Age and sex specific allometric growth of antlers in *Rangifer tarandus*: variability in the pattern of resource allocation

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Abstract

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Natalka A. Melnycky

Sex-specific tradeoffs between body mass (linked to survival) and costly antlers (linked to reproductive success) are expected in sexually dimorphic ungulates. Unique among cervidae, female reindeer (*Rangifer tarandus*) possess antlers, providing an opportunity to investigate sex- and age-specific patterns of these tradeoffs. Using long-term (1996-2011) individual-based data (e.g. age, body mass, antler length) from a semi-domestic reindeer population in northern Finland, we established antler and body mass growth patterns and assessed the trends of resource allocations towards antlers relative to body mass, using allometric analysis. Sexual dimorphism was apparent in antler and body mass growth curves. Antler growth of males exhibited a steep incline without a plateau by five years, while body mass growth had a less steep incline with a slight decline of growth by five years of age. After an initial incline, female antler and body mass growth patterns showed a plateau near the age of three. All age and sex categories, apart from yearling males and mature females, exhibited positive allometry of antlers, meaning the rate of increase in antler length was higher than that of body mass. Relative allocation of resources towards antlers was highest in female calves, with both sexes exhibiting high allometric exponents as calves and decreasing allocations in yearlings. Male adults increased allocations, while females tended to decrease allocations further with age. Our results exhibit a varying allocation strategy towards antlers, relative to body mass, in reindeer, with clear age-specific sexual dimorphism in relative allocations.

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Contribution of Authors

As the first author, I was responsible for the conception, design, set-up, data analysis and the writing of the manuscript related to this thesis. The manuscript was co-authored by Dr. Robert B. Weladji, Dr. Øystein Holand and Dr. Mauri Nieminen who supervised the work and provided mentorship. Dr. Weladji assisted with the statistics and correction of the manuscript. Dr. Holand advised on experimental design, coordination of fieldwork and data collection, and provided feedback on earlier versions of my analysis. Dr. Mauri Nieminen helped with data collection and provided past data in Finland.

Table of Contents

List of Figures

List of Tables

Age and sex specific allometric growth of antlers in *Rangifer tarandus*: variability in the pattern of resource allocation

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Introduction

The concept of resource allocation is essential to understanding patterns of variation in life history traits (Kojola 1991, Cichoń 1997, Loison and Strand 2005). Nutritional efforts should be directed towards maximizing an individual's fitness (Cichoń 1997, Festa-Bianchet et al. 2004, Weladji et al. 2005) by allocating resources towards appropriate traits (Emlen 1997). Thus, in order to maximize fitness, tradeoffs between traits may be necessary (Agrawal et al. 2010). The terminal investment hypothesis (TIH) states that an organism should allocate resources as a function of remaining potential for reproduction (Clutton-Brock 1984, Fessler et al. 2005). The TIH helps rationalize why older red deer (*Cervus elaphus*) mothers give birth to calves in higher condition and with higher survival rates than young mothers; they are investing more into lactation to compensate for declining condition and reduced future potential for reproduction (Clutton-Brock 1984). Conversely, if future reproductive potential is high, the TIH suggests that an organism should invest conservatively in current reproduction to ensure resource availability in the future and vice versa (Fessler et al. 2005). Tradeoffs between traits should be plastic rather than static and should be influenced by the age, condition, and reproductive status of the individual as well as the availability of resources (Emlen 1997).

Secondary sexual traits (SST), such as antlers, are exaggerated phenotypic traits that evolved under sexual selection, are expected to be strongly condition dependent and costly to produce and maintain, hence they are an honest reflection of quality (Kodric-Brown et al. 2006, Vanpe et al. 2007, Bergeron et al. 2008). The size of SST has subsequently been correlated with dominance and reproductive success (Clutton-Brock 1982, Lincoln 1992, Côté et al. 1998, Holand et al. 2004a, Thomas and Barry 2005, Vanpe et al. 2007). The costs associated with SST production would suppress selection of these traits (Goss 1983, Holand et al. 2004a) unless allocation towards SSTs provides an advantage to individuals through increased fitness (Bergeron et al. 2008). Antlers are model systems in which to investigate resource allocations to SSTs as they are easily measured and dependent on body condition, age, and body size, and yearly renewal is costly (Kiltie 1985, Høymork and Reimers 1999). Advantages of large antlers in roe deer (*Capreolus capreolus*) can translate into reproductive success and increased fecundity regardless of age and body size (Vanpe et al. 2007). However, it is extremely difficult to know if large antlers alone increase total lifetime reproductive success without the influence of body size (Kruuk et al. 2002) as body mass is considered to be one of the most important life history traits (LaBarbera 1989, Calder 1996, Couturier et al. 2010).

Like antlers, body mass in ungulates is reflective of dominance (Hirotani 1990), good foraging skills, fighting success (Clutton-Brock 1982), increased reproductive fitness (Fournier and Festa-Bianchet 1995, Weladji et al. 2005), longevity, and survival (Loison et al. 1999a). Mating success has been found to be largely dependent on both body size and antler size traits (Kojola 1991), thus to ensure high lifetime reproductive success, tradeoffs between resource allocations towards SSTs and body mass should be moderated by future reproductive potential and current availability of resources (Vanpe et al. 2007).

Neither the cost of a given increment of investment, nor its impact on future reproduction remain constant over a lifetime (Clutton-Brock 1984). For example, smaller individuals may feel a larger cost associated with a given increment of reproductive effort, than a larger individual (Clutton-Brock 1984). Accordingly age can play a major role in SST investment. The age of an individual can limit the availability of resources to allocate towards SST, as resources can be constrained in young and old ungulates, by body growth and senescence (aging) respectively (Ericsson et al. 2001, Weladji et al. 2002, Reimers et al. 2005, Vanpe et al. 2007). The development and subsequent regress of antler size in cervids is affected by the nutritional status of the individual (Bender et al. 2003) and therefore also by age. Given that antlers represent costly SSTs, which are shed annually, it might be assumed that they offer no benefit to the bearer before sexual maturity, and indeed could decrease an individual's chance of survival by reducing the resources available for body growth at the risk of reduced peak body size (Kojola 1991, Stewart et al. 2000, Fessler et al. 2005, Bergeron et al. 2008). This might suggest resources should instead be allocated towards somatic growth, especially in calves which must guarantee a threshold weight to survive their first winter (Loison et al. 1999b, Gjøstein et al. 2004) and whose early life growth may determine adult body size (Loison et al. 1999b). Elk (*Cervus elaphus nelsoni*) bulls have been seen to allocate more resources towards antlers upon reaching maturity than when they are juveniles and attained peak body size before peak antler size, indicating a precedence of body mass over antler development in juvenile cervids (Bender et al. 2003).

Body mass and antler size are not mutually exclusive and are positively correlated (Stewart et al. 2000, Weladji et al. 2005). The strength of the correlation between antler size and body size can be evaluated by an allometric relationship. Allometry is the variation of shape among individuals of the same species and developmental stage, and is expected to be positive for all signal traits under directional sexual selection (Bonduriansky 2007). It has also previously been used to examine resource allocations

(Lincoln 1992, Weladji et al. 2005). Across taxa, SSTs consistently show a positive allometric relationship with body size, suggesting that resources are allocated differentially to SSTs rather than to overall body size (Kodric-Brown et al. 2006). However, the plasticity of allometric relationships between SSTs traits and morphological traits at varying ages and resource constraints have not been investigated in depth (Emlen 1997, Tomkins et al. 2005). Data on a single population, monitored over a relatively short period of time is ideal when examining allometric relationships and resource allocations towards SSTs (Emlen 1997).

