marreros, N., Ryser-Degiorgis, M.-P., Keller, L. F., & Neuhaus, P. (2012). Male reproductive pattern in a polygynous ungulate with a slow life-history: the role of age, social status and alternative mating tactics. *Evolutionary Ecology*, *26*, 187–206. doi:10.1007/s10682-011-9486-6

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, *9*, 442–446.

Wolf, M. & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*, 3959–3968.

Wolff, J. O. (1998). Breeding strategies, mate choice, and reproductive success in American bison. *Oikos*, *83*, 529–544.

Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behaviour*, *16*, 229-249.

TABLES

Table 1: Composition and characteristics of subdominant males and mating groups over four years. ASR = Adult sex ratio.

Year	**Subdominant males (*n*)**	**Number of males by age**						**Average male weight (kg ± SD)**	**Average male age (years ± SD)**	**Total times chased by dom. male (*n*)**	**Mating groups (*n*)**	**Average ASR ± SD**
		1	**2**	**3**	**4**	**5**	**6**					
2009	17	3	3	4	4	2	1	110.10±21.37	2.60±1.30	203	300	0.39±0.17
2010	21	4	6	4	5	1	1	104.21±21.34	2.41±1.17	302	275	0.41±0.12
2013	6	1	2	2	0	1	0	97.45±16.67	1.91±0.83	309	47	0.30±0.27
2014	8	3	2	2	0	1	0	90.66±22.48	1.61±0.94	336	61	0.41±0.22
Total	45[1]	11	13	12	9	5	2	105.12±21.92	2.39±1.23	1150	683	0.39±0.17

[1] Total number of subdominant males over all four years of data does not equal the sum of subdominant males in each year as some males were present in multiple years.

Table 2: Parameter estimates ± standard errors with corresponding t-values and p-values for a generalized linear mixed model of subdominant male risk frequency score (frequency of being chased or displaced by dominant male in each group each day) with subdominant male identity as random effect. All years are in comparison to 2014. Weight parameter is scaled to units of kilograms × 100. Bold p-values indicate statistical significance ($\alpha = 0.05$).

Parameter	**Estimate ± SE**	**t- value**	**p-value**
Year (2009)	-1.136±0.318	-3.58	**0.002**
Year (2010)	-0.607±0.315	-1.93	0.071
Year (2013)	0.030±0.351	0.08	0.933
Observation	0.223±0.016	13.60	**<0.001**
Age	0.113±0.159	0.71	0.487
Day number	0.101±0.051	1.98	**0.049**
Day number^2	-0.010±0.003	-3.38	**0.008**
Avg. sex ratio	-2.50±0.426	-5.86	**<0.001**
Weight	-1.95±0.906	-2.15	**0.046**
Dom. Ag. score	1.59±0.218	7.28	**<0.001**

Table 3: Parameter estimates ± standard errors with corresponding t-values and p-values for a generalized linear mixed model of subdominant male flight initiation distance in meters with subdominant male identity as random effect. Weight parameter is scaled to units of kilograms × 100. Trial1 parameter is the trial number of flight initiation trials per group per day. Trial2 parameter is the trial number of flight initiation trials per subdominant male for the entire season. Bold p-values indicate statistical significance (α = 0.05).

Parameter	**Estimate ± SE**	**t- value**	**p-value**
Weight	8.04±3.49	2.31	0.057
Starting distance	0.287±0.067	4.28	**<0.001**
Trial1	-4.538±1.397	-3.25	**0.002**
Trial2	-9.784±3.303	-2.96	**0.004**

