The Company of **Biologists**

RESEARCH ARTICLE

Daily energy expenditure in the face of predation: hedgehog energetics in rural landscapes

Carly E. Pettett[1,*], Paul J. Johnson[1], Tom P. Moorhouse[1], Catherine Hambly[2], John R. Speakman[2] and David W. Macdonald[1]

ABSTRACT

Failure to balance daily energy expenditure (DEE) with energy intake can have an impact on survival and reproduction, and therefore on the persistence of populations. Here we study the DEE of the European hedgehog (*Erinaceus europaeus*), which is declining in the UK. We hypothesise that there is a gradient of suitable habitat for hedgehogs in rural areas, which is a result of fewer food resources, a higher risk from predation by badgers (*Meles meles*) and colder ambient temperatures, as distance to the nearest building increases. We used the doubly labelled water method to obtain 44 measurements of DEE from hedgehogs on four predominately arable sites, to determine the energetic costs associated with proximity to buildings, on sites with and without badgers. The mean±s.e.m. DEE was 508.9±34.8 kJ day^{-1}. DEE increased the further a hedgehog was from buildings during the study, possibly as they ranged larger distances on arable land, supporting the hypothesis that hedgehogs select villages owing to the lower energy demands in comparison to arable farmland. Hedgehogs had an approximately 30% lower DEE on sites with badgers. We speculate that on badger-occupied sites, hedgehogs may restrict movement and foraging in response to a threat from predation and thus have reduced DEE. Therefore, hedgehogs may also seek refuge in villages where the perceived threat of predation is lower and foraging is unrestricted. In a broader context, we demonstrate that individual differences in DEE can aid in understanding habitat selection in a patchily distributed species.

KEY WORDS: Arable farmland, Doubly labelled water, Landscape of fear, *Meles meles*, Predation risk

INTRODUCTION

Energy balance is essential in all animals for survival and reproduction. The cost of homeostasis, particularly body temperature regulation, in mammals can be high (Nagy, 1987), and small mammals must maintain a high metabolic rate to maintain endothermy (McNab, 1983). However, energy must also be allocated for activity, growth and reproduction (Brown et al., 2004). An animal's field metabolic rate, or daily energy expenditure (DEE), measures the total energy individuals spend under differing environmental and physiological conditions.

An individual's survival (Zub et al., 2011) and reproduction (Rutkowska et al., 2011; Speakman, 2008) depend on the balance between energy input and output, and so examining differences in DEE between populations of declining species, and how this is affected by environmental factors, may reveal which environmental factors are particularly contributing to that species' decline.

There are two competing hypotheses regarding environmental conditions and DEE, both based on the positive correlation between mass-independent resting metabolic rate (RMR) and DEE (Speakman et al., 2003). In poor quality habitats, e.g. those with dispersed resources or a harsh climate, individuals may have higher energy demands and therefore RMR and DEE may be forced up (Speakman et al., 2003). Conversely, RMR and DEE may be restricted in poor quality habitats because of low availability of resources, which may result in lower energy available to invest in growth and reproduction (Bozinovic et al., 2007; Burton et al., 2011; Speakman et al., 2003). Additionally, energy expenditure increases with locomotion (Covell et al., 1996; Kenagy and Hoyt, 1989) and ranging behaviour varies in response to resource availability (Ford, 1983).

Predation risk is likely to affect an individual's behaviour and, therefore, energetic expenditure (Lima, 1998; McNab, 1986). Under a perceived threat of predation, individuals may expend energy by fleeing (Kenagy and Hoyt, 1989), or as a result of increased physiological stress (Boonstra et al., 1998; Tidhar et al., 2007). Individuals may also be forced to alter habitat use (Kotler et al., 1991) or restrict foraging to avoid predation (Banks et al., 1999; Ergon et al., 2004). Thus, predator presence can indirectly affect survival through reducing individuals' body mass and reproductive success (Ergon et al., 2004; Hik, 1995; Monarca et al., 2015a,b).

