Energetic costs of male reproduction in a scramble competition mating system

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Summary
1. The assumption that the primary limitations on reproductive success differ between the sexes is inherent in traditional sexual selection theory. Although the energy that can be allocated to reproduction is assumed to be the main limitation to females, the ability to attract and defend oestrous females is assumed to be the primary limitation to males.
2. Estimates of the energetic costs of reproduction in male mammals are, however, limited and have largely been obtained from sexually dimorphic species exhibiting female defence mating systems. These studies often reveal that the energetic cost of male reproduction is similar to or even exceeds that of females, and therefore challenge long-held assumptions of inter-sexual reproductive limitations, but their generality is little known.
3. We coupled measurements of energy expenditure with detailed behavioural observations of reproductive male North American red squirrels (Tamiasciurus hudsonicus). This species displays minimal sexual dimorphism and exhibits a scramble competition mating system, under which sexual selection favours enhanced mate searching effort by males.
4. We conducted the study over 2 years characterized by a substantial variation in upcoming natural food availability and across two study populations that experienced either natural food abundance or an ad libitum food-supplementation to investigate the influence of resource availability on male reproductive energy expenditure.
5. Under natural conditions, mean energy expenditure of males across the 2 years was high, approximating that of females during lactation. Furthermore, in the anticipation of high upcoming natural food availability and resultant offspring survival, expenditure approximately doubled (from 290 ± 7 to 579 ± 73 kJ day−1). When current food availability (and consequently the density of receptive females) was experimentally elevated, males displayed the highest levels of energy expenditure we recorded (873 ± 98 kJ day−1).
6. Our results provide compelling evidence that the energy available for reproductive allocation places a strong limitation on reproduction in male North American red squirrels and contribute to previous work suggesting that high and limiting energetic costs of male reproduction may be a general feature of mammalian reproduction.

Key-words: daily energy expenditure, life history, mating system, North American red squirrel, sexual selection

Introduction
By definition, females invest heavily in individual gametes but produce them in relatively low numbers, whereas males expend relatively little on individual gametes but produce them in vast quantities (Parker, Baker & Smith 1972; Bell 1978). In therian mammals, this initial asymmetry in resource allocation becomes further exaggerated by internal offspring development, lactation and (in most species) sole parental care of dependent offspring by females (Clutton-Brock 1991). This fundamental difference has given rise to a set of assumptions underlying traditional sexual selection theory. Specifically, that male reproductive success is primarily limited by the number of mates that can be acquired, while female success is predominantly limited by the energetic resources that can be allocated to reproduction (Bateman...
Breeding energy expenditure, estimated using the doubly labelled water technique or from daily mass loss of capital breeders, is expressed as daily energy expenditure (DEE) and as sustained metabolic scope (susMS) calculated by expressing DEE as a multiple of resting metabolic rate (RMR).

Table 1. Estimated reproductive energy expenditure of male mammals in relation to mating system and male breeding mass (kg)

