Scaling of antler size in reindeer (*Rangifer tarandus*): sexual dimorphism and variability in resource allocation

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Male cervids face trade-offs in allocating resources to body mass (linked to survival) and antlers (linked to reproductive success). Reindeer (*Rangifer tarandus*) are unique among cervids because females also possess antlers, providing an opportunity to investigate sex- and age-specific patterns of resource allocation to body mass and antlers. Using long-term (1996–2011) data on 560 reindeer, we examined how body mass and antler length varied with age and sex, and the relative allocation of resources toward antlers using scaling analysis. Body mass and antler length increased through age 5 years in males but plateaued in females at age 3 years, with males 59% greater in body mass and 146% longer in antler length by age 5 years. All age and sex categories, except yearling males and mature females, had a positive scaling (a scaling exponent greater than isometry) of antlers with body mass, with the highest relative allocation of resources toward antlers in female calves. Relative allocation toward antlers tended to increase with age in males but decrease with age in females. The observed patterns in antler and body growth are likely a reflection of sex-specific life-history strategies of reindeer whereby females have offspring yearly from puberty and males have an increased number of offspring as they mature.

Key words: allometry, antler growth, *Rangifer tarandus*, resource allocation, trade-offs

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 toward maximizing an individual's fitness (Cichoń 1997; Festa-Bianchet et al. 2004; Weladji et al. 2005) by allocating resources toward traits linked to reproductive success (Emlen 1997). Limited resources force trade-offs between morphological traits. To maximize fitness, allocations of resources should be plastic rather than static and should be influenced by the animal's age, body condition, reproductive status, availability of resources, and remaining potential for reproduction (Clutton-Brock 1984; Emlen 1997; Fessler et al. 2005; Agrawal et al. 2010).

Secondary sexual traits (SSTs), such as antlers, are exaggerated phenotypic traits that evolved under sexual selection. SSTs are expected to be energetically costly to produce and maintain, thus are considered to be honest reflections of phenotypic quality and body condition (Kodric-Brown et al. 2006; Vanpe et al. 2007; Bergeron et al. 2008). The costs associated with the production and maintenance of

SSTs should suppress selection of these traits (Goss 1983; Holand et al. 2004a) unless SSTs provide an advantage to individuals through increased fitness (Bergeron et al. 2008). For example, 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, antler size is not easily decoupled from body size when determining influence on lifetime reproductive success (Kruuk et al. 2002). Not only are body mass (BM) and antler size not mutually exclusive (Stewart et al. 2000; Weladji et al. 2005), but BM alone is considered to be the most apparent and important life-history trait in all species, because BM is a reflection of energy stores needed for future survival and reproduction (LaBarbera 1989; Calder 1996; Couturier et al. 2010) and in ungulates is reflective of increased reproductive

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fitness (Fournier and Festa-Bianchet 1995; Weladji et al. 2005; Mainguy et al. 2009).

The relative allocation of resources to SSTs such as antler size (Stewart et al. 2000; Weladji et al. 2005) can be evaluated using scaling relationships. Because of directional sexual selection, SSTs are expected to differ from isometry (i.e., proportional to BM—Bonduriansky 2007). Across taxa, SSTs consistently show positive scaling (i.e., scaling exponent > isometry), suggesting that resources are allocated differentially to SSTs than to body size (Lincoln 1992; Weladji et al. 2005; Kodric-Brown et al. 2006). However, the scaling relationships between SSTs and morphological traits at varying ages and resource constraints have not been investigated in depth (Emlen 1997; Tomkins et al. 2005).