We use the European hedgehog (*Erinaceus europaeus* Linnaeus 1758) as a model species for studying the effects of habitat productivity and predator presence on DEE. The hedgehog is declining and patchily distributed in the UK (Aebischer et al., 2011; Hof, 2009; Roos et al., 2012), and declines are thought to be more severe in rural areas (JNCC, 2010). Arable land is typically under-selected by dispersing hedgehogs, which show an attraction to urban habitats such as rural villages (Doncaster, 1992, 1994, 2001), potentially because of poor habitat quality on arable land, in combination with the presence of their main predator, the badger [*Meles meles* (Linnaeus 1758)] (Hof et al., 2012; Micol et al., 1994).

Hedgehogs prey on macroinvertebrates (Yalden, 1976; Wroot, 1984) and arable land may be unfavourable owing to a lack of prey, resulting from agricultural intensification (Macdonald and Feber, 2015a,b; Moreby and Southway, 1999; Robinson and Sutherland, 2002; Wilson et al., 1999). Residential areas have abundant mowed grass habitats – e.g. amenity grassland and garden lawns (Doncaster, 1992, 1994) – which typically have higher earthworm abundance than arable fields (Kruuk et al., 1979). Hedgehogs may also benefit from supplementary feeding in gardens (Hubert et al., 2011; Morris, 1985) and warmer ambient temperatures than on arable land (Hubert et al., 2011). Badgers are more abundant on open farmland than in rural villages (Neal and Cheeseman, 1996), and hedgehog presence is

[1]Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxfordshire OX13 5QL, UK. [2]Energetics Research Group, Zoology Department, University of Aberdeen, Aberdeen AB24 2TZ, UK.

*Author for correspondence (carly.pettett@gmail.com)

C.E.P., 0000-0002-4390-0696

negatively correlated with the abundance of their setts (Micol et al., 1994; Young et al., 2006). Although foxes and domestic dogs also prey on hedgehogs (Reeve, 1994), badgers may be particularly detrimental to hedgehogs because they are intraguild predators, also competing for earthworms (Doncaster, 1992; Neal, 1986; Polis et al., 1989).

In rural landscapes, hedgehog food availability, temperature and relative safety from badger predation are all likely to decrease with increasing distance from buildings (Fig. 1). Our study investigated variations in hedgehog DEE and ranging behaviour along a gradient of habitats from rural villages to arable farmland at sites with and without resident badger populations, to dissect the causes of hedgehogs' apparent preference for villages and gardens. We predicted that hedgehogs that spend more time further from buildings would have higher energetic costs than those remaining closer to buildings. These costs could arise from physiological stress from badger presence (Ward et al., 1996), having to increase foraging range to meet energy requirements, or experiencing increased costs of thermoregulation. Alternatively, hedgehogs may have lower energy expenditure further from buildings if they restricted their activities to avoid predation (Hof et al., 2012), as hedgehogs may be smaller because of restricted foraging (Monarca et al., 2015a,b), or if their energy expenditure were constrained owing to insufficient food resources.

MATERIALS AND METHODS
Study design
We selected four study sites in England, two in North Norfolk (UK grid refs: TF 96061 25469 and TG 16716 36586) and two in North Yorkshire (SE 90511 81822 and SE 68646 24715). Each site comprised a predominately arable farm with a rural village within 2.5 km of the farmstead (Figs S1–S4, Table S1). Each village consisted of houses and rural gardens with village edge habitats, including small pasture fields and amenity grassland. In each, country sites were selected such that badgers were present at one and absent from the other, to test the effect of badger presence on DEE. Badger presence was determined by surveys in autumn 2013 and spring 2014 by inspecting woodland, coppices and hedgerows for setts, latrines and tracks.

Hedgehog capture
Adult hedgehogs were captured by hand using red-filtered spotlights (Clulite, Cluson Engineering Ltd, Petersfield, UK)

Fig. 1. Gradient of habitat suitability for hedgehogs in predominately arable rural areas.

across the four sites in July–September 2013 and April–September 2014 (Natural England License 2014/SCI/0298, HO PIL 30/10293). Hedgehogs were found by walking along hedgerows of arable fields, scanning pasture fields, walking along roads in the villages and scanning gardens. Hedgehogs were anaesthetised using a portable anaesthesia system with a mix of isoflurane (IsoFlo, Zoetis, London, UK) and oxygen (2%).