<table>
<thead>
<tr>
<th>Species</th>
<th>Mating system</th>
<th>Male breeding mass</th>
<th>RMR a (kJ day -1 )</th>
<th>Male breeding DEE b,c (kJ day -1 )</th>
<th>Male breeding susMS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southern elephant seal (Mirounga leonina)</td>
<td>Female defence d</td>
<td>2092 d</td>
<td>128 969 l</td>
<td>324 506 k,h,e</td>
<td>2.52</td>
</tr>
<tr>
<td>Northern elephant seal (Mirounga angustirostris)</td>
<td>Female defence d</td>
<td>1441 d</td>
<td>93 246 d</td>
<td>207 363 k,e</td>
<td>2.22</td>
</tr>
<tr>
<td>Gray seal (Halichoerus grypus)</td>
<td>Female defence d</td>
<td>298 e</td>
<td>23 688 f</td>
<td>103 414 h,e</td>
<td>4.37</td>
</tr>
<tr>
<td>Red deer (Cervus elaphus)</td>
<td>Female defence g</td>
<td>200 g</td>
<td>18 614 g</td>
<td>63 000 b,h,a</td>
<td>3.38</td>
</tr>
<tr>
<td>Antarctic fur seal (Arctocephalus gazella)</td>
<td>Female defence h</td>
<td>92 e</td>
<td>8513 i</td>
<td>54 560 b,e</td>
<td>3.44</td>
</tr>
<tr>
<td>Yellow-bellied marmot (Marmota flaviventris)</td>
<td>Female defence i</td>
<td>241 k,i</td>
<td>371k,l</td>
<td>2434 k,l</td>
<td>6.60</td>
</tr>
<tr>
<td>Fat-tailed dunnart (Georychus capensis)</td>
<td>Female defence m</td>
<td>0.02 m</td>
<td>9.30</td>
<td>68 800 c,a</td>
<td>7.44</td>
</tr>
<tr>
<td>(Sminthopsis crassicaudata)</td>
<td>Scramble competition n</td>
<td>364 n</td>
<td>50 948 o</td>
<td>86 178 b,n</td>
<td>1.52</td>
</tr>
<tr>
<td>Moose (Alces alces)</td>
<td>Scramble competition n</td>
<td>313 n</td>
<td>24 701 n</td>
<td>89 160 b,n</td>
<td>3.61</td>
</tr>
<tr>
<td>Hooded seal (Cystophora cristata)</td>
<td>Scramble competition n</td>
<td>92 e</td>
<td>8513 i</td>
<td>2036 b,e</td>
<td>2.39</td>
</tr>
<tr>
<td>Harbour seal (Phoca vitulina)</td>
<td>Scramble competition n</td>
<td>0.42 116 i</td>
<td>375 1</td>
<td>3.24</td>
<td></td>
</tr>
<tr>
<td>Namaqua mole rat (Bathyergus janetta)</td>
<td>Scramble competition n</td>
<td>0.27 166 i</td>
<td>407</td>
<td>2.45</td>
<td></td>
</tr>
<tr>
<td>North American red squirrel (Tamiasciurus hudsonicus)</td>
<td>Scramble competition n</td>
<td>0.07 n</td>
<td>72.50 o</td>
<td>137 o</td>
<td>1.89</td>
</tr>
<tr>
<td>Cape mole rat (Georychus capensis)</td>
<td>Scramble competition n</td>
<td>0.062 n</td>
<td>710 o</td>
<td>201 o</td>
<td>2.82</td>
</tr>
<tr>
<td>North American brown lemming (Lemmus trimucronatus)</td>
<td>Unknown</td>
<td>0.06 n</td>
<td>24-40 n</td>
<td>201 c,n</td>
<td>8.25</td>
</tr>
</tbody>
</table>

Breeding energy expenditure, estimated using the doubly labelled water technique or from daily mass loss of capital breeders, is expressed as daily energy expenditure (DEE) and as sustained metabolic scope (susMS) calculated by expressing DEE as a multiple of resting metabolic rate (RMR).

*Estimated for male breeding mass using intra- or inter-specific allometric equations, assuming 1 kcal = 4184 kJ and/or 19.2 kJ L -1 O 2 for respiratory quotient (RQ) = 0.81; *estimated from daily weight loss assuming all reproductive expenditure is derived from accumulated body reserves, that weight loss consists of 85% fat loss and 15% protein loss yielding 39 and 5.6 kJ g -1 respectively; *estimated using the doubly labelled water technique; *Lindenfors, Tullberg & Biuw (2002); *from pooled data Table 2 in Galimberti et al. (2007); *estimates using energy available for reproductive allocation estimated from pinniped allometric equation in Lavigne et al. (1986); *Clutton-Brock et al. (1982); *Bobek et al. (1990); *Jiang & Hudson (1994); *Armitage (1991); *Salsbury and Armitage (1994); *Salsbury and Armitage (1995); *Lee & Cockburn (1985); *Nagy (1987); *estimated from all dayurid spp. included in Lovegrove (2000); *Van Ballenberghe & Miquelle (1993); *Schwartz et al. (1988); *Mysterud et al. (2005); *Regelin et al. (1985); *Scantlebury et al. (2006); *E. Ben-Ezra, S. Woods & M. M. Humphries, unpublished data; *Peterson et al. (1976); *Lovegrove (2000).
year. We predicted that, if energetically costly, search effort would correlate positively with natural resource abundance and be elevated under simulated mast crop conditions.