FIGURES

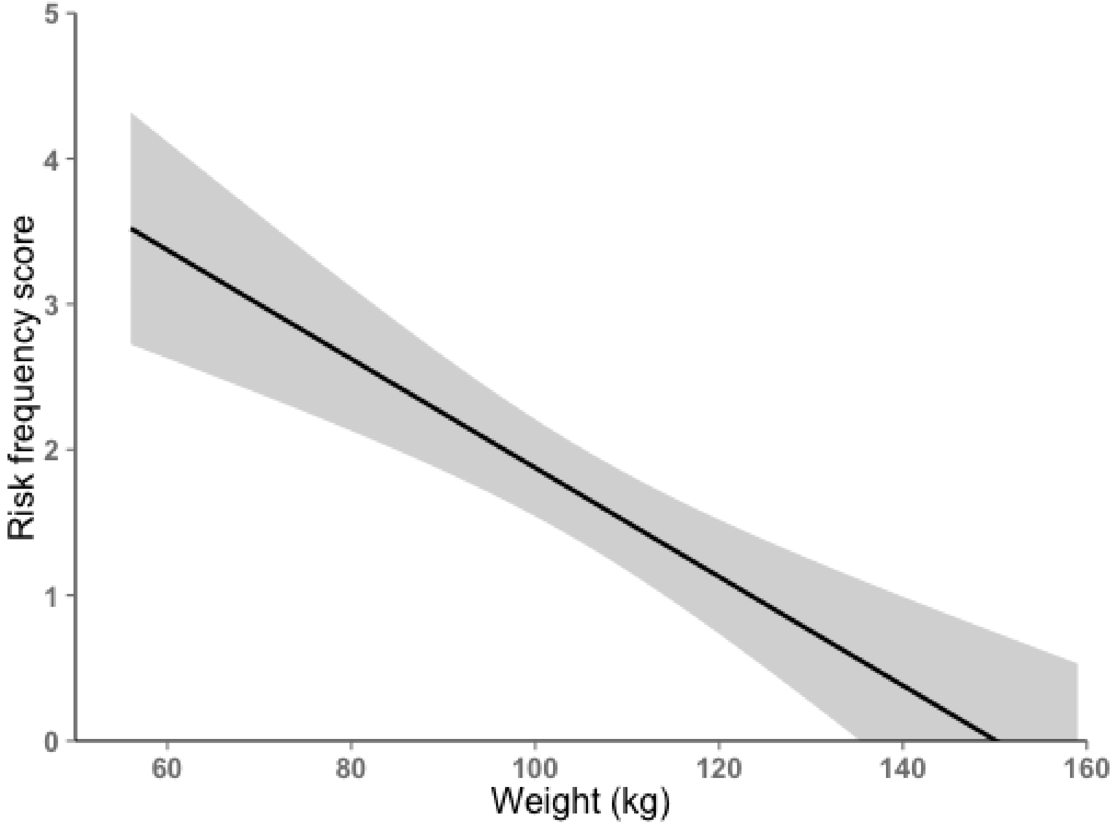

Figure 1: Risk frequency as measured by propensity to penetrate into a mating group in relation to subdominant male weight in kilograms. The black line represents the model predictions and the grey area represents the 95% confidence interval.