Under anaesthesia, hedgehogs were weighed, sexed and fitted with a 10 g radio-tag (Biotrack, Dorset, UK), which was glued to a patch of clipped spines on the rump using epoxy resin. The radio-tags used were 0.87–1.84% of the hedgehog's body mass, in the range of values known to have no effect on DEE in small mammals (Berteaux et al., 1996a). Hedgehogs were marked with six 1 cm pieces of coloured heat-shrink tubing, which were glued over spines in a patch on the rear (Molony et al., 2006). As DEE may vary with reproductive state in small mammals (Fletcher et al., 2012; Kenagy et al., 1989; Key and Ross, 1999; Poppitt et al., 1993, 1994), we measured testes length, or checked for signs of lactation and pregnancy. Hedgehogs were given 3 weeks to become accustomed to the radio-tag and then re-captured for energetics experiments.

Doubly labelled water experiments
DEE was measured by the doubly labelled water (DLW) technique (Butler et al., 2004; Lifson et al., 1955; Nagy, 1980, 1983). In addition to the 32 hedgehogs tagged 3 weeks prior, 12 hedgehogs were captured during the DLW experiments, and were simultaneously fitted with a tag and injected with DLW.

The DLW dose given was 0.6 ml of 61,3671 ppm ^{18}O and 33,4163 ppm ^{2}H, injected ventrally and subcutaneously under anaesthesia (conditions described above). To calculate the exact dose hedgehogs received, administered trials were conducted in the laboratory to assess the mean volume of DLW left in the syringe after injection (in ml, to four decimal places). After injection, hedgehogs were placed in a recovery box whilst the isotopes reached equilibrium in the body. Hedgehogs were then re-anesthetised and an initial 100 μl blood sample was taken from the left hind leg. In 2013, hedgehogs were held for 1 h before the initial blood sample (time based on species of a similar body mass with the same method of injection; see Speakman, 1997a), but this proved to be insufficient time for the isotopes to reach equilibrium in some individuals. Two hours was sufficient, and this interval was used during the 2014 season.

After recovery from anaesthesia, hedgehogs were released at the point of capture. They were re-captured for a second 100 μl blood sample, from the right hind leg, as close to 96 h after release as possible. Collecting samples across 96 h minimises daily variability in DEE (Speakman et al., 1994; Berteaux et al., 1996a,b). Blood samples were also taken from two hedgehogs at each site before injection, to obtain a measure of the background levels of the isotopes in the local environment. All blood samples were flame-sealed in heparin-free glass capillaries (Vitrex Medical, Herlev, Denmark) and capillary ends were dipped in sealing wax to prevent air leaks. Samples were stored at 4°C until analysis.

Blood sample analysis
The blood-filled capillary tubes were vacuum distilled (Nagy, 1983) and the resulting water samples were analysed for their enrichment of ^{2}H and ^{18}O on a liquid water isotope analyser (Los Gatos Research, San Jose, CA, USA). Fifteen replicates were measured for each sample, which were run alongside three global water standards – SMOW, SLAP and GISP – and three in-house laboratory standards, encompassing the range of enrichments expected. Measures of the degree of enrichment of ^{2}H and ^{18}O in the water
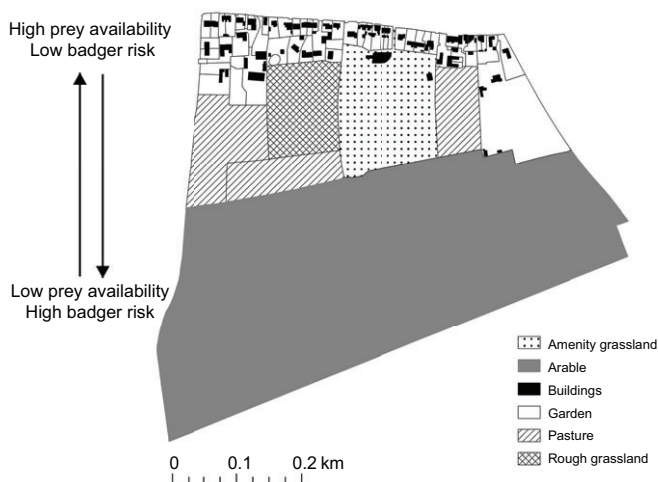
samples were converted into DEE measures using a single pool model (eqn 7.17 in Speakman, 1997a,b), the optimal method for small mammals (Speakman, 1997a; Speakman and Król, 2005). In 2013, six of the 14 individuals had low isotope enrichments in the initial blood sample, indicating that the isotopes had not reached equilibrium in the body during the 1 h holding period. For these animals, their initial enrichment values were estimated based on initial enrichment readings of other hedgehogs that had reached equilibrium in the 2013 dataset, the known volume injected and the individual's body mass. There was no evidence for differences in DEE between these six individuals and the other individuals in the 2013 dataset (ANOVA, $F_{1,12}=0.43$, $P=0.52$).