Materials and methods

A free-ranging population of red squirrels was studied near Kluane National Park in the southwest Yukon Territory (YT; 61° N, 138° W) in 2004 and 2005. Squirrels were resident on three study grids. Two 40-ha grids (KL and SU) were immediately adjacent to one another and bisected by the Alaska highway, while the other 60-ha grid (AG) was c. 5 km away. Details of the study landscape (Krebs, Boutin & Boonstra 2001) and population (e.g. Humphries & Boutin 2000; Boutin et al. 2006; McAdam et al. 2007) have been reported previously. Briefly, both males and females defend individual food-based territories, centred on a food cache (midden). Population densities range from c. 1.5 to 5.3 squirrels ha\(^{-1}\) in response to food availability. During the 2 years of this study, available food was low and squirrel densities remained below 2.2 squirrels ha\(^{-1}\) (S. Boutin, unpublished data). Individuals were captured in live traps (Tomahawk Live Trap, Tomahawk, WI, USA) placed on, or in the immediate vicinity of, their middens and checked every 90 min. All individuals born into the study population were originally handled in their natal nest, and had there received unique alphanumeric ear tags in both ears (to ensure that animals could be identified in the rare event of a lost tag). Ages of such focal males (n = 32) were known with certainty. Any immigrating adults received ear tags on first capture, and for these focal males (n = 10), age is treated as a minimum estimate (i.e. age = 1 in year of first capture). Each individual was also given a unique combination of one or two coloured wires, threaded through their ear tags, on first capture of the season to allow for identification from a distance. The Biosciences Animal Policy and Welfare Committee at the University of Alberta approved all protocols for the capture and handling of red squirrels.

ENERGY EXPENDITURE

The breeding season daily energy expenditure (DEE) of 22 males was measured in 2004 and that of 27 males was measured in 2005 [n = 15 (control), n = 12 (food-add)] using the DLW technique (Lifson et al. 1955; Speakman 1997). Seven of these males were measured in both years. The DLW technique estimates the carbon dioxide (CO\(_2\)) production of animals based on the differential washout of injected hydrogen (\(^{2}\)H) and oxygen (\(^{18}\)O) isotopes (Nagy, Girard & Brown 1999; Speakman 2000; Anderson & Jetz 2005; Nagy 2005). It has been previously validated by comparison with indirect calorimetry in a range of small mammals (e.g. Speakman & Kröl 2005) and provides an accurate measure of DEE over periods of several days (Speakman et al. 1994; Berteaux et al. 1996).

Squirrels were captured, weighed and injected intraperitoneally with 0.5 mL of DLW [10% APE enriched \(^{18}\)O water (Enritech, Rehovot, Israel) and 99% \(^{2}\)H enriched water (MSD Isotopes, Pointe-Claire, QC, Canada) mixed in a ratio of 20 : 1]. Squirrels were held in the trap, following injection, for a 60-min equilibration period to allow the isotopes to equilibrate in the body (Kröl & Speakman 1999) and then bled via a clipped toenail to obtain initial blood samples for isotope analysis. Some animals (n = 4) were blood sampled without injection to estimate the background isotope enrichments of \(^{2}\)H and \(^{18}\)O. This is the best way to evaluate background isotope enrichments without taking an additional blood sample from all the measured individuals (Speakman & Racey 1987). Blood samples were heat sealed into two 100-µL glass capillaries. Squirrels were then released at the site of capture and recaptured, weighed and bled 3–5 days later, at as close as feasible to a whole 24-h period (Speakman & Racey 1988), to estimate isotope elimination rates. The range of deviation from 24 h was 0.03–8.28 h (25th percentile = 0.53 h, median = 1.32 h, 75th percentile = 2.63 h). Capillaries that contained the blood samples were then vacuum distilled (Nagy 1983), and water from the resulting distillate was used to produce CO\(_2\) and H\(_2\) following the methods of Speakman et al. (1990) for small-sample equilibration for CO\(_2\) and of Kröl, Murphy & Speakman (2007) for small-sample pyrolysis for H\(_2\). The isotope ratios \(^{18}\)O : \(^{16}\)O and \(^{2}\)H : \(^{1}\)H were analysed using gas source isotope ratio mass spectrometry (Isoprime IRMS and Isochrom μG; Micromass, Manchester, UK). Isotope enrichments were converted to values of DEE using a single pool model, as recommended for this size of animal by Speakman (1993), assuming a respiratory quotient (RQ) of 0.8. There are several alternative approaches for the treatment of evaporative water loss in the calculation (Visser & Schekkerman 1999). We used equation 7.17 from Speakman (1997), which assumes a fixed evaporation of 25% of the water flux. This approach has been established to minimize error in a range of conditions (Visser & Schekkerman 1999; Van Trigt et al. 2002). Both DEE and body mass values were subsequently log$_{10}$-transformed prior to the analysis. Indices of ambient temperature (\(T_A\)) during DEE sampling intervals were obtained by calculating the mean hourly temperature recordings between each individual’s initial and final blood sample, as recorded by a nearby weather station in Haines Junction, YT (Haines Junction Environment Canada Station, http://climate.weatheroffice.ec.gc.ca; 60° N, 137° W; c. 25 km from the study site). The DLW technique has been used successfully in this study population (Humphries & Boutin 2000; Humphries et al. 2005) and the animal use committee at McGill University approved all protocols for its use in this study.