Within the cervidae family, reindeer/caribou (*Rangifer tarandus*) are the only species in which females are antlered (Høymork and Reimers 1999, Holand et al. 2004a, Thomas and Barry 2005). Reindeer have moved towards reduced sexual dimorphism in weaponry and body markings (Geist and Bayer 1988), however, the antler growth and casting cycles of females remain out of phase with those of male reindeer (Espmark 1971, Høymork and Reimers 1999). Selection for antlers in male reindeer is very strong, due to the direct benefit of breeding success via access to females through intrasexual combat (Kiltie 1985, Kruuk et al. 2002). Alternatively, female antlers offer an indirect benefit towards reproduction through increased resource protection during the winter, or increased rank during agonistic intraspecific interactions (Espmark 1971, Kojola 1989, Reimers 1993, Høymork and Reimers 1999, Thomas and Barry 2005). Although indirect, the evolution of antlers in females suggests a large benefit in life-history strategies, and should encourage allocation of resources towards antlers (Kiltie 1985). Nevertheless reports of antlerless females (Schaefer and Mahoney 2001, Cronin et al. 2003), suggests a large cost due to conflicting physiological demands for antler growth, gestation and lactation, and therefore a larger tradeoff and weaker selection of antlers in females than in males (Kiltie 1985, Reimers 1993). *Rangifer* begin developing antlers within their first year (Lincoln 1994) unlike other cervids, whose growth begin at puberty. As both male and female reindeer have comparable antlers, reindeer provide an opportunity to study resource allocations towards SSTs from birth to old age. The asynchronous growth, shedding, and age-related significance of antlers among sexes provide another perspective with which to help interpret these tradeoffs between traits.

Many studies have investigated intersexual differences in body mass in reindeer (Reimers et al. 2005), antler mass in males (Clutton-Brock 1982), and hornlike organs in female ungulates (Kiltie 1985, Schaefer and Mahoney 2001). Intersexual comparisons of resource allocations towards antlers and body mass, however, are lacking or limited to calves (Weladji et al. 2005). The aim of this study is to examine resource allocations towards antlers as a tradeoff with body mass in reindeer, relative to age and sex, through the use of an extensive individual-based data set. Our objectives were to: (1) establish absolute antler and body mass growth curve patterns for each sex; and (2) assess the trends of allometric exponents (antler length relative to body mass), given the age and sex of individuals. We further compared the different allometric exponents in a resource allocation context, where a higher exponent is indicative of a relatively higher allocation to antler growth. Both sexes are predicted to show a pattern of steady increase of body mass and antler size until reaching peak near maturity and a decrease at time of senescence. Females are predicted to show an earlier and paired peak of body mass and antler size corresponding to an earlier age at maturity. Males are predicted to show a later peak of antler size compared to body mass reflecting a focus on somatic growth until peak reproductive age when resources are allocated towards antler growth. Calves are predicted to have low relative allocations towards antlers, focusing on somatic growth until reaching maturity while, yearlings are predicted to increased allocations towards antlers as they near maturity, for both males and females. Adult males are predicted to have the highest relative allocations towards antlers, significantly higher than females who are also predicted to increase their allocations relative to younger individuals.

Materials and Methods

Reindeer study area and research herd

Data collected since 1996 on a semi-domestic reindeer herd in Kutuharju Field Reindeer Research station (69°N, 27°E) in Kaamanen, Finland was used to investigate allometric patterns of antlers in relation to body mass. The herd is considered "semi-domestic" since the reindeer feed, move and mate freely under a system of free-range management (Hirotani 1990). The experimental herd (~ 100 animals) is maintained by Finnish Game and Fisheries Research, which allows for the continuous collection of anatomical and behavioral data. During the rutting season (mid September to late October) the herd is kept within two large, fenced enclosures; Lauluvaara (13.6 km^2) and Sinioavi (13.4 km^2). These sites are predominately covered by birch (*Betula*) spp. and pine (*Pinus syestris*) forests and have many bogs and lakes. During calving the mothers and calves are kept in a calving area (10 ha), and at this time newborn calves are ear tagged, sexed and weighed. For the remaining year the herd is free-range within a 45 km^2 enclosure. During the winter, animals are supplemental fed daily with a concentrate (Poronherkku).

Data collection

Before the rutting season of each year (September 15-20), animals of known age were weighed to the nearest kilogram (noted as BM) and antler length (main beam, in cm and noted as AL hereafter, Fig 1) measured (Høymork and Reimers 1999, Toigo et al. 2006, Plard et al. 2011). Recording body mass, just before rut is the ideal time of measurement as males lose substantial and varying amounts of mass during the rut (Geist and Bayer 1988, Thomas and Barry 2005, Tennenhouse et al. 2011). Only lengths of antler without velvet were used for analysis; length expected to be a reliable proxy of antler size (Vanpe et al. 2007). Both antlers were measured for each animal unless one antler was damaged, whereupon only the remaining antler was measured. The mean of left and right antler lengths was used in all analyses. If one antler length was unavailable, the remaining antler length was used in lieu of an average value. Existing data collected from 1996 to 2001, 2004 to 2008 and 2011 inclusively, was used when at least one antler was measured, with a corresponding pre-rut body mass. When limiting the dataset to ages 0-5, a total of 288 antler measurements from 220 males, and 674 antler measurements from 340 females were used for the analysis (Table 1). The full dataset includes an additional 551 measurements from females aged 6 to 14 (Table 1).

Statistical analysis

(1) Antler and body mass growth

When establishing antler and body mass growth patterns, the data were separated by sex due to the differences in ages available (Male age 0-5, Female ages 0-14) and fit by a series of age-dependent linear mixed effects models including as variables; null (no age); continuous; quadratic; three (age 0, 1, 2-5) and four (age 0, 1, 2, 3-5) age-class for males; and four (age 0, 1, 2-5, 6+) and five (age 0, 1, 2, 3-5, 6+) age-class for females. Female data were fit once for ages 0-14 and again for ages 0-5 for ease of comparison with male growth trends. Body mass was corrected for Julian date of weighing. We included combinations of sampling and birth year, and individual identity (ID) as random terms, to account for year effects (Vanpe et al. 2007, Weladji et al. 2010, Mahoney et al. 2011), and repeated measurements of individuals among years, respectively (Machlis et al. 1985). With an information-theoretical approach, model selection was performed using Akaike's Information Criterion (AIC) with the smallest AIC value indicating the best-fit model and a criterion of parsimony if a change of AIC between the two best models was less than 2 (Burnham and Anderson 2002, Symonds and Moussalli 2011). All analyses were performed using the R 2.12.0 statistical package (R Development Core team 2010), with a level of significance set to $\alpha < 0.05$.