Ranging behaviour

Hedgehogs were radio-tracked from 21:00 to 04:00 h, obtaining at least three tracking fixes per hedgehog per evening, during the 96 h post release using a hand-held three-element yagi directional antenna and a TRX-1000S receiver (both Wildlife Materials, Murphysboro, IL, USA). GPS location and habitat found at the site of each fix were

Table 1. A range of models constructed to assess the predictors of hedgehog daily energy expenditure (DEE; kJ day^{-1}), measured by the doubly labelled water (DLW) method, and the distance a hedgehog travelled in a 4 day release period

Model	logLik	R^2	AICc	ΔAICc	W
DEE					
Dist+Year+Sex+Site	−1.44	0.53	22.99	0.00	0.38
Dist+Year+Sex+Site+Mass	−0.41	0.55	24.11	1.12	0.22
DayL+Dist+Year+DayQ +Sex+Site	1.10	0.58	24.47	1.48	0.18
DayL+Dist+Year+DayQ +Sex+Mass	−3.18	0.49	26.48	3.49	0.07
DayL+Dist+Year+DayQ +Sex+Site+Mass	1.73	0.60	26.78	3.79	0.06
DayL+Dist+Year+Sex+Site +Mass	−0.27	0.56	27.20	4.21	0.05
DayL+Dist+DayQ+Sex +Site+Mass	−1.16	0.54	28.98	5.99	0.02
DayL+Year+DayQ+Sex +Mass	−7.84	0.37	29.95	6.96	0.01
DayL+Dist+Year+DayQ +Site+Mass	−1.93	0.52	30.53	7.54	0.01
Year+Sex+Mass	−9.68	0.32	30.95	7.96	0.01
DayL+Year+DayQ+Sex +Mass	−7.28	0.39	31.67	8.68	0.00
DayL+Year+DayQ+Mass	−9.84	0.31	33.95	11.0	0.00
DayL+DayQ+Mass	−11.84	0.25	35.25	12.3	0.00
DayL+Dist+Year+DayQ +Sex+Site+Mass+Dist×Site	3.27	0.27	35.94	13.0	0.00
Dist+Site	−13.71	0.18	41.70	18.7	0.00
Dist+Site+Dist×Site	−12.50	0.23	48.29	25.3	0.00
Distance travelled					
Dist+Sex	−19.38	0.42	47.78	0.00	0.60
Day+Dist+Sex	−18.96	0.43	49.50	1.72	0.26
Dist+Sex+Site	−17.38	0.47	51.86	4.08	0.08
Day+Dist	−22.59	0.33	54.21	6.42	0.02
Day+Dist+Sex+Site	−17.09	0.48	54.29	6.50	0.02
Dist+Site	−20.70	0.39	55.66	7.88	0.01
Day+Dist+Site	−20.59	0.39	58.29	10.5	0.00
Day+Sex	−27.00	0.18	63.03	15.2	0.00
Day+Sex+Site	−26.53	0.20	70.18	22.4	0.00

logLik, log likelihood for each model; AICc, corrected Akaike's information criterion; ΔAICc, difference in AICc between the model and the model with the lowest AICc; W, weight given to this model; Dist, mean distance each hedgehog was found to the nearest building during energetics experiments; DayL, linear term of day in the season, with 1 April being assigned day 1; DayQ, quadratic term of day.

recorded. The distance travelled by each hedgehog during the release period was calculated using the location analysis program Ranges7 (Ranges 7, Anatrack Ltd, Dorset, UK). We used ArcGIS to measure the distance of each location fix to the nearest building, and calculated the mean for the 96 h release period for each hedgehog.