Within the family Cervidae, reindeer–caribou (*Rangifer tarandus*) is the only species in which females have antlers (Hymork and Reimers 1999; Holand et al. 2004a; Thomas and Barry 2005). Antler growth and casting cycles in females are asynchronous with those of male reindeer (Espmark 1971; Hymork and Reimers 1999). Because the selective pressures on antler growth differ between the sexes, so should the resources allocated toward them. Male reindeer use antlers in intrasexual combat during the breeding season, with victors accessing more females (Kiltie 1985; Kruuk et al. 2002). In contrast, antlers offer an indirect benefit to reproduction in females through acquisition and protection of food resources, because larger antlers can correspond to increased rank during agonistic intraspecific interactions over isolated food patches in winter and superior food patches in summer (Espmark 1971; Kojola 1989; Reimers 1993; Hymork and Reimers 1999; Thomas and Barry 2005). The need to secure food resources over the winter becomes more prevalent when females are pregnant, because they need to acquire resources for themselves, their fetus, and often their yearling calf (Espmark 1964). The presence of antlerless females in some herds (Kiltie 1985; Reimers 1993; Cronin et al. 2003), however, suggests a weaker selection for antlers in females than in males.

Not only might allocation of resources to antlers in reindeer differ with sex, but also with age. Antler size in cervids is affected by body condition (Bender et al. 2003; Hamel and Côté 2009), which tends to be lower in young, growing ungulates and in old, senescent ungulates (Ericsson et al. 2001; Weladji et al. 2002; Reimers et al. 2005; Vanpe et al. 2007). Therefore, resources should primarily be allocated toward somatic growth, rather than antlers, in calves, because early growth may determine adult body size (Loison et al. 1999) and increase overwinter survival (Loison et al. 1999; Gjstein et al. 2004). Similarly, resources allocated toward antlers should be limited by body maintenance in senescent animals (Clutton-Brock 1982), resulting in a lower scaling exponent.

In this study, we examined resource allocation to BM and antler length (AL) in reindeer within sex and age classes, using a large (560 animals), long-term (1996–2011) data set from a semidomestic herd in Kaamanen, Finland. We expected AL and BM to increase with age until senescence in both males and females (quadratic growth), but that females would have an earlier and paired peak of BM and AL at 3 years when they would be expected to invest resources in pregnancy instead of BM and AL. In contrast, we predicted that BM of males would peak before AL because young males would focus on somatic growth until peak reproductive age when resources are allocated toward antler growth. In addition, we expected the relative allocation of resources to AL, as measured from the scaling exponent of the relationship between BM and AL, to be positive (i.e., > 0.33, the isometric relationship between a volume [mass] and a length measure of the body) for all sex and age classes. We expected both males and females to have the highest scaling exponents for AL when mature, but not senescent, and males to have higher scaling exponents for AL across age classes.

MATERIALS AND METHODS

Reindeer study area and research herd.—Data collected since 1996 on a semidomestic reindeer herd in Kutuharju Field Reindeer Research Station (69°N, 27°E) in Kaamanen, Finland, were used to investigate scaling patterns of antlers in relation to BM. The experimental herd (~100 animals) was 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 was held within 2 large (approximately 15-km^2) fenced enclosures. The fenced area was predominately covered by silver birch (*Betula pendula*), downy birch (*Betula pubescens*), and pine (*Pinus sylvestris*) forests, and consisted of several bogs and lakes. During calving, the mothers and calves were kept in a calving area (0.1 km), and at this time newborn calves were ear tagged, sexed, and weighed, thus age was known for all individuals. For the remaining year the herd was held within a 45-km^2 enclosure. During the winter, animals were supplementally fed daily with pelleted reindeer food containing milled oat, barley, wheat, molasses, and minerals (Poron-Herkku; Raisio Feed, Raisio, Finland).

Data collection.—We weighed animals to the nearest kilogram in mid-September, just before rut when males lose varying and large amounts of weight (Geist and Bayer 1988; Thomas and Barry 2005; Tennenhouse et al. 2011). We measured the length (cm) of main beams of antlers (AL; Supporting Information S1, DOI: 10.1644/11-MAMM-A-282. S1) after velvet was shed and growth completed, from September to December (Lincoln 1994; Hymork and Reimers 1999; Plard et al. 2011). AL has been found to be a reliable proxy of overall antler size (Vanpe et al. 2007). Both antlers were measured unless 1 antler was damaged, whereupon only the remaining antler was measured. The mean of left and right ALs was used in all analyses. If 1 AL was unavailable, the remaining AL was used in lieu of an average value. Existing data collected from 1996 to 2001, 2004 to 2008, and 2011, inclusively, were used when at least 1 antler was measured, with a corresponding prerut BM. When limiting the data set to ages 0–5 years, a total of 288 antler measurements from 220 males, and 671 antler measurements from 340 females were