(2) Allometric analysis

The allometric relationship, with the form: $y = ax^b$, is analyzed as a linear regression by taking the log of both sides to yield: $\log(y) = \log(a) + b * \log(x)$. The parameter y is the response variable, in this case the antler length (AL); a describes the intercept; x is the explanatory variable, body mass (BM); and b is the allometric exponent or the slope of the following equation: $\log(AL) = \log(Intercept) + b * \log(BM)$. If two traits with the same power (length, area, volume, etc.) exhibit an isometric relationship, b will equal 1 (= isometric growth) and anything greater than this is considered positive allometry ($b > 1$). However, since our allometric relationship links a length (AL) with a volume (BM), positive allometry will be observed if $b > {}^{1}\!/_{3}$ (Weladji et al. 2005, Plard et al. 2011).

We regressed log (AL) of all individuals with a series of mixed linear effects models using all possible combinations of: log (BM), age, sex, birth year, Julian weighing date, and sampling year as explanatory variables. We also included interactions between age, sex, and BM variables. Individual identity was included as a random term to account for repeated measurements on individuals among years. We fit models using data of both sexes aged 0-5, which included age categories calves (age 0), yearling (age 1), and adult (age 2-5). Model selection was once again performed using Akaike's Information Criterion (AIC). The model best fitting the data was used to calculate allometric exponents for mature females alone (age 6-14). We compared allometric exponents (slope) between sexes and age categories using their 95% CI, whereby allometric exponents with overlapping CI are not significantly different.

The age categories; calf (age 0); yearling (age 1); adult (age 2-5); mature (6-14, for females only), were set *a priori* as they are biologically relevant categories. Calf antlers are important in establishing rank over wintering grounds (Henshaw 1968, Holand et al. 2004a) and yearling males have been known to attempt copulation (Holand et al. 2004b). Although weight can influence age at first pregnancy, many female reindeer can become reproductively receptive by the age of two (Reimers 1983a). Lastly, senescence has been seen in reindeer between the ages of 7 and 11.5 (Holand et al. 2004a, Reimers et al. 2005, Weladji et al. 2010), as well as a reduction in calf birth-weight (Weladji et al. 2010) and a change in dominance relationships (Kumpula et al. 1991) by the age of 6.

Results

(1) Antler and body mass growth

Sexual dimorphism was apparent for both antler and body mass growth patterns. Males exhibited a steady increase of antler size without a clear plateau and only a slight decline in growth in later ages (Fig 2). Alternatively, after a steady increase in antler size females had a plateau of antler growth around age three (Fig 2). For individuals aged 0-5, the growth patterns of absolute antler size were best described by a quadratic relationship for both females (estimate ± SE; age: 8.64 ± 0.65, age^2: -1.01 ± 0.12; Fig 2) and males (age: 20.39 ± 1.22, age^2: - 0.810 ± 0.29; Fig 2). Antler growth in females aged 0-14, was best described by a five age-category (0, 1, 2, 3-5, 6+) model (Table 2, Fig 3). All of the best-fitted models included year and ID as random terms (Table 2).

Once more body mass growth of males exhibited a steep incline however, with a decline in body mass growth in ages four and five, more discernable than in antler growth (Fig 2). Females once more exhibited a steady incline of body growth before reaching a plateau of size near the age of three (Fig 2). The pattern of body mass growth for males aged 0-5 was best described by a quadratic relationship (age: 20.39 ± 1.22, age^2: -0.81 ± 0.29; Fig 2, Table 3). Female body growth patterns were best-fitted by a four-age category model (0, 1, 2, 3-5) for females aged 0-5 (Fig 2) and by a five-age category model (0, 1, 2, 3-5, 6+) for females aged 0-14 (Fig 3, Table 3). Female body mass growth patterns both exhibiting a steady increase before reaching a plateau near three years of age (Fig 2, 3). All models retained year and ID as random terms.

(2) Allometric analysis

The best model explaining change in log antler size included log of body mass, sex, age (0, 1, 2-5), as well as their two and three way interactions as explanatory variables (Table 4, 5). Year collected was the only additional explanatory variable retained in the best model. All age categories and both sexes, showed positive allometric growth of antlers with body mass with all but yearling males and mature females being significant (with 95% CI's not crossing the isometric line; Table 6; Fig 4). With an allometric exponent of 0.35, mature females approached a change in antler length at an equal rate with body mass, or an isometric relationship.

When compared to all other female age categories, antler length increased at a much higher rate with body mass in female calves (Fig 4, 5). Only calves significantly differed in their relative allocations from other female age categories, however there was a clear trend of decreased allocation towards antlers relative to body mass with age in females (Table 6, Fig 4). Indeed, mature females did not significantly differ from an isometric relationship of equal allocation towards antlers relative to body mass increase (Table 6, Fig 4).

Although no male age categories significantly differed in their rate of increase in antler with body mass, there was a trend of relatively larger allocations for calves, reduced allocations from yearlings and greatest relative allocations of resources towards antlers as adults (Table 6, Fig 4). Yearlings were the only male age category whose allometric relationship did not significantly differ from an isometric relationship (Fig 4).

When comparing between sexes, the slopes of the allometric regression of body mass on antler length were significantly higher in female than male calves (Table 6, Fig 4, 5). There was no significant different between female and male yearlings slopes, and there was a tendency for the rate of increase in antler relative to body mass to be higher for males than female adults (Table 6, Fig 4, 5). Additionally mature females allocated significantly less towards antlers at a given body mass than male adults (Table 6, Fig 4). The relative allocations towards antlers of females and males shift from high allocations in calves and low allocations in yearlings for both sexes, to a continual decline in allocations in female adults and increased allocations in male adults (Fig 4, 5).

Discussion

(1) Antler and body mass growth

Our data exhibits strong sexual dimorphism in growth curves of antler length and body mass. Although there were no antler measurements for males above five years of age with which to investigate senescence, the lack of a clear plateau in male growth curves cannot be fully attributed to this limitation in the data. When female data were limited to the age of five, a stabilization of growth was still seen by the age of three, suggesting that antlers have not yet reached their peak in males, while stabilizing earlier in females. This can be explained by the added costs associated with gestation and lactation in females (McPherson and Chenoweth 2012) reducing the resources available for antler growth, as well as the importance of antlers in males to ensure successful mating during the rut. In both moose and red deer males, maximum antler length was not reached until ten years of age (Lincoln 1994, Stewart et al. 2000, Kruuk et al. 2002). If a similar trend is true in male reindeer, it may explain the lack of a plateau in the antler length growth curve, as the ages of our samples were too young to detect a decrease in antler length associated with senescence.

The steep growing curve of body mass in females before reaching a plateau around three years of age coincides with the age of maturity and when most females become pregnant (Reimers 1983b). The coinciding plateau in the antler growth curve may reflect the allocation of energy towards child bearing, and away from SSTs once puberty is reached. Additionally, body mass is closely correlated with longevity (Speakman 2005), which can subsequently be linked with individual fitness, as the longer an individual lives the more offspring they can have (Weladji et al. 2006). In females who can only bear one offspring a year, resources allocated towards body mass once sexually mature would be beneficial, to ensure that their limited number of offspring are fit and healthy. Alternatively male antler size relative to their rivals, can determine yearly offspring count. With large antlers and high rank, males can sire many offspring in a season, however the strong link with body mass is still present. By allocating relatively more towards antlers, in addition to maintaining steady growth in body mass, males focus more on current reproductive success, making a tradeoff between current reproductive potential and somatic growth or survival.