Ambient temperature

To measure differences in temperature we placed data loggers (Thermochron ibutton DS1921G, Maxim Intergrated, CA, USA; accuracy: 0.5°C) on a stake 30 cm off the ground in a range of habitats, including arable fields, hedgerows of arable fields, farm buildings, amenity grassland and village gardens. Loggers recorded hourly from 19:00 to 07:00 h.

Statistical analysis

We wished to test the effect of proximity to buildings and site, categorised by having badgers or not, on DEE in hedgehogs. We constructed a series of linear models in R (R Foundation for Statistical Computing, Vienna, Austria) corresponding to different plausible hypotheses, as recommended by Anderson (2008), listed in Table 1. Explanatory variables included: mean distance to buildings, site, the day in the study period, the quadratic effect of day, year, individual body mass and sex. Ambient temperature correlated with day in the season and the quadratic term of day in the season in this study ($R^2=0.21$), as temperature increased from April until July and began to fall again in August. Therefore, we included day in the season, with 1 April set as day 1 for each year, and the quadratic term of day in the analysis of hedgehog DEE and ranging behaviour. Owing to badger abundance plausibly correlating with increasing distance to buildings, the interaction between site and distance to building was included. Hedgehog ID was not added as a random effect as repeated measures were carried out on only three hedgehogs, and therefore the effects of pseudoreplication from this source were deemed to be negligible. The continuous explanatory variables were scaled to two standard
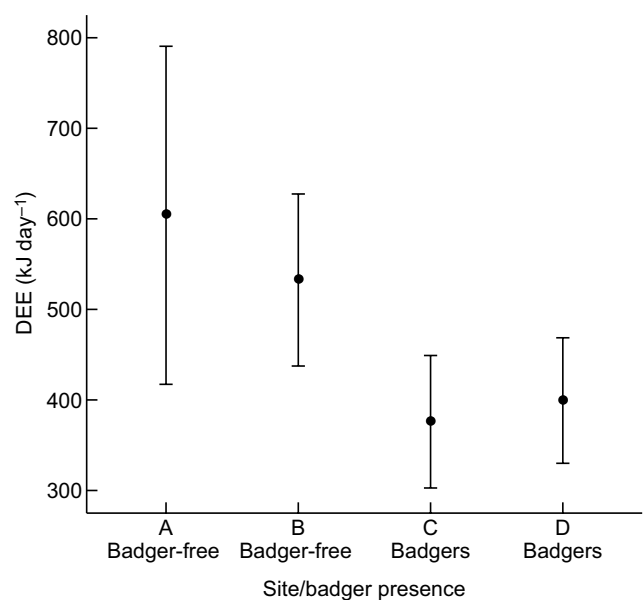

Fig. 2. Effect of site and badger presence on 44 measurements of hedgehog daily energy expenditure (DEE), measured by the doubly labelled water (DLW) method. Bars indicate the 95% confidence interval of the mean. Sites A and C were in North Yorkshire and sites B and D were in Norfolk [site difference measured by general linear model (GLM), mean P-value from top three models=0.029].

Table 2. The significance of variables in the three best fitting models with the lowest AIC to explain variability in hedgehog daily energy expenditure (DEE; kJ day⁻¹), measured by the doubly labelled water method (DLW), and the distance a hedgehog travelled in a 4 day release period

