

Competition between Eurasian red and introduced Eastern grey squirrels: the energetic significance of body-mass differences

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Daily energy expenditure (DEE) was measured in sympatric populations of red and grey squirrels using the doubly labelled water technique. Grey squirrels had significantly higher DEEs than red squirrels. However, the difference between the species was not separable from the effects of body mass on DEE. The DEEs of both species were in accordance with published allometric predictions incorporating body mass and ambient temperature. The differences in energetic requirements and social dominance, both consequences of body size, may represent means by which grey squirrels exert more interspecific competition on red squirrels than do conspecifics, potentially driving populations below viable levels in some sites.

Keywords: body mass; conservation; daily energy expenditure; doubly labelled water; red squirrel; grey squirrel

1. INTRODUCTION

Studies of energetics have provided insight into some pressing conservation problems (Gorman *et al.* 1998). Grey squirrels are just one of many introduced species to have caused a threat to a native congener (Macdonald *et al.* 2001). The potential significance of different energy requirements as a consequence of differences in body mass is examined here in relation to the competition between red and grey squirrels.

Competition for food has been proposed as the most likely mechanism by which grey squirrels (body mass *ca.* 570 g) have excluded red squirrels (body mass *ca.* 300 g) throughout much of the British Isles since their introduction at the end of the nineteenth century (Kenward & Holm 1989; Gurnell & Pepper 1993; Skelcher 1997; Kenward *et al.* 1998), and more recently in northern Italy (Wauters *et al.* 1997; Wauters & Gurnell 1999). Previous studies have found their diets to be largely similar when the two species are allopatric, with red squirrels specializing on coniferous seed and grey squirrels specializing on the mast of large-seeded broad-leaved trees (Tittensor 1977; MacKinnon 1978; Tonkin 1983; Moller 1983, 1986). Niche overlap in sympatry was estimated to be 75% in one conifer plantation in northern England (Wauters *et al.* 2000) and 77% in the site where this study was conducted (Bryce 2000), indicating that there is considerable potential for dietary competition. Daily food requirement is closely related to field metabolic rate (FMR) when there is no substantial export of energy (Nagy 1994; Speakman 1997). Hence, in this study, field energy expenditures were estimated, to provide a quantitative comparison of the energy requirements of the two species.

Body mass has been found to be important in intraspecific social dominance in red (Wauters & Dhondt 1989, 1992) and grey squirrels (Pack *et al.* 1967; Allen & Aspey 1986). Therefore, a grey squirrel would be

expected to displace a red squirrel. Frequent observations have been made of red and grey squirrels in close proximity without any interaction (Reynolds 1981; Wauters & Gurnell 1999); hence, most encounters appear to be passive. However, subtle social interactions are predicted to favour the larger grey squirrel (Bertram & Moltu 1986). Several studies have reported difficulties in trapping red squirrels where grey squirrels are present (Skelcher 1993; Kenward & Hodder 1998; Bryce 2000). These observations provide some evidence that grey squirrels may claim more exclusive access to prime food sources, including baited traps.

Holarctic tree squirrels do not hibernate in winter, as this is the time of highest seed abundance (Reynolds 1985). Instead, they focus activity around the middle of the day between January and March, minimizing exposure to extreme temperatures (Tonkin 1983; Reynolds 1985; Kenward 1985, 1992; Wauters & Dhondt 1987; Wauters *et al.* 1992) and remaining in their dreys for up to 22 h a day (Pauls 1978, 1981). Millar & Hickling (1990) predicted that larger species should deposit relatively more fat prior to potentially inclement conditions than smaller species. In broad-leaved woodland, allopatric grey squirrels have been found to increase their body mass by 23% over winter, compared with only 12% for red squirrels (Kenward & Holm 1989). However, in purely coniferous forests, with access only to smaller conifer seeds, grey squirrels have been reported to have very low levels of body fat (P. Lurz, personal communication).

We set out to examine the relationships between daily energy expenditure (DEE), body mass and ambient temperature in red and grey squirrels. A theoretical competition coefficient was derived to describe the impact of adding one grey squirrel, as opposed to one red squirrel, to the total number of sympatric squirrels, based on their relative energetic requirements. These predictions assume that food availability limits squirrel numbers. This assumption is deemed to be reasonable because,

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although other factors may be involved, squirrel population densities are primarily determined by food availability (Nixon *et al.* 1975; Gurnell 1983; Kenward & Holm 1989; Andren & Lemnell 1992; Wauters & Lens 1995).