A few things should be kept in mind when reviewing the relationships discussed above. Unexplained variability within female growth curves may be partially due to the pregnancy status of females during antler growth, and should be included in future antler and body mass growth models. Pregnant females retain their antlers until after calving in May (Geist and Bayer 1988, Høymork and Reimers 1999, Schaefer and Mahoney 2001), which suggests that antlers are important in obtaining the additional resources needed for pregnant females during the winter in order to fulfill the physiological demands associated with pregnancy. Furthermore, antler mass has been shown to be lighter in non-pregnant young and old females (Thomas and Barry 2005) and may also be true for antler length for females pregnant the year prior to growing. That being said, our population has a pregnancy rate of near 100% and including pregnancy would likely not result in a better-fitting model.

Herd-specific differences in antler measurements have been found as these differences are closely linked to nutritional status (Høymork and Reimers 1999), population sizes (Mahoney et al. 2011), latitudinal changes (Geist 1987) and area-specific differences in body growth (Reimers 1983a). As our data were taken from one population and not a mixture of populations, we are free from these confounding factors. Although the data available to us are exceptional, studies on other reindeer populations should be included in the literature in order to better understand herd-specific differences in antler growth. Lastly, tine numbers were not considered in this analysis and together with length should be considered in future studies, as tine numbers can drastically differ between ages and can be dependent on resource availability (Bowyer et al. 2001, Mahoney et al. 2011).

(2) Allometric analysis

Our results confirm the findings of many studies in which SSTs have positive allometric exponents (Bonduriansky 2007). Almost complete widespread positive allometric exponents within our population suggest that with larger body mass, resources are directed towards antlers at an exponential rate. However, the extent of this tradeoff in resource allocation between antlers and body mass fluctuates according to age and individual body condition. Secondary sexual traits have been strongly linked to reproductive success (Gould and Gould 1997), thus increased allocation towards SSTs with higher body mass is expected. Male-male contests linked to sexual selection encourage the selection of larger SSTs, which may reflect higher quality individuals. Adult and yearling reindeer with larger antlers more often initiate and win a fight with other males (Barrette and Vandal 1986) thus securing their rank, potentially preventing future battles and safeguarding the siring of many females. Antlers can also be used to showcase superior quality from a distance and to prevent dangerous and energetically costly battles (Gould and Gould 1997, McPherson and Chenoweth 2012).

The morphology of immature males usually resembles that of females until sexual maturity is reached, as exaggerated sexual dimorphism is unnecessary costly in early life (Gould and Gould 1997). This was evident in our findings within yearlings whose pattern of allocations towards antlers relative to body mass did not differ between sexes. In other words, among yearlings, antler length did not increase at a much greater rate with body mass in males than in females. Antlers are a burden to bear, being heavy and making navigation through shrub difficult. Males, who have a chance of becoming high ranked, would benefit from large antlers as they may result in many offspring. However, younger males or males in poor condition would best avoid the extra burden of large SSTs and focus on survival in order to have a chance to sire offspring in the future. Large allometric exponents within adult males especially reflect this trend, with males in higher body condition exhibiting proportionally larger antler growth.

Although antlers first evolved in males, primarily as offensive and defensive weaponry against conspecifics during mating season (Kiltie 1985, Thomas and Barry 2005), our results indicate that antlers in females also receive significant resources as calves and yearlings, and are playing a major role in their life-histories. Female reindeer are suggested to have evolved and retained antlers as weapons in intra-specific and intersexual competition (Geist and Bayer 1988, Hirotani 1990, Schaefer and Mahoney 2001). Due to stressful conditions and gregarious behavior in winter, defense of snow craters from conspecifics is needed to secure resources (Espmark 1971, Kojola 1989, Reimers 1993). Another force selecting for antlers in females, may be intraspecific competition or prevention of unwanted advances from juvenile males who retain their antlers for the first part of the winter (Henshaw 1968, Geist and Bayer 1988, Holand et al. 2004a). Although many life-history traits are thought to improve either mating survival or reproductive success (Andersson 1994), antlers in females may act to enhance both, by increasing rank, securing resources, preventing unwanted juvenile suitors during the rut and thus increasing the quality and longevity of their offspring (Holand et al. 2004a, Holand et al. 2004b).

A positive allometric exponent in reindeer calves has been previously seen in reindeer (Weladji et al 2005). Heavy calves allocate exponentially more resources towards antlers than light calves and the contrast between the strategies of heavy and light individuals is significantly different in female calves than in yearlings, adults and mature females. A supporting theory for this trend is that females have been predicted to establish rank early on in life, and maintain that rank throughout their life (Henshaw 1968, Taillon and Côté 2006). Antler length has been linked to dominance and rank in this population (Holand et al. 2004a), so high allocation to antlers early on in life, may be advantageous if rank is kept stable after establishment, ensuring future access to resources since resource attainment is subsequently linked to reproductive success (Holand et al. 2004a). Removal of antlers in adult females has been shown to negatively influence dominance rank (Kiltie 1985, Holand et al. 2004a), though age was still correlated with rank for females with and without antlers.

Barrette and Vandal (1986) determined that at a close range antler size made no difference to the outcome of antagonistic encounters between adult females. This is contrary to Holand et al. (2004a) who found that antler threats preceded displacement as the most common agonistic interactions at feeding sites between females. Either way, antlers play a part of agonistic encounters at feeding sites (Kumpula et al. 1991), which may explain why antlerless females are more often found in environments with abundant food supply, low snow cover, and smaller populations (Schaefer and Mahoney 2001). Later in life, rank may have a greater influence on reproductive success than antler length does (Holand et al. 2004a), as rank may ensure resources and large body mass, which has been linked to offspring survival and birth weight (Barrette and Vandal 1986). Allocation towards female antler length at a young age by establishing rank early may circumvent their inability to allocate as much towards antlers at older ages due to constraints associated with gestation. Additional research on female rank establishment is required to enhance our understanding of the importance of antlers in calves, especially since *Rangifer* are unique within cervidae as they begin growing their antlers within weeks of birth (Blake et al. 1998).

Male calves were seen to have positive allometry, allocating more resources to antlers relative to body mass, in comparison to yearlings that did not significantly differ from isometry. Overwinter resource competition can be intense for calves, as they are low ranked, need to acquire plenty of resources to prevent mortality during their first winter (Kojola and Helle 1996, Loison et al. 1999b). Additionally, calves are highly dependent on their mothers who are often pregnant and in great need of resources themselves (Henshaw 1968, Barrette and Vandal 1986, Adamczewski et al. 1993). Reindeer calves are more sensitive to environmental changes than are adults (Helle and Kojola 1994) and male calves may be more sensitive to mortality risks than females (Loison et al. 1999b). All resources should thus be focused on body maintenance and only on antlers once a threshold is reached. This can accentuate the contrasts between ‘strong’ and ‘weak’ calves, making the slope of the allometric regression between antler length and body mass more apparent.

Although reindeer young are considered precocial they follow their mother closely shortly after birth which is indicative of a considerable need of active maternal defense (Clutton-Brock 1982). As reindeer milk has high content of milk solids compared to that of ungulates, it provides calves with an advantage of large food resources prior to lush summer vegetation, without needing to search for it (Gjøstein et al. 2004). Calves with fit mothers may not be as limited by resources due to earlier gestation (Holand et al. 2006), or higher ranked mothers over the winter which can increase their own rank

(Veiberg et al. 2004), and can allocate more towards antlers relative to body mass, as a result. Though findings elsewhere suggest that reindeer calves rely heavily on mothers to provide food during their first winter, it has also been argued that offspring must quickly become self-sufficient to survive harsh winter conditions (Henshaw 1968). Mother-calf association ends much faster in males than with females (Hirotani 1990) and females more often feed from a mothers' feeding crater over winter than do males (Kojola and Helle 1996). This may explain the drastic drop in resources allocated towards antlers in yearling males, as they have much reduced resources available.