Response	Variables in model	d.f.	F	P	Effect size	95% CI
DEE	Distance to buildings	1,37	4.624	0.038*	0.004	0.001, 0.006‡
	Year 2014	1,37	24.25	0.00002***	0.094	−0.657, −0.274‡
	Sex Male	1,37	3.397	0.073	−0.164	−0.335, 0.008
	Site B No badgers	3,37	3.294	0.031*	−0.187	−0.400, 0.027
	Site C Badgers				−0.144	−0.479, 0.191
	Site D Badgers				−0.345	−0.595, −0.096‡
DEE	Distance to buildings	1,36	4.715	0.037*	0.004	0.002, 0.007‡
	Year 2014	1,36	21.74	0.00004***	−0.443	−0.636, −0.250‡
	Sex Male	1,36	4.976	0.032*	−0.184	−0.357, −0.011‡
	Site B No badgers	3,36	3.359	0.029*	−0.144	−0.366, 0.077
	Site C Badgers				−0.093	−0.434, 0.248
	Site D Badgers				−0.332	−0.580, −0.083‡
	Body mass	1,36	3.198	0.082	0.121	−0.066, 0.307
DEE	Distance to buildings	1,35	4.909	0.033*	0.004	0.001, 0.006‡
	Year 2014	1,35	5.415	0.026*	−0.355	−0.664, −0.045‡
	Sex Male	1,35	8.329	0.007**	−0.202	−0.376, −0.027‡
	Site B No badgers	3,35	3.497	0.026*	−0.323	−0.571, −0.075‡
	Site C Badgers				−0.165	−0.492, 0.161
	Site D Badgers				−0.333	−0.582, −0.084‡
	Day linear	1,35	7.541	0.009**	0.149	−0.190, 0.488
	Day quadratic	1,35	12.343	0.001**	0.518	−0.022, 1.059
Locomotion	Distance to buildings	1,41	22.953	0.00002***	0.555	0.315, 0.796‡
	Sex Male	1,41	6.950	0.012*	0.315	0.074, 0.556‡
Locomotion	Day	1,40	0.765	0.387	−0.109	−0.361, 0.143
	Distance to buildings	1,40	22.821	0.00002***	0.524	0.272, 0.776‡
	Sex Male	1,40	6.910	0.012*	0.322	0.079, 0.564‡
Locomotion	Distance to buildings	1,38	23.302	0.00002***	0.618	0.368, 0.868‡
	Sex Male	1,38	7.056	0.012*	0.299	0.056, 0.542‡
	Site B No badgers	3,38	1.208	0.320	−0.236	−0.534, 0.062
	Site C Badgers				0.078	−0.386, 0.543
	Site D Badgers				−0.142	−0.495, 0.211

The reference categories were: Sex, Female; Year, 2013; Site, A No badgers.
*P<0.05; **P<0.01; ***P<0.001.
‡95% confidence interval of the effect size does not contain zero.

deviations following Gelman (2008). For assessing the effects of proximity to buildings and badger presence on ranging behaviour during the energetics studies, linear models were constructed with the distance travelled by each hedgehog in the 96 h release period as the response variable (Table 1). To test for statistically significant differences in the nightly ambient temperature of rural habitats, a linear mixed model was constructed with habitat and site as fixed explanatory variables and date and time as random factors. All results are presented as means±s.e.m.

RESULTS

Forty-four measurements of DEE in free-living hedgehogs were obtained (see Table S2 for details of study subjects). The mean DEE was 508.9±34.8 kJ day⁻¹ with a mean body mass of 808.1±18.9 g. There was large variation in DEE between individuals in the study, ranging from 227 kJ day⁻¹ to a rate over five times greater at 1272 kJ day⁻¹. No difference in mean DEE was observed between hedgehogs given time to acclimatise (and those injected and tagged at the same time (501.6±40.2 versus 528.2±71.8 kJ day⁻¹; ANOVA, $F_{1,42}$=0.25, P=0.62).

We obtained 382 GPS fixes for hedgehogs during the 96 h release period. We obtained over 11,000 measurements of ambient temperature.

Hedgehog density

Despite aiming to capture equal numbers of hedgehogs in village habitats and on arable land, only two of the 44 hedgehogs in the energetics study were found in arable fields. Seventeen hedgehogs

were found in village edge habitats including amenity grassland, small pasture fields and set-aside. The majority of hedgehogs (25) was found in village habitats such as gardens and road verges. Although 36
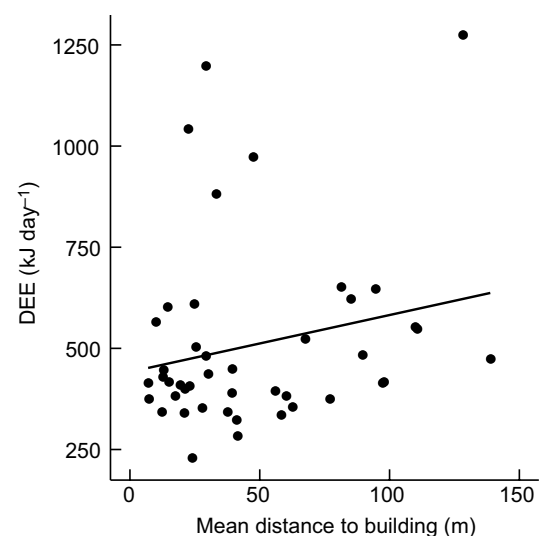