TABLE 1.—Antler length and body mass of reindeer (*Rangifer tarandus*) of 340 females and 220 males from the Kutuharju Field Reindeer Research Station collected from 1996 to 2011. Data are represented as medians for age, and means ($\pm$ *SE*) for body mass and antler length, with range in parentheses.

	n	Birth year	Age (years)	Body mass (kg)	Antler length (cm)
Female	1,125	1984–2011	4 (0–14)	73.26 $\pm$ 0.45 (31–106)	37.74 $\pm$ 0.33 (1–67)
Female	671	1991–2011	2 (0–5)	66.97 $\pm$ 0.61 (31–101)	33.88 $\pm$ 0.44 (1–67)
Male	288	1992–2011	0 (0–5)	68.54 $\pm$ 1.63 (31–152)	43.13 $\pm$ 1.49 (8.5–115.5)
Overall	1,413	1984–2011	3 (0–14)	72.32 $\pm$ 0.49 (31–152)	38.72 $\pm$ 0.40 (1–115.5)

used for the analysis (Table 1). The full data set included an additional 454 measurements from females aged 6–14 years (Table 1). We ensured that ethical standards were met while performing the measurement as per the Concordia University Animal Research Ethics Committee guidelines (certificate AREC-2011-WELA), which is in line with the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011).

To examine allocations toward SSTs in reindeer, we used biologically relevant age categories set a priori: calf (age 0 year), yearling (age 1 year), adult (ages 2–5 years), and mature (ages 6–14 years, for females only). Calf antlers are important in establishing rank on overwintering grounds (Henshaw 1968; Holand et al. 2004a) and yearling males have been known to copulate, although with varying success (Holand et al. 2004b; Roed et al. 2005). Male reindeer can reach puberty at 6 months; however, most reach peak reproductive age as adults at 4 years (Kojola 1991). Although BM can influence age at 1st pregnancy, most female reindeer 1st become pregnant as yearlings (Reimers 1983a), with 3-year-olds having 82% probability of being pregnant (Ropstad 2000). Last, senescence has been seen in reindeer between the ages of 7 and 11.5 years (Holand et al. 2004a; Reimers et al. 2005; Weladji et al. 2010), with a reduction in calf birth mass (Weladji et al. 2010) and a change in dominance relationships (Kumpula et al. 1991) by the age of 6 years.

Statistical analysis.—To establish AL and BM growth patterns across all ages, the data were separated by sex because of the differences in ages available (male, ages 0–5 years and female, ages 0–14 years) and fit by age-dependent linear mixed-effects models including variables: null (no age); continuous; quadratic; 3 (age 0, 1, and 2–5 years) and 4 (age 0, 1, 2, and 3–5 years) age class for males; and 4 (age 0, 1, 2–5, and 6+ years) and 5 (age 0, 1, 2, 3–5, and 6+ years) age class for females. Female data were fit once for ages 0–14 years and again for ages 0–5 years for ease of comparison with male growth trends. BM was corrected for Julian date of weighing. As random terms, we included combinations of sampling and birth year to account for year effects (Forchhammer et al. 2001; Vanpe et al. 2007; Weladji et al. 2010; Mahoney et al. 2011), and individual identity to account for repeated measurements of individuals among years (Machlis et al. 1985). 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 2 best models was less than 2 (Burnham and Anderson 2002). Akaike weights (ωs), representing the relative

probability for a model to be the best among considered models, were calculated (Wagenmakers and Farrell 2004; Barton 2012). Goodness of fit of the chosen model was determined by calculating a likelihood-ratio–based pseudo-*R*-squared value (Kramer 2005; Barton 2012). All analyses were performed using the program R version 2.12.0 (R Development Core Team 2010), with $\alpha = 0.05$.