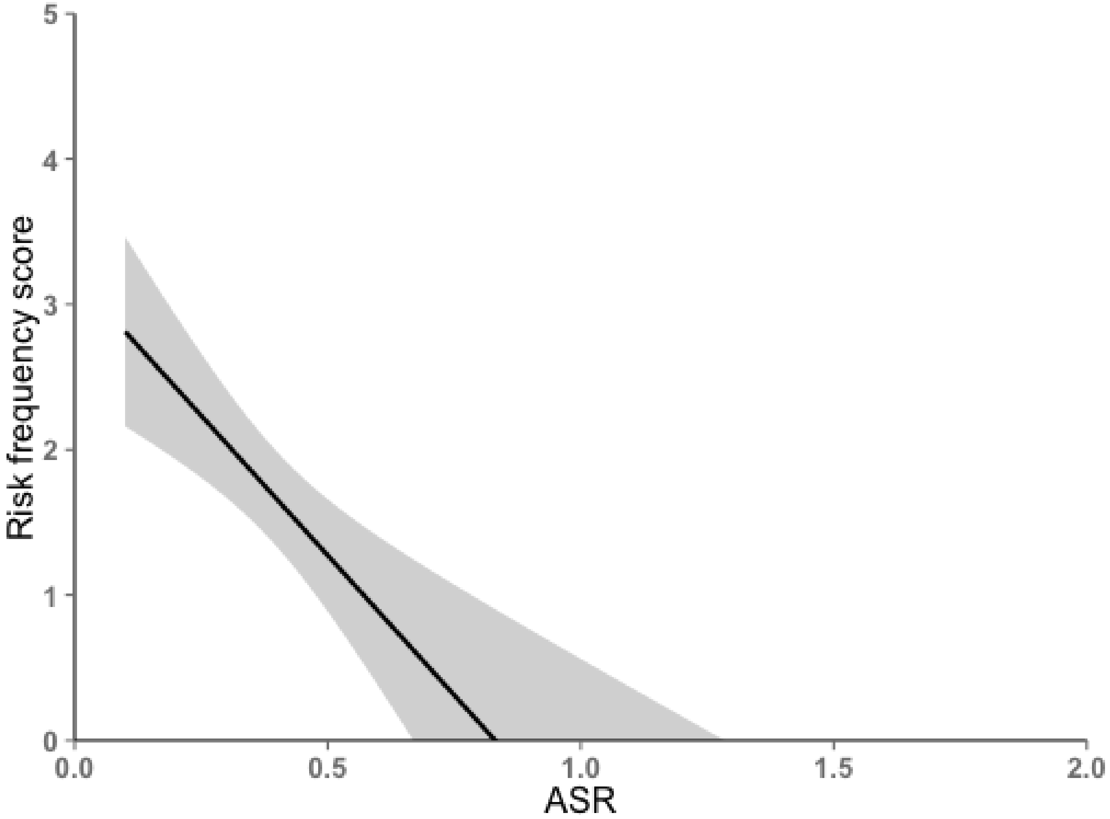

Figure 2: Risk frequency as measured by propensity to penetrate into a mating group in relation to the adult ratio of males to females (ASR) in the mating group. The black line represents the model predictions and the grey area represents the 95% confidence interval.