Fig. 3. Relationship between 44 measurements of hedgehog DEE during a 96 h release period and the hedgehog's mean distance to buildings during this period. Distance travelled was calculated from the distance between hourly radio-tracking fixes (GLM, mean P-value from top three models=0.036).
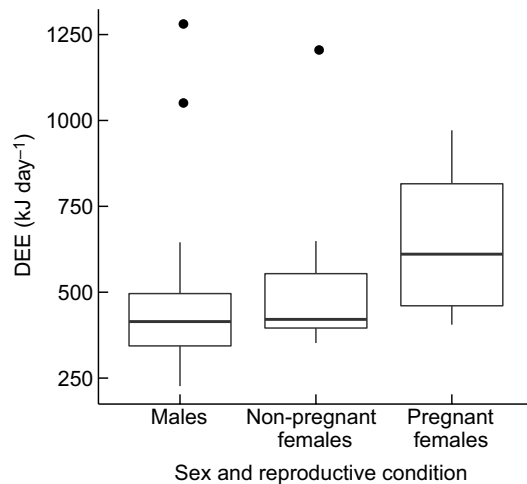
Fig. 4. Effect of sex and reproductive condition on 44 measurements of hedgehog DEE, measured by the DLW method. Pregnant females included hedgehogs thought to be pregnant or lactating. Analysis included 26 measurements of DEE in males, 12 females and six pregnant or lactating females (sex difference measured by GLM, *P*-value from top three models=0.037).
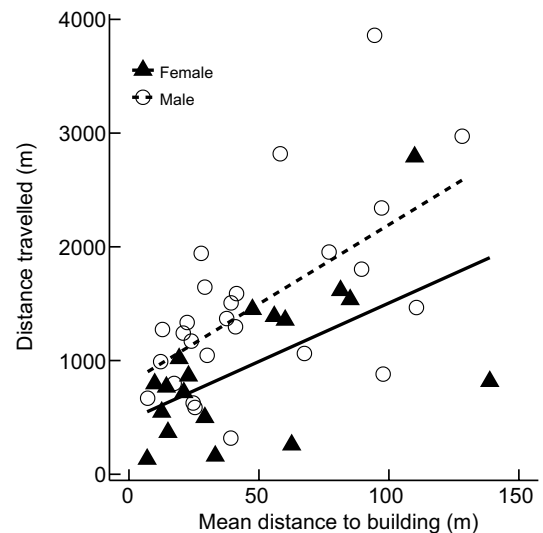

Fig. 5. Relationship between the mean distance that male (M) and female (F) hedgehogs were found from buildings and distance travelled. Distance travelled was measured during a 96 h release period and was calculated from the distance between hourly radio-tracking fixes. There were 26 measurements of males and 18 of females (GLM, effect of distance from buildings on distance travelled: *P*-value from top three models=0.00002; effect of sex on distance travelled: *P*-value from top three models=0.012).

hedgehogs did use arable land at some point during the 96 h release period, only 13 hedgehogs spent 30% or more of their time on arable land. Hedgehog density varied with site; 2.85 times more hedgehogs (134 compared with 47) were encountered on sites where badgers were absent, with the same sampling effort on each site.

Daily energy expenditure

DEE was approximately 30% lower on sites where badgers were present (Fig. 2, Table 2), and increased with the mean distance hedgehogs were found from buildings (Fig. 3, Table 2). The interaction between site and distance to buildings did not feature in the top models, selected by AIC (Table 1), indicating that there was no evidence that the distance effect differed among sites. Female hedgehogs had higher energy expenditure than males (560.7±55.3 and 473±44.2 kJ day^{-1}, respectively; Table 2). Six hedgehogs were in the late stages of pregnancy or lactating during the energetics experiments and these had a higher DEE than did non-pregnant females (648.8±95.8 and 516.7±66.8 kJ day^{-1}, respectively; Fig. 4). DEE was significantly higher in 2013 than in 2014 (Table 2). There was also evidence for a quadratic effect (with DEE being highest mid-season; Table 2).