We examined scaling of AL with BM using a power function (i.e., $y = ax^b$) and determined the intercept and scaling exponents for this relationship by running a linear regression through log-transformed variables (scaling exponent is b, in: $\log(AL) = \log(\text{intercept}) + \times\log(BM)$). Linear mixed-effects models were used to determine which explanatory factors (age, sex, birth year, Julian weighing date, and sampling year), in addition to log(BM), best explained variation in allocations toward AL (i.e., response variable). We used all possible combinations of variables including interactions between age, sex, and log(BM), and included identity as a random term to account for repeated measurements between years. Models were fit using data limited to ages 0–5 years, which included calves (age 0 year), yearlings (age 1 year), and adults (ages 2–5 years) of both sexes. Model selection was once again performed using AIC, with ωs calculated (Wagenmakers and Farrell 2004; Barton 2012) and goodness of fit of the chosen model determined by using a likelihood-ratio–based pseudo-*R*-squared value (Kramer 2005; Barton 2012). The chosen model was used to calculate scaling exponents for each age and sex category and for mature females (age 6–14 years). Exponents were compared using 95% confidence intervals (*CI*s), whereby exponents with overlapping *CI*s were not significantly different.

RESULTS

Body mass and AL increased with age in both male and female reindeer, but the difference in BM and AL between the sexes increased through age 5 years, at which point males were 59% larger in BM and had antlers 146% longer (Fig. 1). The pattern of BM growth for males aged 0–5 years was best described by a quadratic relationship and appears to plateau in older individuals ($R^2 = 0.87$, age: 20.39 $\pm$ 1.22, age^2: –0.81 $\pm$ 0.29; Fig. 1b; Supporting Information S2, DOI: 10.1644/ 11-MAMM-A-282.S2). BM in females showed a steady increase before reaching a plateau near 3 years of age (Fig. 1b; Supporting Information S3b, DOI: 10.1644/ 11-MAMM-A-282.S3). Female body growth patterns were best fitted by a 4 age-class (0, 1, 2, and 3–5 years) model for
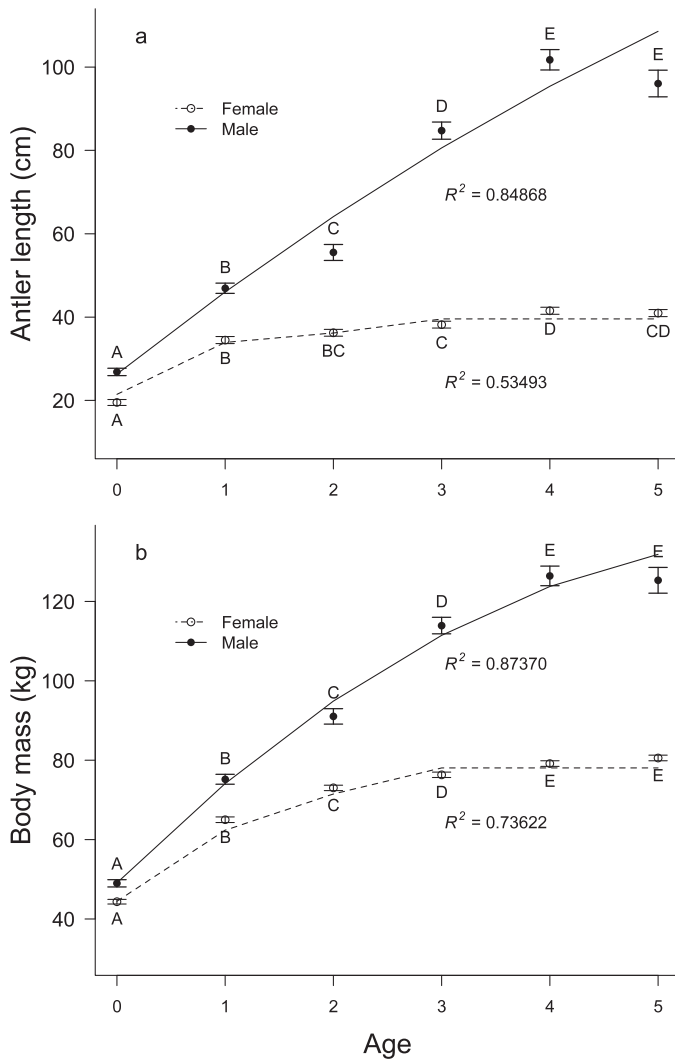
Fig. 1.—Least-square means (± *SE*) adjusted for year, in relation to age (year) of a) antler lengths (cm) and b) body mass (kg) of reindeer (*Rangifer tarandus*) from the Kutuharju Field Reindeer Research Station, 1996–2011. Means with the same letter are not significantly different according to a Tukey–Kramer multiple comparisons test (α = 0.05). Trend lines of the fixed factors of the best-fit models are displayed.