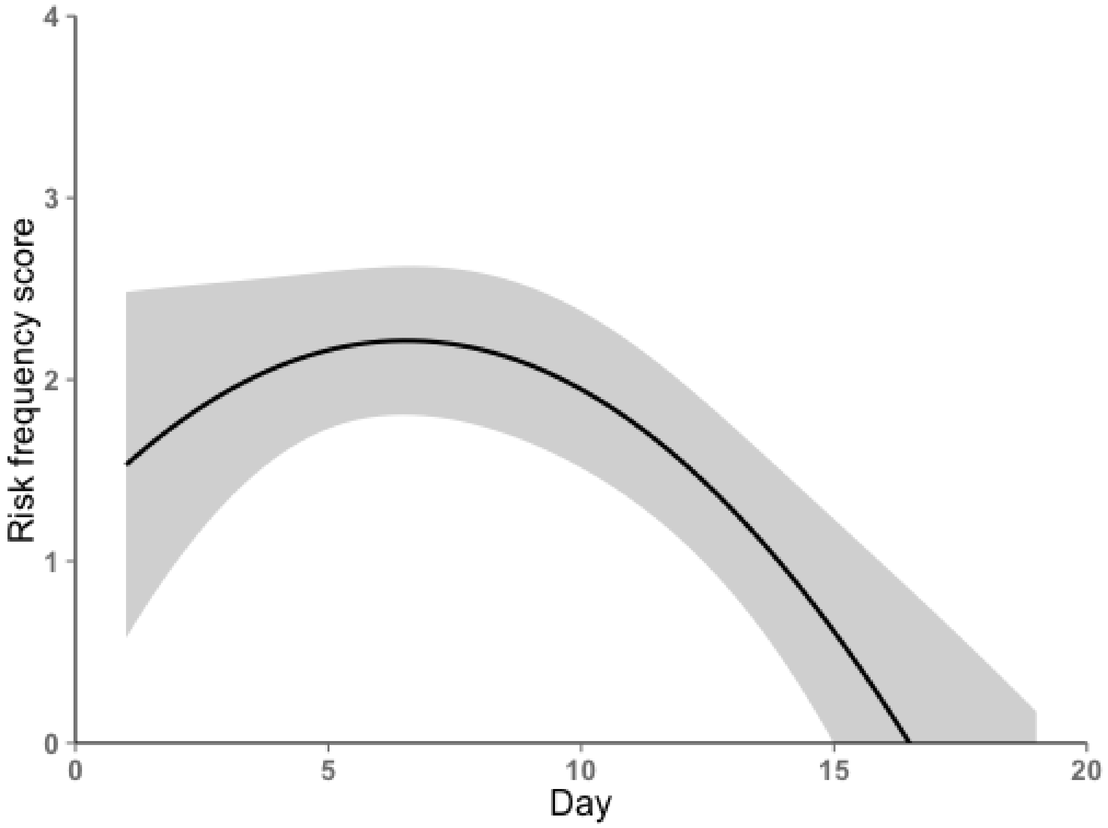

Figure 3: Risk frequency as measured by propensity to penetrate into a mating group in relation to day of mating season since start of data collection each year. The black line represents the model predictions and the grey area represents the 95% confidence interval.

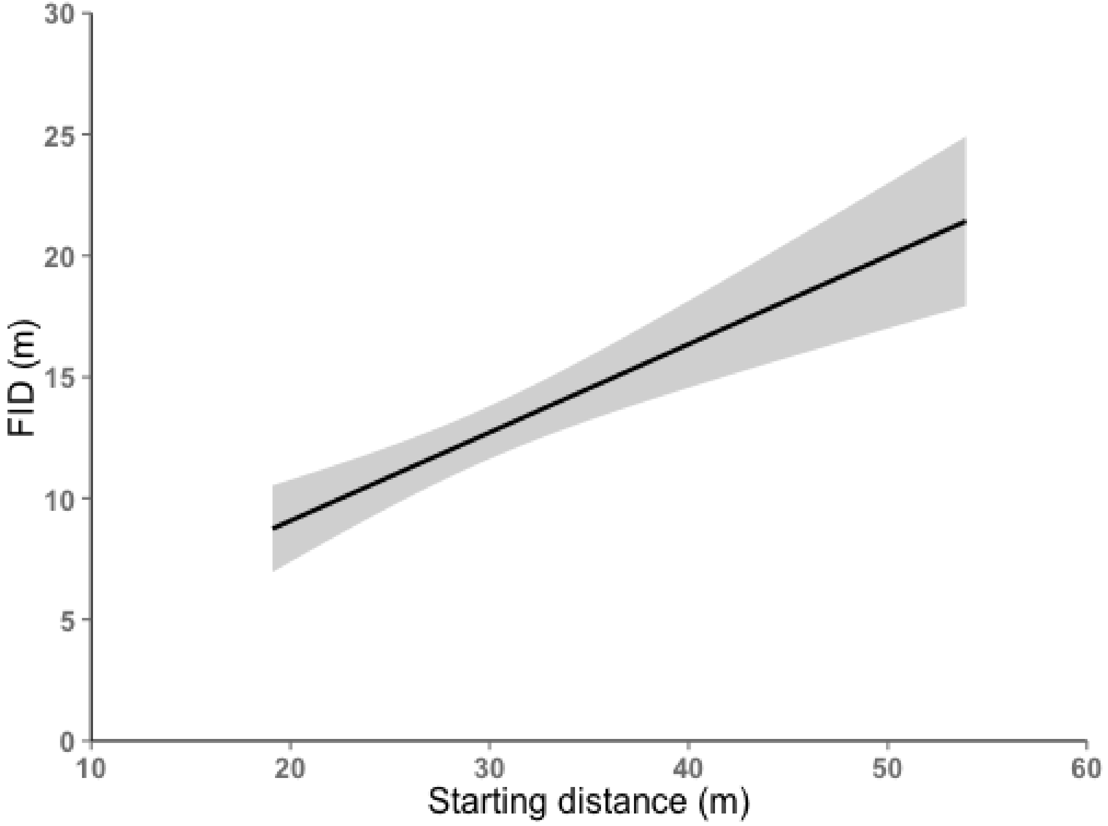

Figure 4: Flight initiation distance (FID) in meters in relation to starting distance in meters of each trial. The black line represents the model predictions and the grey area represents the 95% confidence interval.