We calculated the sustained metabolic slope (SusMS; Drent & Daan 1980) as DEE scaled to resting metabolic rate (i.e. DEE/RMR). SusMS, which reaches a limit variously suggested to be around 4 x RMR (Drent & Daan 1980) to 6–7 x RMR (Hammond & Diamond 1997), is widely recognized as a useful index of how hard an animal is working and enables comparisons across both sexes and species. We used a standard value of 166 kJ day$^{-1}$ for RMR. This value was obtained through coordination with other projects (E. Ben-Ezra, S. Woods & M. M. Humphries, unpublished data) and represents the mean RMR of 18 males from this population measured during the winter (January and February) over 2 years (2007 and 2008). Because RMR increases with mass (McNab 2002), we first compared the mean mass of the males in each of the year-grid combinations (2004 and 2005 control and 2005 food-supplemented) and those in the RMR trials. Mass did not differ significantly among the groups (ANOVA: F$\(_{2,5}\) = 1.37, P = 0.26) and we consequently used the same standard RMR value for all comparisons.

REPRODUCTIVE EFFORT

In the scramble competition mating system of red squirrels (Lane et al. 2008), the breeding season home range size of males provides an informative measure of their reproductive effort and correlates positively with their reproductive success (Lane et al. 2009). Home range sizes [n = 22 (2004), 13 (2005)] of males on the two control study grids (KL and SU) were quantified in both 2004 and 2005, using previously established protocols (Lane et al. 2009). Study grids were staked and flagged at 15- or 30-m intervals to provide spatial
references for all location data. All trap locations of individuals were recorded and the locations of any individuals seen opportunistically (for example, during regular trapping rounds) were noted. Individuals were also outfitted with radio-collars (model PD-2C; 4 g; Holohil Systems Limited, Carp, Ontario) and behavioural focal points were conducted (recording spatial locations every 30 s for 10 min) to augment our spatial data. In two cases \( n = 1 \) (2004); \( n = 1 \) (2005) males were known to have moved to a different territory during the mating season. Due to the difficulties in distinguishing these spatial movements from forays to search for reproductive females, these males were not included in analyses.

**RESOURCE LEVELS**

Natural resource levels were quantified by recording an index of the spruce cones produced, using previously established protocols (e.g., Humphries & Boutin 2000; McAdam & Boutin 2003; Boutin et al. 2006). Cones ripen in the late summer and are clipped and hoarded by squirrels in August and September to be consumed over the following winter and spring. Consequently, resources available for reproduction in the current year are produced in the previous autumn (Boutin et al. 2006). The average number of visible cones on one side of the top 3 m of each of 172 trees distributed among the control grids \( n = 85 \) (KL), \( n = 87 \) (SU) was recorded in July 2003, 2004 and 2005. Because our index of cone abundance can vary over 3 orders of magnitude (Humphries & Boutin 2000), these values were ln-transformed prior to the analysis.

To simulate mast crop-level food conditions on one study grid (AG), supplemental food was provided, in the form of ad libitum natural peanut butter (no salt or sugar added), to all resident individuals beginning in the winter of 2004. Peanut butter is nutritionally similar to spruce cones and 1 kg of peanut butter provides the approximate caloric equivalent of 5000 spruce cones (calculated from Brink & Dean 1966; Nienstaedt & Zasada 1990). Individuals were provided with an elevated feeder, centred over their midden that contained 1 kg of peanut butter. Peanut butter was replaced, prior to depletion, throughout October–May. This ensured constant food availability through the winter and into the following breeding season.