2. METHODS

(a) *Field measurements*

The study was based in Craigvinean Forest (a Forest Enterprise plantation of *ca.* 2000 ha), Dunkeld, Perthshire, UK, 3°40' W, 56°34' N. The forest is predominantly coniferous, containing spruce (*Picea abies* and *Picea sitchensis*), Scots pine (*Pinus sylvestris*), larch (*Larix decidua*) and Douglas fir (*Pseudotsuga menziesii*), with adjoining riparian corridors of ash and wych elm (*Fraxinus excelsior*, *Ulmus glabra*), mixed woodland with planted oak (*Quercus robur*) and beech (*Fagus sylvatica*).

Between April 1998 and March 1999, doubly labelled water (DLW) samples were obtained from 11 red and 19 grey squirrels. Sampling took place in each of three seasons defined by food availability: March–June (spring shortage), July–October (autumn abundance) and November–February (over winter). We attempted to sample the same squirrels in each season; however, few were recaptured in winter. Hence, the individuals sampled comprised a mixture of repeated measures and independent samples.

In all, 20 cage traps, at a density of *ca.* two traps per hectare, were pre-baited for three days and then set for up to ten days in each season. Cage traps consisted of mink traps (Fuller Engineering Ltd, East Grinstead, UK) modified with wooden base boards and nest boxes. Traps were placed 1–2 m above the ground, in trees or on platforms. Squirrels were individually marked with a combination of tail clips, transponders (Trovan™, R. S. Biotech, Finedon, UK) and radio-collars (Biotrack, Wareham, UK). Squirrels were weighed to the nearest 5 g using a Pesola spring balance, and injected with the H²O¹⁸ isotope by intrapericardial injection. Squirrels were then placed back in the traps, which were covered and left undisturbed for a period of at least 1 h. Blood was then removed from the tip of the tail and collected in 100 µl capillary tubes, which were flame sealed using a butane torch. Squirrels were released, and recaptures were attempted after intervals as close to 24 h as possible (Speakman & Racey 1988; Speakman *et al.* 1994). Traps were checked regularly so that squirrels were not in the traps for prolonged periods. A second blood sample was obtained on recapture. No more than three samples were obtained for any one squirrel within any seven-day period. The total sample sizes were 25 measurements on 11 individual red squirrels and 54 measurements on 19 individual grey squirrels. Syringes were weighed before and after injection to an accuracy of 0.001 g to calculate the volume of DLW injected. Water samples were collected, for each squirrel, from the nearest running source to establish background levels of the isotopes. Ambient temperature was recorded using the dry-bulb reading from a whirling hygrometer.

(b) *Laboratory analysis*

Blood samples were distilled using the pipette method of Nagy (1983). Mass-spectrometric analysis of deuterium enrichment was performed using H₂ gas, produced from the distilled water after reaction with LiAlH₄ (after Bocek *et al.* 1973). Reactions were performed inside 10 ml Vacutainers (Beckton Dickinson Ltd, Cowley, UK) as detailed in Krol & Speakman (1999).

For analysis of ¹⁸O enrichment, distilled water was equilibrated with CO₂ gas using the small-sample equilibration technique (Speakman *et al.* 1990). Pre-weighed Vacutainers were injected with 10 µl of distilled water and re-weighed (to the nearest 0.0001 g) to correct for differences in the amount of water added. Subsequently, the Vacutainers with the samples were injected with 0.5 ml CO₂ of a known oxygen isotopic enrichment and left to equilibrate at 60 °C for 16 h.

To estimate the injectate enrichment, the original injectate was diluted with tap water (five different solutions, ±0.0001 g) in proportions similar to those expected in the injected squirrels (*ca.* 0.2 g injectate and 19–31 g water) (Speakman 1997). Mass-spectrometric analyses of ²H and ¹⁸O were performed on five subsamples of each solution and five subsamples of tap water. The enrichment of injectate was calculated for the five different solutions (Speakman 1997) and then averaged.