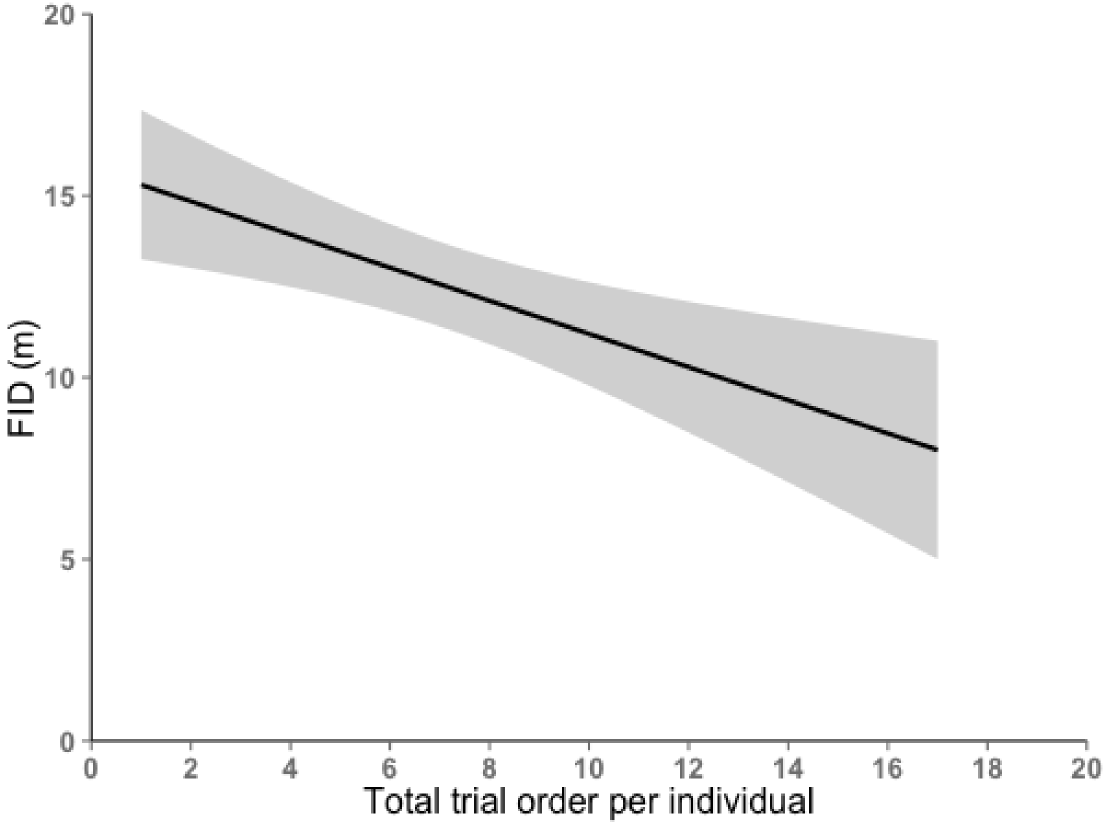

Figure 5: Flight initiation distance (FID) in meters in relation to total trial order for each subdominant male. The black line represents the model predictions and the grey area represents the 95% confidence interval.