**STATISTICAL ANALYSES**

A general linear model (GLM) with a three-way interaction term (year \( \times \) age \( \times \) searching effort) was used to investigate the interactive effect of these variables on DEE of control males during the breeding season. One record from each male that was measured in both years \( n = 7 \) was randomly selected. Year was incorporated as a two-level (2004 and 2005) categorical variable and age class was incorporated as a three-level categorical variable [yearling \( n = 10 \), mature \( 2–4 \) years old; \( n = 11 \) and old \( 25 \) years old; \( n = 16 \)], following previously established protocols (Descamps et al. 2009). Search effort, represented as the log_{10} transformed home range size, was incorporated as a continuous variable. Ambient temperature, log_{10}-transformed body mass and the number of data points used (range: 7–485) in the home range calculations were also included as covariates. Due to our limited sample size, we did not include grid as a categorical variable. However, in previous analyses (Lane et al. 2009), including grid as a factor was not shown to influence the relationship between male-breeding season home range size and either mating or reproductive success. To analyse the within individual variation in DEE across the 2 years, a paired-sample \( t \)-test was used. This analysis was restricted to control males sampled in both years \( n = 7 \).

A GLM was used to determine whether the DEEs of males on the food-supplemented grid \( n = 12 \) differed from those of males on the control grids \( n = 15 \) in 2005. A complicating factor in this analysis is that food supplemented females breed earlier than control females (Kerr et al. 2007). Males on AG were thus measured earlier than KL and SU in an attempt to pair DEE measurements by reproductive chronology rather than Julian date. The inclusion of \( T_w \) as a covariate, however, should control for temperatures being warmer later in the season. Log_{10}-transformed body mass was also included as a covariate in the analysis and the treatment \( \times \) age class interaction was included to investigate whether the effects of resource availability varied across age classes. All analyses were implemented in \( r \) (ver. 2.6.0; R Core Development Team, Boston, MA, USA) and values are presented as mean ± 1 SE.

**Results**

The red squirrel breeding season on the control grids (KL and SU) extended from 5 March to 19 May in 2004 and 21 March to 17 July in 2005. On the experimental grid (AG) in 2005, the breeding season extended from 28 February to 3 May. We measured the DEE of males during the peak periods of these breeding seasons (Fig. 1). On the control grids, the mean breeding season DEE across the 2 years was 407 ± 38 kJ day⁻¹ \( n = 37 \). In comparison with the mean winter RMR of males in this population \( 166 \) kJ day⁻¹; E. Ben-Ezra, S. Woods & M. M. Humphries, unpublished

**Fig. 1.** Histogram showing the total number of oestrous females (white bars) and doubly labelled water-sampled males (black bars) across the breeding seasons on the control grids in 2004 (a) and 2005 (b) and the food-supplemented grid in 2005 (c). Oestrous dates of females were determined either through behavioural observation of mating behaviour (\( n = 43 \)) or by back-calculating 35 days from parturition dates (\( n = 150 \)). Dates are relative to the first observed oestrous bout and are grouped into 5-day bins. Individual males were sampled for 3–5 days and so may be present in more than one date bin.
The three-way interaction (year × search effort × age class) is significant; we do not attempt to interpret the lower-order interactions or independent component variables. Because the three-way interaction (year × search effort × age class) is significant, we do not attempt to interpret the lower-order interactions or independent component variables.

Table 2. Degrees of freedom, coefficients, standard errors and statistical significance (including F-statistics and P-values) for terms retained in the final general linear model of breeding season daily energy expenditure of male North American red squirrels on control grids.

<table>
<thead>
<tr>
<th>Term</th>
<th>d.f.</th>
<th>Coefficient</th>
<th>SE</th>
<th>F</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year × search effort × age class</td>
<td>1, 18</td>
<td>-2.12</td>
<td>0.67</td>
<td>10.08</td>
<td>0.005</td>
</tr>
<tr>
<td>Year × search effort</td>
<td>1, 18</td>
<td>n.a.</td>
<td>n.a.</td>
<td>12.10</td>
<td>0.003</td>
</tr>
<tr>
<td>Year × age class</td>
<td>1, 18</td>
<td>n.a.</td>
<td>n.a.</td>
<td>22.10</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Search effort × age class</td>
<td>1, 18</td>
<td>n.a.</td>
<td>n.a.</td>
<td>0.35</td>
<td>0.56</td>
</tr>
<tr>
<td>Year</td>
<td>1, 18</td>
<td>n.a.</td>
<td>n.a.</td>
<td>46.86</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Search effort</td>
<td>1, 18</td>
<td>n.a.</td>
<td>n.a.</td>
<td>1.79</td>
<td>0.20</td>
</tr>
<tr>
<td>Age class</td>
<td>1, 18</td>
<td>n.a.</td>
<td>n.a.</td>
<td>16.59</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Log mass</td>
<td>1, 18</td>
<td>1.56</td>
<td>0.46</td>
<td>9.55</td>
<td>0.0006</td>
</tr>
<tr>
<td>Ambient temperature</td>
<td>1, 18</td>
<td>-0.01</td>
<td>0.01</td>
<td>15.32</td>
<td>0.001</td>
</tr>
</tbody>
</table>