A downward trend in allometric exponents with age in females reflects higher allocation of resources towards body mass with age. Body mass has strong correlations with offspring birth mass and survival (Cameron et al. 1993), and the chance of having offspring if you are a female is very high (Kruuk et al. 2002). Hence, it may be advantageous to allocate resources towards body mass rather than focusing on antlers, as has been previously noted, to ensure longevity (Weladji et al. 2005). The maintenance of these costly SSTs in females is likely due to the benefit of remaining antlered in the winter when resource constraints are high, adult males are antlerless (Lincoln 1994), and larger antlered females keep their resources during intrasexual competition (Barrette and Vandal 1986). Unsurprisingly, the rate of increase in antler length with body mass was higher in adult males than females, supporting the greater importance of antlers in prime male individuals, given that antler size in ungulates, even once corrected for body size, has been significantly correlated with breeding success (Kruuk et al. 2002). Although female reindeer prioritize more resources towards SSTs than other cervidae females, it remains that males will prioritize their antlers more because of the greater selection pressure as fewer males are reproductively successful compared to females (McPherson and Chenoweth 2012).

Conclusions

Reindeer antler growth patterns are sex-specific as expected; females showed a clear plateau from the age of three, while this trend was much less pronounced in males who showed seemingly linear antler growth until age five. There was consistent positive allometry, therefore high relative allocations towards antlers across sex and age categories. Females showed a decrease in relative allocations to antlers with increased age, while after a decrease for yearlings, males tended to increased allometric exponents with increasing age, with adult relative allocations being nearly significantly higher for males as compared to females. Calves of both sexes showed larger relative allocations towards antlers than expected, with female calves allocating more than any other age category. These results shed light on the evolutionary significance of antlers in female reindeer and the varying allocations towards SSTs at different life-history stages within reindeer. More thorough behavioral studies on antler use in calves are warranted.

Table 1. Summary statistics of reindeer (*Rangifer tarandus*) antler length and body mass data of 340 females and 220 males from the Kutuharju Field Reindeer Research station collected, from 1996 to 2011. Data is represented as medians for age, and means (± SE) for body mass and antler length, with range in brackets.

	n	Birth year	Age (median)	Body mass (kg)	Antler length (cm)
Female	1125	1984 - 2011	4 (0 - 14)	73.26 ± 0.45 (31 - 106)	37.74 ± 0.33 (1 - 67)
Female	674	1991 - 2011	4 (0 - 5)	66.97 ± 0.61 (31 - 101)	33.88 ± 0.44 (1 - 67)
Male	288	1992 - 2011	0 (0 - 5)	68.54 ± 1.63 (31 - 152)	43.13 ± 1.49 (8.5 - 115.5)
Overall	1413	1984 - 2011	3 (0 - 14)	72.32 ± 0.49 (31 - 152)	38.72 ± 0.40 (1 - 115.5)

Table 2. Summary of model selection of linear mixed effects models describing age-specific changes in absolute antler size in *Rangifer tarandus*, with the chosen model in **bold**.

Model	df	AIC	ΔAIC
Males 0-5:			
Null	4	2671.851	550.365
Age	5	2126.891	5.405
Age^2	**6**	**2121.486**	**0**
Three Age	6	2282.922	161.436
Four Age	7	2133.997	12.511
Females 0-5:			
Null	4	4440.201	341.256
Age	5	4187.385	88.44
Age^2	**6**	**4098.945**	**0**
Three Age	6	4143.212	44.267
Four Age	7	4097.1	-1.845
Females 0-14:			
Null	4	7816.061	601.939
Age	5	7397.334	183.212
Age^2	6	7260.46	46.338
Four (F) Age	7	7229.438	14.412
Five Age	**8**	**7214.122**	**0**

Note: Model selection was conducted using Akaike Information Criterion (AIC). ΔAIC is the difference in AIC between the given model and the best model (lowest AIC or most parsimonious if ΔAIC from the lowest AIC is less than 2) with the best model in **bold**. Null = without age; Age = age as a continuous variable; Age+Age^2 = Age fitted as a quadratic variable; Three Age = age fitted as a factor with three classes (0, 1, 2-5 years); Four Age = age as a factor with four classes (0, 1, 2, 3-5); Four (F) Age = age as a factor with four classes for females (0,1, 2-5, 6+); and Five Age = model with age fitted as a factor with five classes for females (0, 1, 2, 3-5, 6+). Random terms for all models include year collected and ID and mean antler length was the response variable.

Table 3. Summary of model selection of linear mixed effects models describing age-specific changes in absolute body mass in *Rangifer tarandus*, with the chosen model in **bold**.

Model	df	AIC	ΔAIC
Males 0-5:			
Null	5	2700.736	591.91
Age	6	2167.572	58.746
Age+Age^2	**7**	**2108.826**	**0**
Three Age	7	2232.863	124.037
Four Age	8	2128.747	19.921
Females 0-5:			
Null	5	4720.208	884.345
Age	6	4116.905	281.042
Age+Age^2	7	3863.358	27.495
Three Age	6	3883.077	47.214
Four Age	**8**	**3835.863**	**0**
Females 0-14:			
Null	5	8253.631	1309.639
Age	6	7684.082	740.09
Age+Age^2	7	7305.958	361.966
Four (F) Age	7	6972.631	28.639
Five (F) Age	**9**	**6943.992**	**0**

Note: Model selection was conducted using Akaike Information Criterion (AIC). ΔAIC is the difference in AIC between the given model and the best model (lowest AIC or most parsimonious if ΔAIC from the lowest AIC is less than 2) with the best model in **bold**. Null = without age; Age = age as a continuous variable; Age+Age^2 = Age fitted as a quadratic variable; Three Age = age fitted as a factor with three classes (0, 1, 2-5 years); Four Age = age as a factor with four classes (0, 1, 2, 3-5); Four (F) Age = age as a factor with four classes for females (0,1, 2-5, 6-14); and Five Age = model with age fitted as a factor with five classes for females (0, 1, 2, 3-5, 6-14). Random terms for all models include year collected and ID and body mass corrected for weighing date was the response variable.

Table 4. Linear mixed effects model selection of allometric relationship of antler size and body mass in *Rangifer tarandus*, with the chosen model in **bold**.

Model	df	AIC	ΔAIC
BM x 3C x SEX + YC	**15**	**523.71**	**0.87**
BM x 3C x SEX + BY + YC	16	522.83	0
BM x 3C x SEX + BY + YC + DW	17	524.51	1.67
BM x 3C x SEX + YC + DW	16	525.59	2.75
BM x 3C x SEX + BY	15	528.77	5.88
BM x 3C x SEX + BY + DW	16	530.23	7.39
BM x 3C x SEX + DW	15	538.18	15.34
BM x 3C x SEX	14	546.89	24.05

Note: BM= log(Body mass); 3C = Age with 3 classes (0, 1, 2-5) ; BY = Birth year; YC = Year collected; DW= Julian weighing date; response variable is log(Antler length). All models include identity as a random term. Model selection was conducted using Akaike Information Criterion (AIC). ΔAIC is the difference in AIC between the given model and the best model (lowest AIC or most parsimonious if ΔAIC from the lowest AIC is less than 2) with the best model in **bold**.