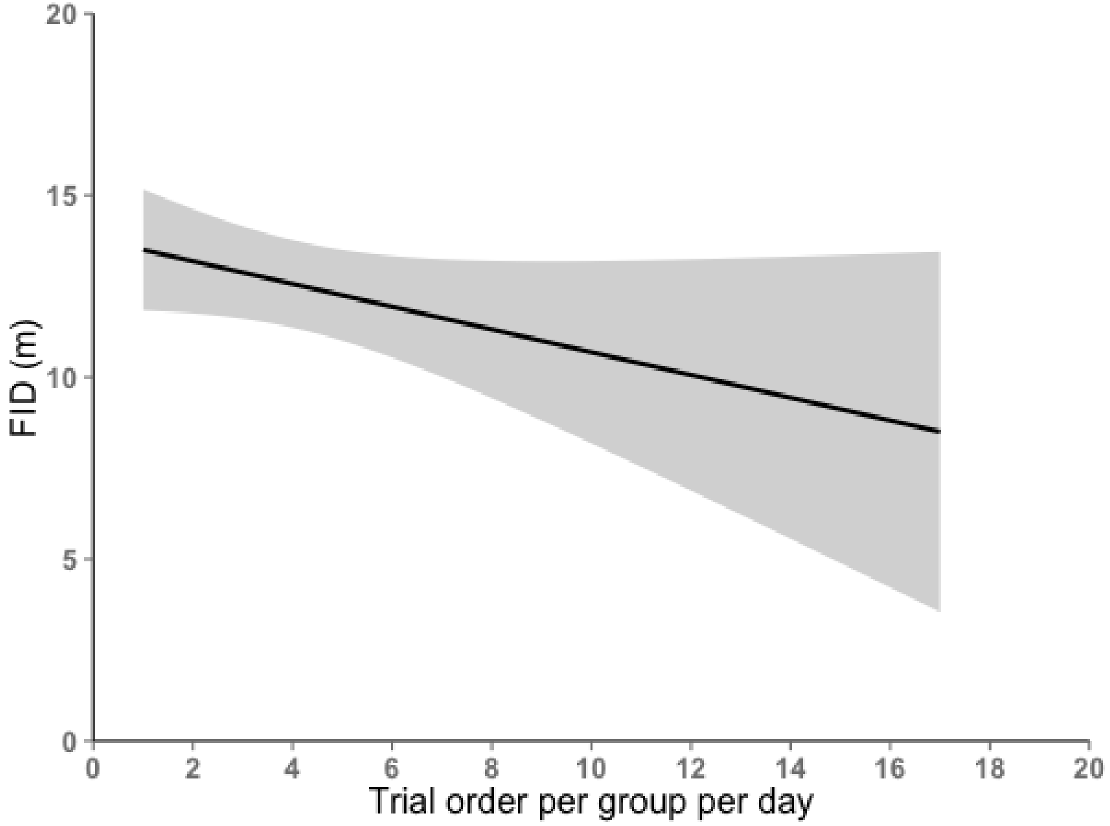

Figure 6: Flight initiation distance (FID) in meters in relation to the order of trials for all subdominant males within a group each day. The black line represents the model predictions and the grey area represents the 95% confidence interval.