The mean DEE of breeding males exhibited substantial inter-annual variation (Fig. 4), despite similar and low levels of available (i.e. produced the previous autumn) food across the two study years (2003 ln-transformed cone index = 0.9; 2004 ln-transformed cone index = 1.0). In anticipation of high upcoming food (2005 ln-transformed cone index = 3.4), however, mean DEE values on control grids in 2005 (579 ± 73 kJ day⁻¹; n = 15) approximately doubled those recorded in 2004 (290 ± 7 kJ day⁻¹; n = 22). These levels of DEE represent susMS values of 3.5 × RMR (2005) and 1.7 × RMR (2004). The highest levels of DEE were recorded from food-supplemented males in 2005 (873 ± 98 kJ day⁻¹; n = 15) approximately doubled those recorded in 2004 (579 ± 73 kJ day⁻¹; n = 15) in the same year (GLM: F₁, 22 = 6.96, P = 0.01; Fig. 4).

Discussion

Over the last three decades, evidence of the high energetic costs of breeding to male mammals (often exceeding the corresponding costs to females) has steadily accumulated (Table 1). Although this pattern seemingly challenges one of the fundamental assumptions of traditional sexual selection theory, it has been largely unknown whether it may hold...
across different mating systems, and therefore be considered a general feature of mammalian reproduction. Here we report a similarly costly energetic allocation to reproduction in a small, relatively monomorphic, male mammal displaying a scramble competition mating system. The breeding season susMS of male red squirrels, exposed to natural food conditions, averaged $c. 2.5 \times RMR$ but single year estimates (2005) were over $3.5 \times RMR$ and, under ad libitum food conditions, were over $5 \times RMR$. This latter value approaches presumed physiological limits and is in the top 20% of published values (Drent & Daan 1980; Hammond & Diamond 1997).

During the winter, both male and female red squirrels make use of exceptionally well-insulated nests and limit their out of nest activities to the warmest parts of the day. As a result, the winter susMS of individuals prior to the breeding season is low (Humphries et al. 2005; S. Woods, Q. Fletcher & M. M. Humphries, unpublished data). Upon commencement of the breeding season, however, males must endure the locomotory and thermoregulatory costs of long distance forays to locate receptive females (Lane et al. 2009). Consequently, the average susMS of breeding males approximates that of lactating females in this population ($2.2 \times RMR$; Humphries & Boutin 2000; M. M. Humphries, unpublished data) and single-year estimates can far exceed this value. However, two caveats need to be addressed when comparing DLW estimates of energy expenditure between male and female mammals. First, these estimates on females do not account for energy exported in milk (Butte, Wong & Hopkinson 2001). They do, however, capture the metabolic requirements of both milk production and for acquiring and assimilating the resources required for milk production. Thus, DLW comparisons of males engaged in reproductive activity with that of lactating females provide useful insight into the metabolic consequences of their respective reproductive investments. Second, estimates of the total energetic costs of reproduction need to incorporate the relative lengths of the reproductive periods to the two sexes. In red squirrels, these periods are remarkably similar in duration for the two sexes. Males are engaged in mating activity during the, on average, 105-day breeding season (Lane et al. 2009; S. Boutin, unpublished data) and the combined length of gestation (35 days) and lactation (70 days) for females is also 105 days (Humphries & Boutin 2000). Consequently, both daily and total reproductive energy investment by males can be similar to, or exceed that, by females.