females aged 0–5 years ($R^2 = 0.74$; Fig. 1b) and by a 5 age-class (0, 1, 2, 3–5, and 6+ years) model for females aged 0–14 years ($R^2 = 0.70$; Supporting Information S2; Supporting Information S3b). All models included year and individual identity as random terms.

Antler growth in males showed no clear plateau by 5 years, whereas antler growth in females appeared to reach a plateau at age 3 years (Fig. 1a). For individuals aged 0–5 years, the growth patterns of absolute AL were best described by a quadratic relationship for males ($R^2 = 0.85$, age: 20.39 ± 1.22, age^2: –0.810 ± 0.29; Fig. 1a) and a 4 age-class (0, 1, 2, and 3–5 years) model for females aged 0–5 years ($R^2 = 0.53$). Antler growth in females aged 0–14 years was best described by a 5 age-class (0, 1, 2, 3–5, 6+ years) model ($R^2 = 0.44$; Supporting Information S3a; Supporting Information S4, DOI: 10.1644/

11-MAMM-A-282.S4). All of the best-fitted models included year and individual identity as random terms (Supporting Information S4).

The best model explaining the scaling of AL given BM included log of BM, sex, age (0, 1, and 2–5 years), their 2- and 3-way interactions, and year ($R^2 = 0.59$; Tables 2 and 3) as variables. Other than yearling males and mature females, all age and sex categories showed positive scaling of AL with BM (with 95% *CI*s exceeding isometry, 0.33; Table 4; Fig. 2). Female calves had a significantly higher scaling exponent for AL than did other age classes of females, and allocation of resources toward antlers relative to BM tended to decrease with age (Table 4; Fig. 2). In fact, scaling of AL in mature females did not significantly differ from an isometric relationship of equal allocation toward AL relative to BM (Table 4; Fig. 2). In contrast, scaling exponents for AL in males did not differ with age class, but the greatest relative allocations of resources toward antlers were as adults (Table 4; Fig. 2). All age classes of males had positive scaling exponents, except yearlings, which did not differ significantly differ from isometry (Fig. 2).

The relative allocation of resources to antlers differed between the sexes. The scaling exponent of AL was significantly higher in female than male calves, but not yearlings or adults, although adult males had a significantly higher scaling exponent for AL than mature females and tended to have a higher exponent than adult females.

DISCUSSION

We found several differences in the patterns of growth in BM and AL and relative allocation of resources to AL in male and female reindeer. Differences in BM and AL growth continued to increase between male and female reindeer until at least 5 years of age, by way of BM and AL reaching an asymptote by 3 years of age in females, and AL not declining by the age of 5 years (the oldest age class available) in males. Juvenile elk bulls (*Cervus elaphus nelsoni*) also attain peak body size before peak antler size, suggesting a precedence of BM over antler development in juvenile male cervids (Bender et al. 2003). These observations differ from those of mountain goats (*Oreamnos americanus*), where horn dimorphism between sexes stabilizes by the age of 2 years (Côté et al. 1998) and BM in males is the strongest trait linked to reproductive success (Mainguy et al. 2009). Indeed these differences are obvious in adults, when reindeer males have antlers up to 48 cm longer than those of females, whereas male goats have horns 14 mm shorter than those of females at a given body size (Côté et al. 1998).