The ratios of ²H to ¹H and ¹⁸O to ¹⁶O were measured using dual-inlet gas source isotope-ratio mass spectrometry (Optima, Micromass IRMS, Manchester, UK) with isotopically characterized gases of H₂ and CO₂ (CP grade gases, BOC Ltd.) in the reference channels. The reference gases were characterized every three months relative to standards distributed to other laboratories. These demonstrated good comparability with the mean results across other laboratories (Speakman *et al.* 1990). Each batch of samples was analysed with triplicates of three laboratory standards to correct for day-to-day variations in the performances of the mass spectrometers. All isotope enrichments were measured in delta (per mil) relative to the working standards, and converted to ppm using established ratios for the reference materials. Measures of isotope enrichment were based on independent analyses of two subsamples of the water distilled from the blood samples.

There has been considerable recent debate over the method by which estimates of isotope enrichment should be converted to CO₂ production (summarized in Speakman 1997). We estimated CO₂ production using the single-pool deuterium equation from Speakman (1997). The error in individual estimates was determined using the iterative procedures outlined in Speakman (1995). Conversion to energy expenditure was made by assuming respiratory quotient (RQ) to be equal to 0.8. All calculations were performed using the Natureware DLW software (Speakman & Lemen 1999).

(c) *Statistical analysis*

Variability in DEE between individuals of each species was investigated using analysis of variance (ANOVA) (applied with SAS PROC GLM (SAS 1985)). The relationships between DEE and body mass, species, sex, season and temperature were also examined using the SAS GLM procedure. As independent variables were not orthogonal, the analyses were repeated, entering the variables in different permutations, to determine the extent of the effects attributed to each variable in sequential models (where there was more than one estimate for the same squirrel in the same season, a mean was used in the analysis).

3. RESULTS

There was some evidence of variation in DEE between individual red squirrels ($F_{3,13} = 2.34$, $p = 0.101$), while this variation was statistically significant in grey squirrels ($F_{13,35} = 2.50$, $p = 0.037$). There were no significant differences in DEE between male and female squirrels in either species, nor were there any significant seasonal

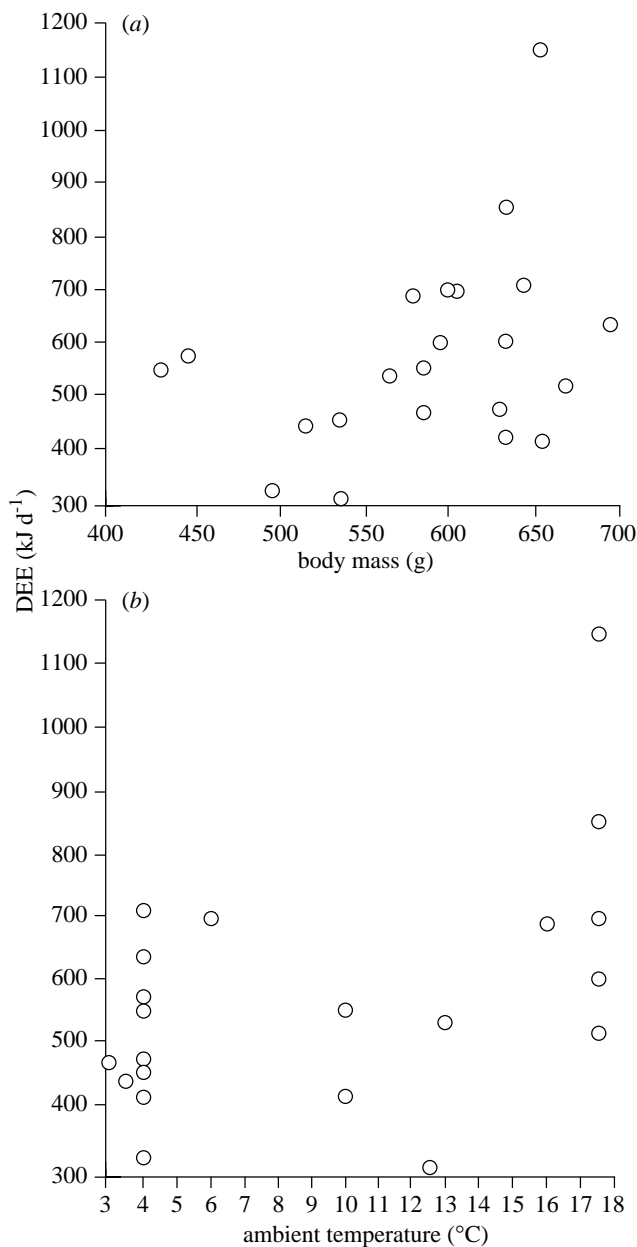


Figure 1. The relationships between daily energy expenditure and (a) body mass and (b) ambient temperature for grey squirrels.