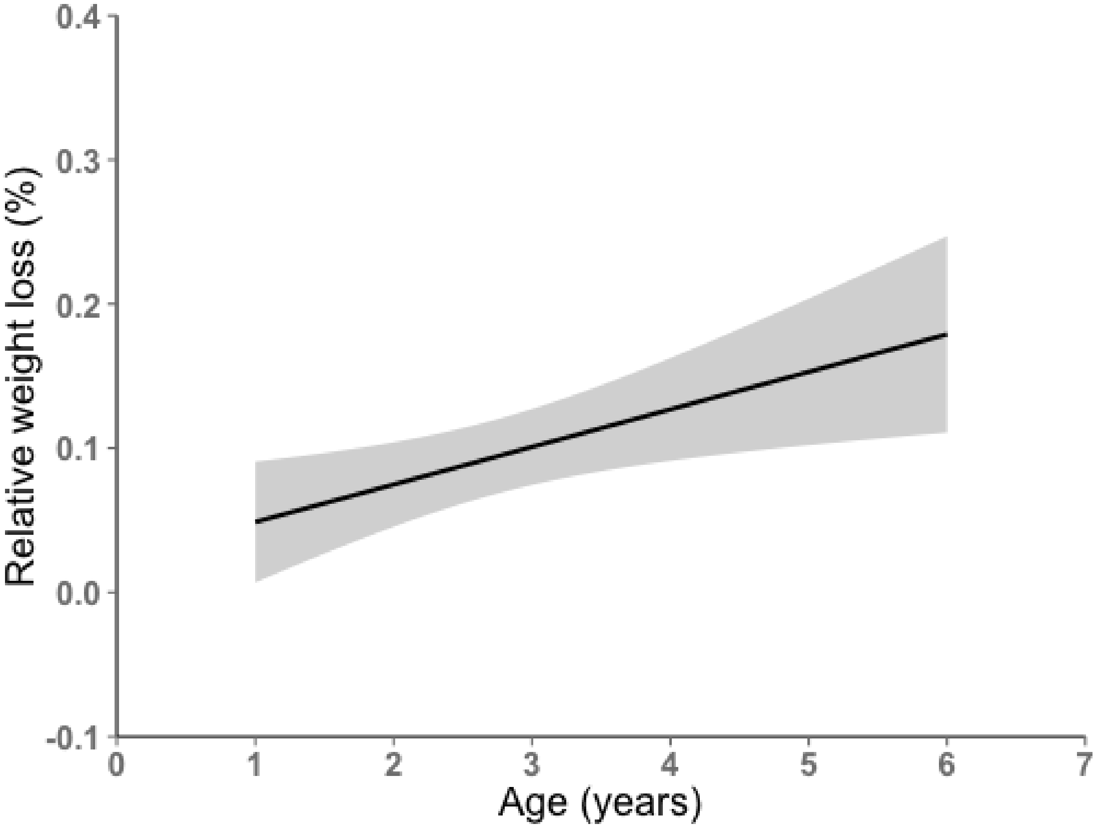

Figure 7: Relative weight loss as a percent in relation to subdominant male age. The black line represents the model predictions and the grey area represents the 95% confidence interval.

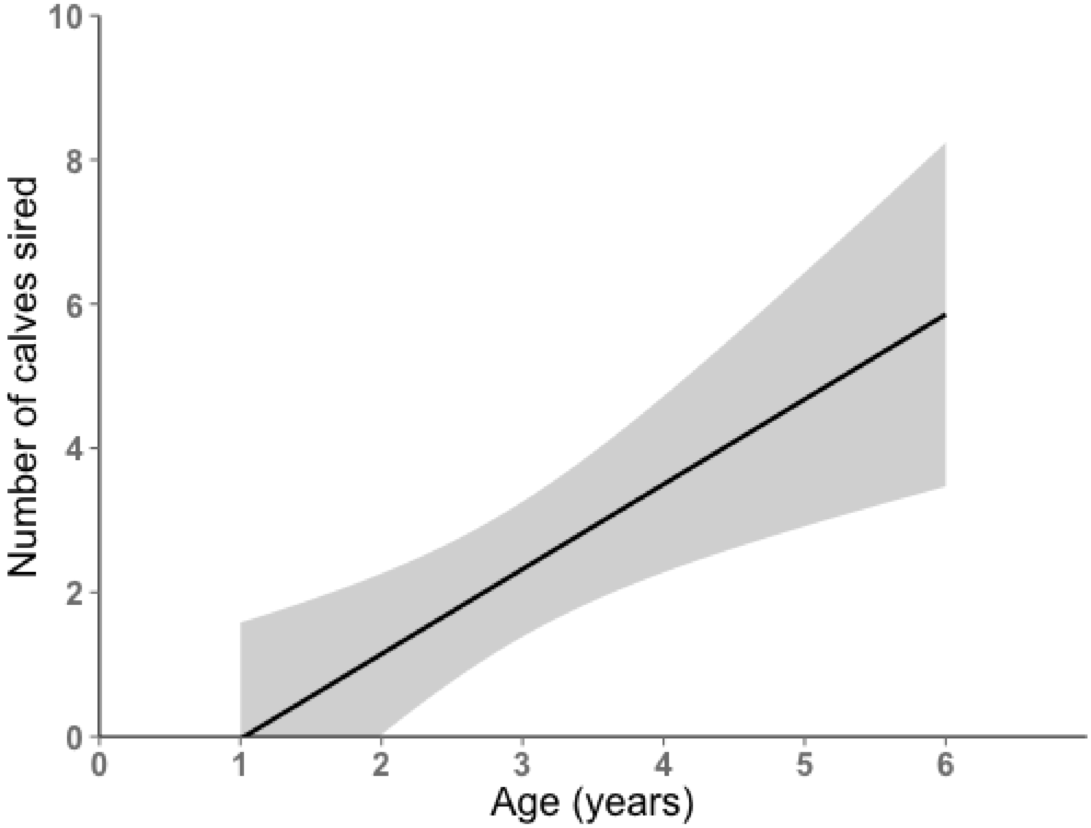

Figure 8: Number of calves sired in relation to subdominant male age. The black line represents the model predictions and the grey area represents the 95% confidence interval of those predictions from the model.