After an initial steep increase in BM growth, females reached a plateau at around 3 years of age, which coincides with the beginning of prime age, when most females are pregnant (Reimers 1983b) and when females are near their peak calf birth masses (Weladji et al. 2010). BM is closely correlated with longevity (Calder 1996), and can subsequently be linked with individual fitness, because longer lives equate to more opportunities of producing offspring (Weladji et al.

TABLE 2.—Model selection results displaying Akaike information criterion (AIC) values, followed by change in AIC (ΔAIC), AIC weight (AIC_ω), and log-likelihood (LogLK) of the linear mixed models assessing the effect of a combination of variables on log(antler length) in reindeer (*Rangifer tarandus*) from the Kutuharju Field Reindeer Research Station collected from 1996 to 2011, with the chosen model in boldface type. BM = log(body mass); 3C = age with 3 classes (0, 1, and 2–5 years); 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	d.f.	AIC	ΔAIC	AIC_ω	LogLK
BM × 3C × SEX + BY + YC	16	522.83	0	0.415	−245.41
BM × 3C × SEX + YC	**15**	**523.71**	**0.87**	**0.268**	**−271.94**
BM × 3C × SEX + BY + YC + DW	17	524.51	1.67	0.180	−245.41
BM × 3C × SEX + YC + DW	16	525.59	2.75	0.105	−246.79
BM × 3C × SEX + BY	15	528.77	5.88	0.022	−249.36
BM × 3C × SEX + BY + DW	16	530.23	7.39	0.010	−249.11
BM × 3C × SEX + DW	15	538.18	15.34	0.000	−254.09
BM × 3C × SEX	14	546.89	24.05	0.000	−254.44
BM	4	638.80	110.96	0.000	−312.90
Null	3	1,383.89	861.05	0.000	−688.94

2006). Furthermore, BM is strongly correlated with birth mass and survival of offspring in reindeer (Barrette and Vandal 1986; Cameron et al. 1993). In females, which can only bear 1 offspring a year, resources allocated toward BM upon sexual maturity increase the chances that their limited number of offspring survive (Weladji et al. 2010), and increase their own survival and future reproduction. The coinciding plateau in the AL growth curves likely reflects the high energetic requirements of pregnancy (Hamel and Côté 2009; McPherson and Chenoweth 2012) in reindeer, which have high chances of yearly pregnancy (Ropstad 2000). Resources are likely limited for antlers and alternatively directed toward maintenance of BM. Indeed, horn growth significantly decreased in lactating female mountain goats aged 4 or 5 years, even when accounting for age (Côté et al. 1998). Alternatively, with large antlers and high rank, male reindeer can sire many offspring in a season (Roed et al. 2005), and thus allocations toward antlers

may lead to a high number of offspring and decrease the need to live long lives to ensure reproductive success.

The dimorphism in allocation toward antlers reflects the sex-specific reproductive strategies of reindeer. Females produce a calf almost yearly, with high costs associated with gestation and lactation (McPherson and Chenoweth 2012). Males have a much larger variation in reproductive success, siring 0 or 1 offspring at younger ages to as many as 20 in older, dominant males (Roed et al. 2005), with energetic costs associated with competition for access to mates (Mainguy and Côté 2008; Tennenhouse et al. 2011). Because antlers are shed and regrown annually, it is more adaptive to delay investments toward antlers when chances of siring young are higher (Stewart et al. 2000). In male moose (*Alces alces*) and red deer (*Cervus elaphus*), maximum AL was not reached until 10 years of age (Lincoln 1994; Stewart et al. 2000; Kruuk et al. 2002). If reindeer are similar, we may have been unable to detect a plateau or decline in AL growth because we lacked data for males > 5 years old.