differences ($F_{1,36} = 0.06$, $p = 0.811$ for sex, and $F_{2,35} = 1.53$, $p = 0.229$ for season); hence, these parameters were removed to simplify the final model. However, the autumn mean DEE for grey squirrels was *ca.* 200 kJ per day higher than the winter mean. Red squirrels exhibited less seasonal difference, with the highest DEE in spring and the lowest in autumn (mean \pm s.e.m. = 389.8 \pm 122.5 kJ per day in spring, and mean \pm s.e.m. = 313.5 \pm 280.6 kJ per day in autumn). The only squirrel to be sampled in all three seasons recorded DEE values of 310 kJ per day in spring (6 °C), 160 kJ per day in autumn (16 °C) and 334 kJ per day in winter (5 °C).

The DEE of grey squirrels was significantly greater than that of red squirrels, but this difference was entirely explained by body-mass differences between the species. There was no evidence of a species interaction with body mass and DEE ($F_{1,35} = 0.0$, $p = 0.98$ for the interaction term),

and so a common linear-regression coefficient, b , was estimated for the two species. DEE increased with body mass: $b = 0.98$ for both species (with non-significantly different intercepts of +30.48 for red squirrels and -3.46 for grey squirrels). This model indicated that there was no evidence for a species effect other than that which could be attributed to the difference in body mass between the species ($F_{1,36} = 0.06$, $p = 0.8047$). However, when adjusting for species, there was evidence that larger squirrels had higher DEEs than smaller ones ($F_{1,36} = 4.28$, $p = 0.045$). This model explained 39% of the variation in DEE.

Overall, there was no significant effect of ambient temperature on DEE. However, when red and grey squirrels were analysed separately, there was a significant tendency for grey squirrels to expend more energy at higher ambient temperatures. In a multiple-regression model, only temperature significantly affected DEE, while body mass did not ($F_{1,19} = 3.46$, $p = 0.079$ and $F_{1,19} = 1.26$, $p = 0.280$, respectively). (The model fitted for this analysis was $\text{DEE} = 97.10 + (11.9 \times \text{temperature}) + (0.60 \times \text{body mass})$; the standard deviations for the slopes were 6.38 and 0.55, respectively.) Figure 1 illustrates these relationships.

4. DISCUSSION

We found some evidence for variation in DEE between individual squirrels. Variation between individuals can be accounted for by the fact that samples of both species included individuals across a range of age classes and reproductive conditions. Other studies have found a high coefficient of variation between individuals at different stages of reproduction (range for small mammals, 7.6%–59.5%) (Stephenson *et al.* 1994). Although intercorrelated with body mass, differences in age and reproductive stage are likely to have affected behaviour and, therefore, activity levels and DEE. However, larger sample sizes would be required to include these as independent variables in the analysis.

In a recent review of FMRs in small mammals, Speakman (1999) derived an equation to predict FMR from body mass and ambient temperature.

$$\log \text{FMR} = 2.22 + (0.670 \times \log_e \text{body mass}) - (0.0236 \times \text{ambient temperature}).$$

(Speakman 1999) (1)

The mean weights of the squirrels sampled here were 322 g for red squirrels and 588 g for grey squirrels. Therefore, at 10 °C we might have expected an FMR of 348 kJ (95% confidence interval, 312.4–387.6 kJ) for red squirrels and 521 kJ (95% confidence interval, 460.8–589.1 kJ) for grey squirrels. The mean DEE for red squirrels across a range of temperatures (3–17.5 °C) was 347 kJ, almost identical to the prediction; for grey squirrels the mean DEE (574 kJ) was 10.2% greater than predicted, but within the 95% confidence interval. From the measured and predicted DEEs we would, therefore, expect grey squirrels to have to consume more than red squirrels to meet their energy expenditure.

Elsewhere, red squirrels' daily consumption of Norway-spruce seeds has been estimated to accrue 393 kJ (Gronwall 1982), while winter estimates in Belgian conifer forests averaged 338 \pm 31 kJ (Wauters *et al.* 1992).