Table 5. Parameter estimates (± SE) for the best-fit linear mixed effects model describing allometric growth of antlers in reindeer (*Rangifer tarandus*) from the Kutuharju Field Reindeer Research station, 1996-2011, using sex (Female as the base), 3 age categories (0,1, 2-5 years; 0 as the base), body mass (BM) and year collected (YC) as variables.

Parameters for the best model	Coefficient	t value
Intercept	-33.58 (+ 5.41) **	-6.2
log(BM)	2.20 (+ 0.19) **	11.11
Age 1	4.92 (+ 1.07) **	4.59
Age 2-5	6.09 (+ 0.87) **	6.94
Sex M	4.78 (+ 0.97) **	4.91
YC	0.01 (+ 0.00) **	5.02
log(BM) x Age 1	-1.24 (+ 0.27) **	-4.6
log(BM) x Age 2-5	-1.51 (+ 0.22) **	-6.78
log(BM) x Sex M	-1.20 (+ 0.25) **	-4.74
Age 1 x Sex M	-3.82 (+ 1.70) **	-2.24
Age 2-5 x Sex M	-7.24 (+ 1.48) **	-4.87
log(BM) x Age 1 x Sex M	1.02 (+ 0.41) **	2.45
log(BM) x Age 2-5 x Sex M	1.81 (+ 0.35) **	5.19

**Significant with $P < 0.05$

Table 6. Allometric exponents (b in $y=ax^b$, ± SE) of reindeer (*Rangifer tarandus*) from Kutuharju Field Reindeer Research station, 1996-2011. An exponent of 1/3 indicates an isometric relationship (same rate of change in antlers as body mass).

	Age Category	Allometric exponent (^{b}) $y = ax^b$	Lower confidence interval 2.5%	Upper confidence interval 97.5%	Sample size (n)
Male	0	1.00 (±0.17)	0.65	1.35	161
	1	0.78 (±0.27)	0.24	1.32	61
	2-5	1.30 (±0.21)	0.88	1.73	66
Female	0	2.20 (±0.19)	1.82	2.59	153
	1	0.96 (±0.20)	0.55	1.37	102
	2-5	0.69 (±0.11)	0.47	0.91	416
	6+	0.35 (±0.09)	0.17	0.54	454

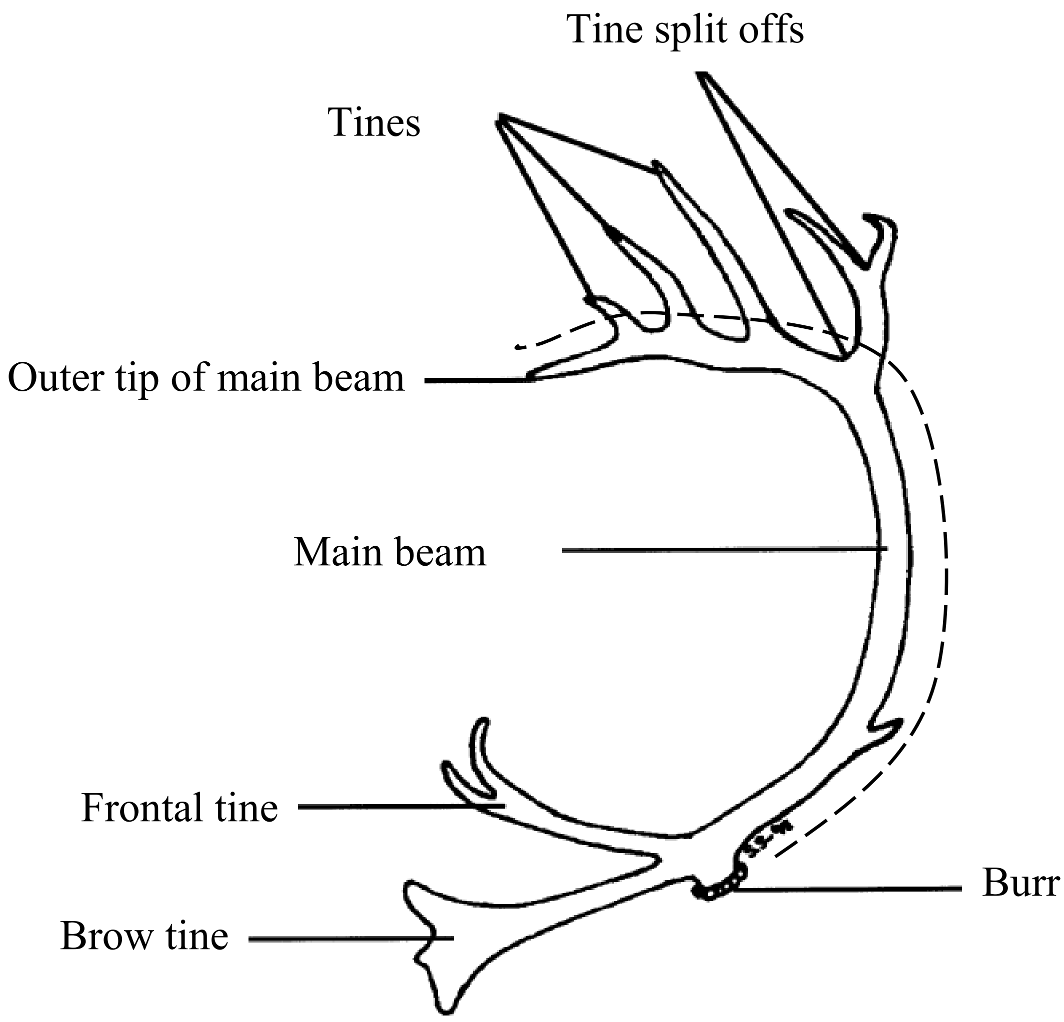

Figure 1. Reindeer (*Rangifer tarandus*) antler nomenclature. Dashed line represents the measuring path for antler length, on the outside of the antler from the burr to the outer tip of the main beam (Markusson and Folstad 1997).