As in many other studies of SSTs, AL in most age and sex classes of reindeer had a positive scaling exponent (Bonduriansky 2007). The relatively high allocation of resources to antlers in reindeer was not surprising because morphological traits linked to reproductive success, such as those used in combat or courtship that have been shaped by sexual selection, tend to have positive scaling, whereas most traits have negative or isometric scaling with body size (Gould and Gould 1997; Bonduriansky and Day 2003; Pomfret and Knell 2006). In species where competitive interactions are dictated by body size, larger individuals will benefit from displaying larger antlers to showcase superior quality from a distance, because this can reduce dangerous and energetically costly battles (Clutton-Brock 1982; Gould and Gould 1997; McPherson and Chenoweth 2012). Indeed, adult and yearling reindeer with larger antlers more often initiate and win fights with other males (Barrette and Vandal 1986). Given that antler size in male ungulates, even when corrected for body size, has been significantly correlated with breeding success, it is unsurprising that allocations toward antlers were higher in adult males than

TABLE 3.—Parameter estimates (± *SE*) for the best-fit linear mixed-effects model describing scaling relationship of antlers in reindeer (*Rangifer tarandus*) from the Kutuharju Field Reindeer Research Station, 1996–2011. Sex (female as the base), 3 age categories (0, 1, and 2–5 years; 0 as the base), log body mass (BM) and year collected (YC) as explanatory variables, identity as a random term, and the response variable being log antler length (AL). An asterisk (*) indicates significance at α = 0.05. M = male.

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) × Age 1	−1.24 (+ 0.27)*	−4.6
Log(BM) × Age 2–5	−1.51 (+ 0.22)*	−6.78
Log(BM) × Sex M	−1.20 (+ 0.25)*	−4.74
Age 1 × Sex M	−3.82 (+ 1.70)*	−2.24
Age 2–5 × Sex M	−7.24 (+ 1.48)*	−4.87
Log(BM) × Age 1 × Sex M	1.02 (+ 0.41)*	2.45
Log(BM) × Age 2–5 × Sex M	1.81 (+ 0.35)*	5.19

TABLE 4.—The scaling of antler length with body mass in reindeer (*Rangifer tarandus*) from the Kutuharju Field Reindeer Research Station, 1996–2011, by age category (calf [0 year], yearling [1 year], adult [2–5 years], and mature [6+ years]). An exponent of 1/3 indicates an isometric relationship (same rate of change in antlers as body mass).

	Age category	Scaling 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

in females (Kruuk et al. 2002). Although female reindeer prioritize more resources toward SSTs than other cervid females, it remains that males prioritize their antlers more, because of greater selection pressures because fewer males are reproductively successful compared to females (McPherson and Chenoweth 2012).

Positive scaling of antlers in male reindeer has been well established (Calder 1996); however, the scaling of antlers in females has not been well documented or explored. Our results indicate that females also allocate significant resources to antlers, and that antlers play an important role in their life-history strategy. In contrast to males that adapted antlers primarily as offensive and defensive weaponry against conspecifics during mating (Kiltie 1985; Thomas and Barry 2005), female reindeer may have evolved and retained antlers as weapons in intraspecific and intersexual competition (Geist and Bayer 1988; Hirotani 1990; Schaefer and Mahoney 2001). Clutton-Brock (2009) suggested that traits that increase competitive success might be influenced more by variation in resource distribution rather than the form of mating systems.
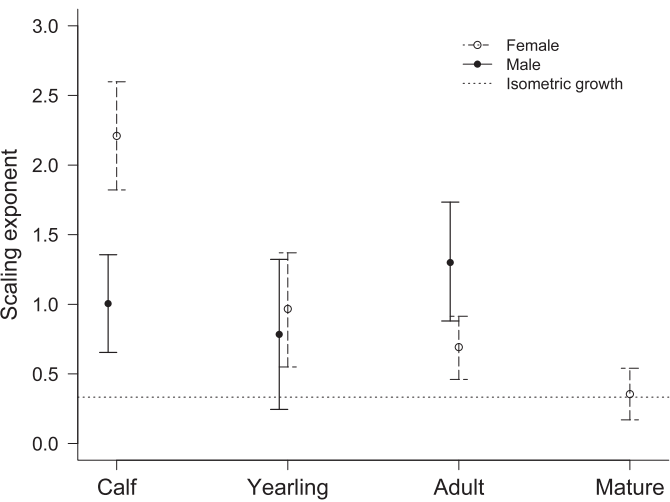
FIG. 2.—Scaling exponents of antlers relative to body mass in age classes calf (0 year), yearling (1 year), adult (2–5 years), and mature (6 years) for semidomestic reindeer (*Rangifer tarandus*) from the Kutuharju Field Reindeer Research Station, 1996–2011, derived from a linear mixed-effects model that includes Year as a factor and individual identification (ID) as a random term. Exponents are displayed with 95% confidence interval bars.