The mean DEE measured here for red squirrels accords well with these values of consumption. However, we would expect consumption to exceed DEE because some energy will be lost, through the inefficiencies of assimilation, as faeces and urine.

Extrapolating further, consider a landscape of 25 ha providing six Scots pine cones per square metre each year (see South 1999; the range estimated in Wauters *et al.* 2000 was 4.8–20 per m²). The annual energy content of this patch can be estimated as 50.1×10^3 kJ, based on the gross energy content of each cone being 3.34 kJ (South 1999). If we assume that squirrels assimilate approximately 75% of the available energy (Ludwick *et al.* 1969; Montgomery *et al.* 1975) then this patch would be predicted to support a maximum of 29.7 red squirrels (1.19 per ha), each using 126 655 kJ per year, or 17.9 grey squirrels (0.72 per ha), each using 209 510 kJ per year. At carrying capacity, we would expect red squirrels to occupy the same habitat at higher densities than grey squirrels, as a consequence of their lower energetic demands. Yet under 'contest' conditions (Gurnell 1987), the same resource landscape with 10 grey squirrels would only be expected to hold another 13.1 red squirrels at carrying capacity (a total of 23.1 squirrels), compared with 29.7 when there were only red squirrels. This suggests a theoretical competition coefficient, whereby one grey squirrel will use up 1.65 times the available food energy of one red squirrel. This prediction probably relies more heavily upon the assumption that grey squirrels will be socially dominant to red squirrels, and hence gain better access to food resources, than on the fact that they have greater energetic requirements. However, the fact that each individual grey squirrel potentially demands more of the available resources would be expected to accelerate resource depletion relative to a situation where there are only red squirrels.

Faced with the generally accepted conclusion that grey squirrels have been responsible for displacing red squirrels throughout much of Britain and parts of northern Italy, it seems that some competitive effect has been manifested. However, red and grey squirrels have experienced prolonged coexistence at our study site, apparently fostered by habitat partitioning (Bryce 2000). Hence, differences in foraging efficiencies, habitat preferences and intraspecific interactions between species and between sites may disrupt and even reverse these predictions. For example, Brown *et al.* (1994) discussed the variety of mechanisms by which temporal and spatial variation in foraging efficiency and patch use have promoted coexistence among desert rodent communities. Hence, where food availability or foraging efficiencies are low, reduced energy requirements as a consequence of lower body mass could favour red squirrels. Indeed, observations of elongated periods of activity (Smith 1999) and reduced fat deposits (P. Lurz, personal communication) suggest that grey squirrels may find it harder to meet their greater energetic demands in purely coniferous forests than in broad-leaved forests. The proportional changes (minima to maxima) in mean weights for other squirrels at this site were 5.9% ($n=9$) for red squirrels and 15.6% ($n=4$) for grey squirrels (Bryce 2000). However, red and grey squirrels differed in their proportional use of coniferous and broad-leaved habitats at this

site, with grey squirrels occupying the more mixed habitats. The seasonal difference in body mass for grey squirrels was less than that reported by Kenward & Holm (1989) for broad-leaved woodland but is not indicative of a purely coniferous habitat.

In conclusion, the implication of the measured energy requirements is that grey squirrels will need to consume more than red squirrels to maintain a positive energy balance. Given their differences in body mass, this finding is not entirely unexpected. Nevertheless, the consequence is that grey squirrels are likely to exert more competition on red squirrels than do conspecifics, through a combination of consuming more food and, possibly, gaining more exclusive access to the available resources, again by virtue of their greater body size. But are these body-mass differences sufficient to bring about the competitive displacement of red squirrels? For this to be the case, these differences would need to be reflected in changes in red-squirrel numbers, either through poor recruitment or increased mortality. Competition with grey squirrels may prevent red squirrels from attaining a minimum breeding weight and so limit reproduction (Wauters & Dhondt 1989). Alternatively, food limitation may reduce red-squirrel survival, most likely of sub-adults (Wauters *et al.* 2000). Yet it could be speculated that grey squirrels do not have the same opportunity to increase reserves in autumn in conifer forests that they do in broad-leaved woodland, and hence do not profit from the same advantages over red squirrels. However, these findings provide evidence for a mechanism by which grey squirrels may replace red squirrels by virtue of their greater body size alone.

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