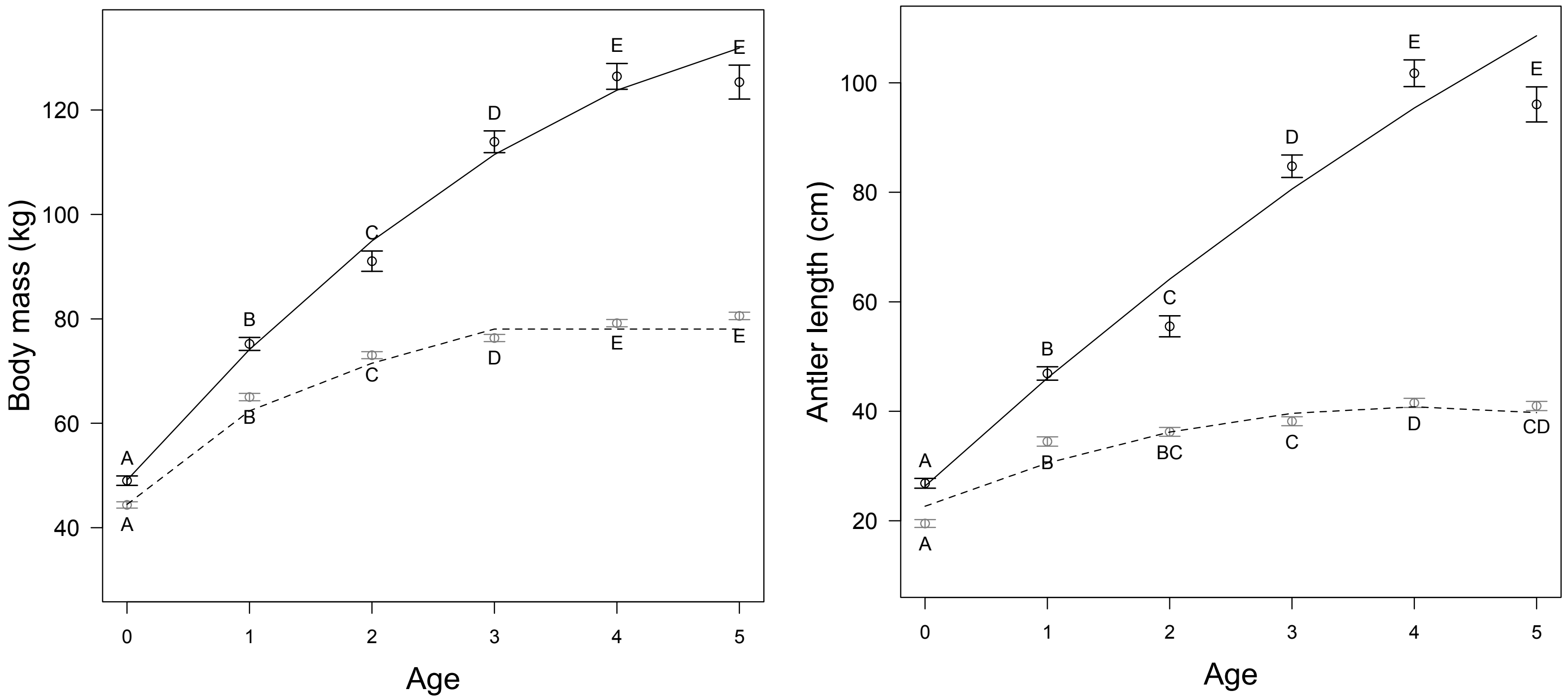

Figure 2. Least square means (± SE), adjusted for year, of antler lengths (cm) and body mass (kg) of reindeer (*Rangifer tarandus*) from the Kutuharju Field Reindeer research station, 1996 to 2011. Means with the same letter are not significantly different according to a Tukey-Kramer multiple comparisons test ($\alpha = 0.05$). Trend lines of the fixed factors of the best-fit quadratic models are displayed for each sex (female = discontinuous line, male = continuous line).

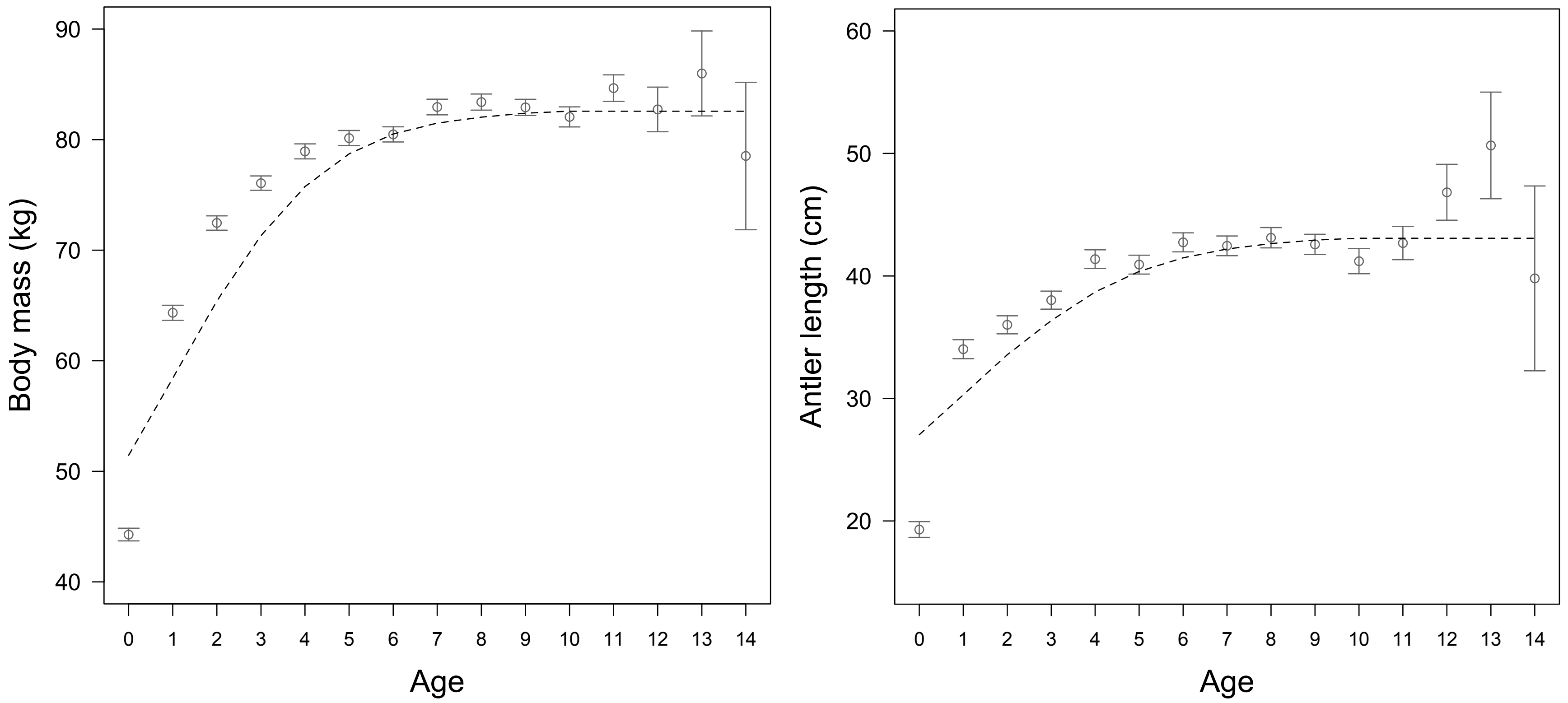

Figure 3. Least square means (± SE) controlled for year, of antler lengths (cm) and body mass (kg), of female reindeer (*Rangifer tarandus*) aged 0-14 from the Kutuharju Field Reindeer research station, 1996 to 2011. Smoothed trend lines display the fixed factors of the best-fit five-age-category growth models.