This may help explain the evolution of antlers in females, and why antlerless females occur more often in environments with abundant food supply, low snow cover, and smaller populations (Schaefer and Mahoney 2001). Another force selecting for antlers in females may be preventing unwanted advances from juvenile males that retain their antlers for the 1st part of the winter (Henshaw 1968; Geist and Bayer 1988; Holand et al. 2004a). Although many life-history traits are thought to improve either survival or reproductive success (Andersson 1994), antlers in females may act to enhance both by securing winter resources and preventing unwanted juvenile suitors during the rut, thus increasing individual and offspring quality and longevity (Holand et al. 2004a, 2004b).

Contrary to our expectations, we found that scaling exponents for AL were higher for female calves than for any other sex or age class. This means that heavy calves allocated exponentially more resources toward antlers than did light calves (Weladji et al. 2005). One reason that allocation of resources to antlers may be especially important in female calves is that females may establish rank early in life, and maintain that rank throughout their life (Henshaw 1968; Taillon and Côté 2006). AL has been linked to dominance and rank in the studied population (Kiltie 1985; Kumpula et al. 1991), thus high allocation to antlers early in life may safeguard future access to resources if rank is kept stable after establishment (Holand et al. 2004a). A similar mechanism is likely less important for males because they do not experience gestation and lactation, and are thus able to allocate resources to antlers later in life and concentrate on somatic condition as juveniles. Similarly, male elk allocate more resources toward antlers upon reaching maturity than they do as juveniles (Bender et al. 2003).

Female reindeer tended to allocate fewer resources toward AL with age, which may have been a response to senescence, in addition to increased energetic demands of gestation and lactation. Although reduced, antlers continue to receive resources in older females, likely serving to increase rank during winter when males are antlerless (Lincoln 1994). Later in life, rank may have a greater influence on reproductive success than does AL (Holand et al. 2004a), because rank may facilitate access to resources and thus large BM. Our results shed light on the evolutionary significance of antlers in female reindeer and the varying allocations toward SSTs at different life-history stages in reindeer. More thorough behavioral

studies on antler use and rank retention in calves are warranted to enhance our understanding of the importance of antlers in calves.

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SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—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, adjusted from Markusson and Folstad (1997).
Found at DOI: 10.1644/12-MAMM-A-282.S1

SUPPORTING INFORMATION S2.—Model selection of linear mixed-effects models describing age-specific changes in absolute body mass in *Rangifer tarandus*, with the chosen model in boldface type. Random terms for all models include year collected and individual identity (ID) and body mass corrected for weighing date was the response variable. LogLK is the log likelihood of the model.
Found at DOI: 10.1644/12-MAMM-A-282.S2

SUPPORTING INFORMATION S3.—Least-square means ($\pm$ *SE*) controlled for year of a) antler lengths (cm) and b) body mass (kg) of female reindeer (*Rangifer tarandus*) aged 0–14 years from the Kutuharju Field Reindeer Research Station, 1996–2011. Smoothed trend lines display the fixed factors of 5-age-category growth models.
Found at DOI: 10.1644/12-MAMM-A-282.S3

SUPPORTING INFORMATION S4.—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 boldface type. Random terms for all models include year collected and individual identity (ID) and mean antler length was the response variable. LogLK is the log likelihood of the model.
Found at DOI: 10.1644/12-MAMM-A-282.S4

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