In the scramble competition mating system of red squirrels, male reproductive success correlates positively with search effort, generating directional positive sexual selection on this trait (Lane et al. 2009). We predicted that, if energy available for reproductive allocation is an important limitation on search effort, elevated individual effort should entail a corresponding energetic cost. DEE did increase with search effort, but this relationship was only observable in the breeding season preceding the mast crop. We suggest, therefore, that reproductive effort does entail an energetic cost, but that it is only observable under conditions of intensified reproductive investment. Although the breeding season home range size of an individual provides a general picture of the area over which he searched for reproductive opportunity, it does not provide an estimate of the intensity of the search effort. For example, a male could increase his effort by making multiple forays to assess the reproductive status of females and our data do not have the resolution to detect this type of increased investment. Future studies quantifying the detailed activity budgets of males, in concert with breeding season home range size, will provide a more comprehensive picture of energetic costs incurred by elevated reproductive effort.

Males also showed contrasting patterns of breeding season DEE among age classes. In general, yearlings and males in the oldest age class expended greater energy than mature males. In addition, at the individual level, while the DEE of mature males was similar, or moderately lower in 2005 when compared with 2004, it more than doubled in older males. Thus, old males that are least likely to survive long enough to experience another mast crop in their lifetime showed an increase in reproductive energy investment, while those that are likely to survive to future breeding seasons (mature age class) showed no increase, as would be predicted if current investment incurs a cost to future survival and reproduction (Williams 1966; Descamps et al. 2007).

Yearling males, as well, showed elevated expenditure. This pattern parallels that seen in females in this population, whereby yearling females and those in the oldest age class pay higher costs to reproduction (measured as future survival) than those in the mature age class (Descamps et al. 2009). These differential costs have been attributed to yearling females still growing during their first year of reproduction. If males are, similarly, still investing energy to their soma, the metabolic investment to growth should compound the investment to reproduction.
The influence of resource abundance on energy expenditure of males proved to be more intricate than we initially predicted. Expenditure of control males varied substantially across 2 years that varied little in available (i.e. cached from the previous year) natural food. However, although available food conditions were similar, upcoming conditions varied substantially. Specifically, the 2004 breeding season preceded a food shortage and the 2005 season preceded a mast crop of superabundant food. As the density of squirrels closely tracks food abundance (S. Boutin, unpublished data), individual males reproducing in breeding seasons preceding mast crops have low current food resources, but they also have few competitors. In addition, any offspring they sire will experience high levels of food following emergence and, as a consequence, high over winter survivorship and recruitment (McAdam & Boutin 2003). Life-history patterns in this population have seemingly evolved to optimize fitness in the context of fluctuating food resources and our results on males indicate that selection has seemingly evolved to optimize fitness in the context of fluctuating food resources and our results on males parallel those previously reported on females (Boutin et al. 2006). Female red squirrels are capable of anticipating upcoming food conditions, evidenced by mean litter sizes increasing, individuals attempting second litters following successful first attempts and a greater proportion of yearlings reproducing in breeding seasons preceding mast crops (Boutin et al. 2006). Our results suggest that males similarly attempt to capitalize on potential fitness payoffs by allocating greater amounts of energy to reproduction in anticipation of high upcoming levels of food.

Our results from the food-supplemented grid, AG, in 2005 approximate what would be seen under natural conditions following a mast crop. Although this study grid, unlike the controls, did not experience the upcoming mast crop, the food supplementation over the previous winter resulted in both high overwinter survivorship of individuals (S. Boutin, unpublished data) and energy available for reproduction. As a result, while both reproductive opportunities (due to a high female density) and energy available for reproduction to males was high, competition for these opportunities was severe (due to a high male density). To capitalize on these opportunities, males invested the greatest mean level of energy observed over the study. These results, as well, parallel those seen in females in years following mast crops, whereby reproductive investment is elevated by breeding earlier in the season and producing faster growing offspring (Boutin et al. 2006).

In conclusion, we have shown that the energetic costs of reproduction to males of a small, relatively monomorphic, mammal with a scramble competition mating system can be high and responsive to potential fitness payoffs. In combination with those reported from other systems (Table 1), these results suggest that high and, potentially limiting, energetic costs to males may be a general feature of mammalian reproduction. To our knowledge, this is the first evidence of male reproductive effort being sensitive to both current and upcoming resource levels. We would predict, however, a similar relationship between current food conditions and reproductive effort in the males of other species, in which individual male effort correlates positively with energetic expenditure (e.g. Galimberti et al. 2007). Furthermore, in resource pulse systems, we would also predict a relationship with upcoming food conditions. Future studies quantifying the energetic costs of reproduction to both sexes, within the context of resource availability, should provide a more general picture of the ecological limits to reproduction, and therefore the action of sexual selection in natural populations.

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