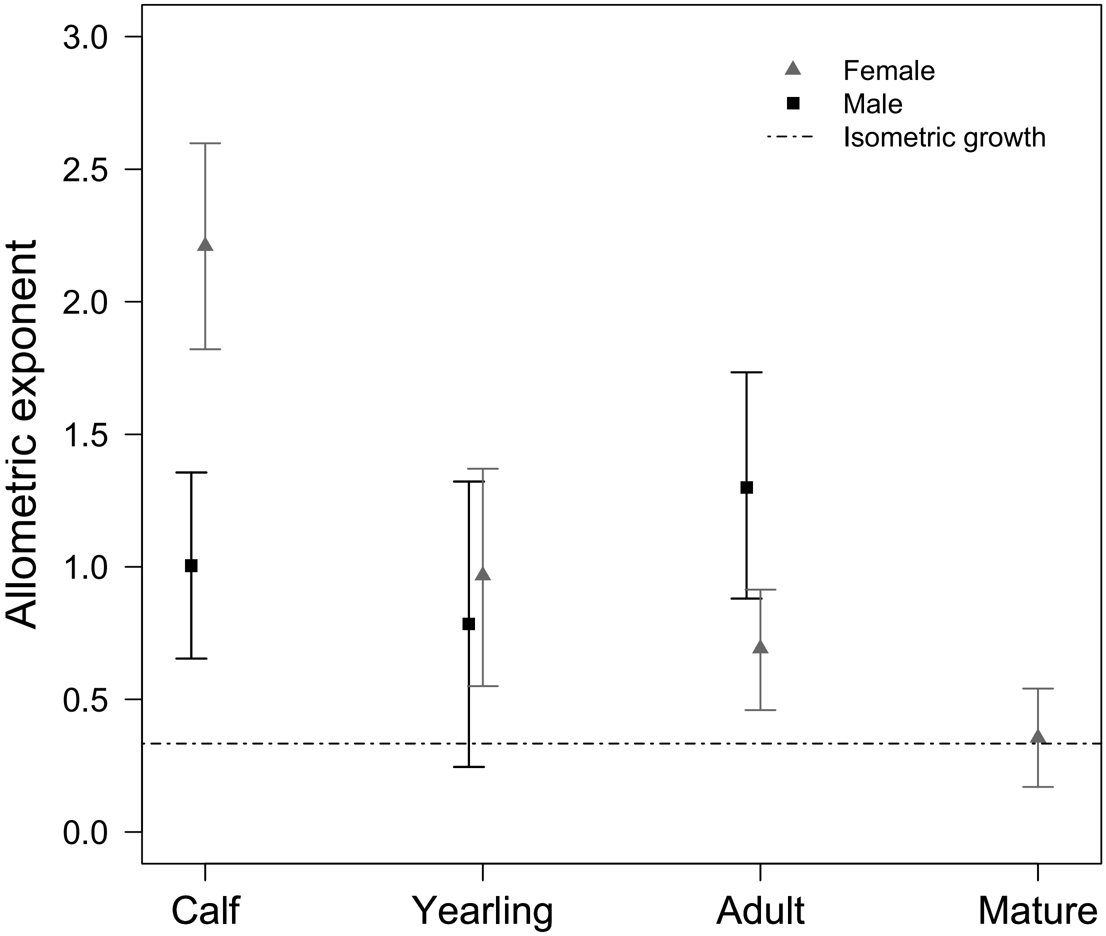

Figure 4. Allometric exponents of age classes, calf (0), yearling (1), adult (2-5) and mature (6+, for females only) of a semi-domestic reindeer herd (*Rangifer tarandus*) from Kutuharju Field Reindeer Research station, 1996 to 2011, derived from a linear mixed effects model which includes Year as a factor and ID as a random term. Exponents are displayed with 95% confidence interval bars and a dashed line depicting isometry.

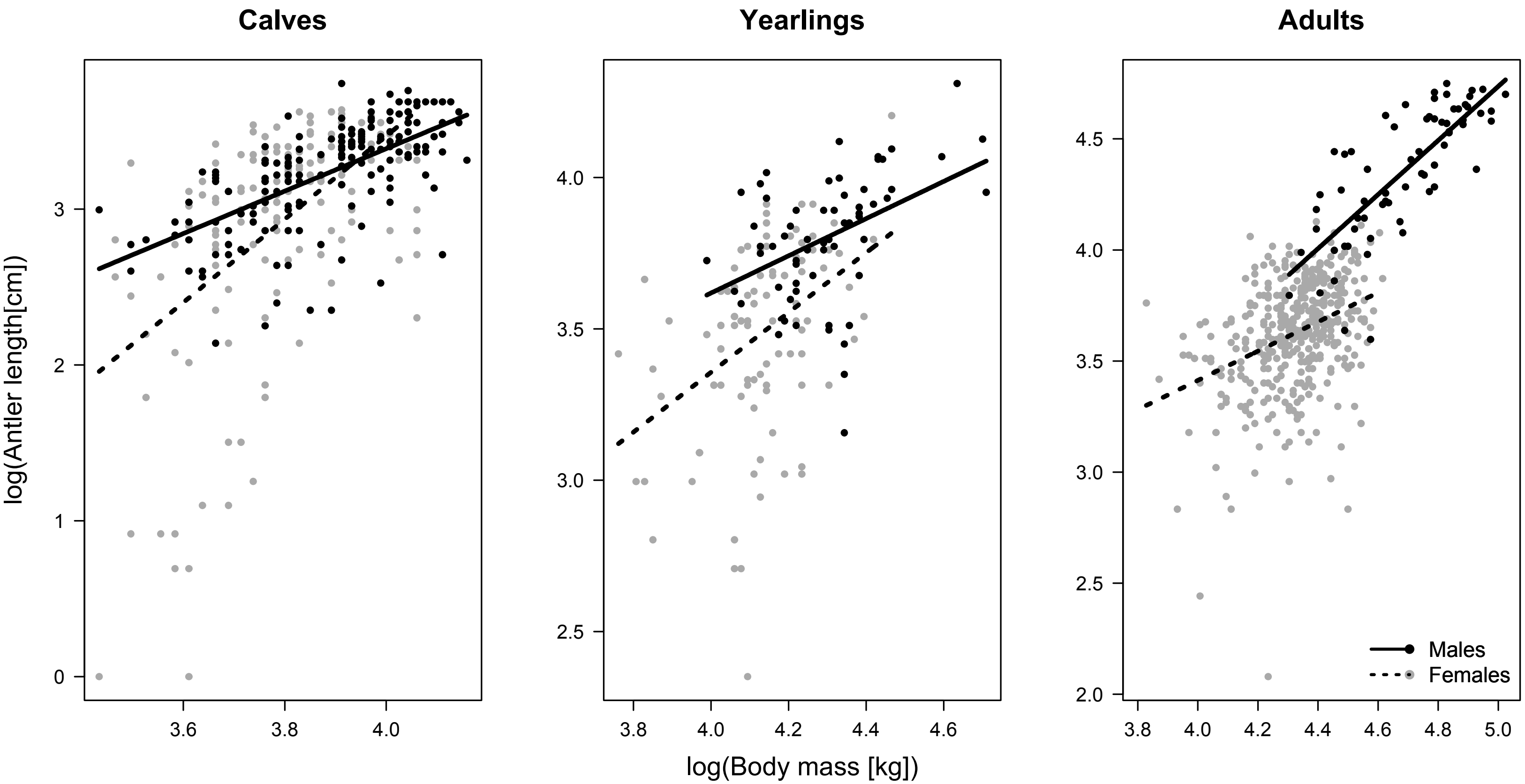

Figure 5. Allometric relationships (log-log regression) between antler lengths and body mass for calf (0), yearling (1), and adult (2-5) of a semi-domestic reindeer herd (*Rangifer tarandus*) from Kutuharju Field Reindeer Research station, 1996 to 2011, derived from a general linear model which includes collection year as a factor.

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