Ranging behaviour

Male hedgehogs travelled 1.5 times further than females during the release period (1483±158 and 949±155 m, respectively), and hedgehogs that spent more time away from buildings also travelled further (Fig. 5). There was no evidence for between-site difference in the mean distance travelled by hedgehogs, including between sites with and without badgers (with badgers: 1259± 140 m, without: 1267±159 m). However, hedgehogs' home range sizes over the whole season were larger on sites where badgers were absent (home range calculated by 100% minimum convex polygon; with badgers: 9.68±1.67 ha; without: 16.67±3.44 ha; C.E.P., T.P.M., P.J.J. and D.W.M., unpublished data).

Ambient temperature

Mean hourly night temperature differed between rural habitat types, being coldest in arable fields (mean 10.7±0.1°C), which were

significantly colder than all other habitat types, and arable hedgerows (11.4±0.1°C), which were significantly colder than all none-arable habitats (Tables 3 and 4). The warmest habitat was village gardens (11.9±0.1°C). There were no differences in the mean ambient temperature between farm buildings, village gardens and amenity grassland (Tables 3 and 4). Day in the season, a proxy for temperature, was positively correlated with DEE. We verified this finding by running the models again and replacing day in the season with the mean logger temperature during the release period. Temperature was present in the model with the third lowest AIC and was significantly positively correlated with DEE ($F_{1,34}$=18.1, P=0.002).

DISCUSSION
Daily energy expenditure
In this study, hedgehogs in badger-occupied sites had a lower DEE than those in badger-free sites. Previous intraspecific studies

Table 3. Significance of variables in a linear mixed-effects model to test for differences in ambient temperature between five rural habitats at five sites in July–October 2013 and April–September 2014

Variable	d.f.	t	P	Effect size	95% CI
Habitat					
Farm buildings	4, 10,955	172.040	<0.0001***	0.201	0.082, 0.319‡
Arable hedge				−0.437	−0.551, −0.323‡
Arable field				−1.077	−1.193, −0.960‡
Village garden				0.039	−0.074, 0.153
Site					
B	3, 353	19.945	<0.0001***	−1.066	−2.153, 0.029
C				−2.857	−3.825, −1.887‡
D				0.108	−0.987, 1.207

Temperature was measured hourly from 19:00 to 07:00 h. The reference habitat is amenity grassland and the reference site is site A.
***P<0.001.
‡95% confidence interval of the effect size does not contain zero.

Table 4. Pairwise *t*-tests between ambient temperatures in five rural habitats with a Bonferroni correction applied

	Amenity grassland	Farm buildings	Arable hedge	Arable field	Village garden
Farm buildings	1.00	–	–	–	–
Arable hedge	<0.0001***	<0.0001***	–	–	–
Arable field	<0.0001***	<0.0001***	<0.0001***	–	–
Village garden	1.00	1.00	0.0004***	<0.0001***	<0.0001***

***$P<0.001$.

of DEE and RMR have shown that in higher productivity habitats, higher RMRs and thus higher rates of DEE may be enabled (Bozinovic et al., 2007; Burton et al., 2011; Speakman et al., 2003) and conversely, DEE may be lower in lower productivity habitats. Although we did not measure the productivity of arable land, the finding that hedgehogs had lower DEE where badgers were present may reflect the inability of hedgehogs to take advantage of available resources when under risk from predation. For example, Hof et al. (2012) found that when badgers were present, hedgehogs stayed closer to hedgerows, and Ward et al. (1997) found that hedgehogs preferred not to forage in the presence of badger odour.

Another possibility is that hedgehogs compensated for the loss of food intake in the face of predation by decreasing their energy use in some way. Studies of predation risk after wildfires in echidnas and antechinuses have found that individuals compensated for loss of foraging opportunity by increasing torpor use (Nowack et al., 2016; Stawski et al., 2015). It could be that hedgehogs lower their body temperature in order to conserve energy when food intake is reduced owing to predation risk. This would result in the lower DEE observed in hedgehogs on sites where badgers were present. Measurements of hedgehog body temperature during radio-tracking would ascertain whether hedgehogs lower their body temperature as a result of predation risk.

Our findings support the suggestion by Hof et al. (2012) and Micol et al. (1994) that arable land represents a 'landscape of fear' for hedgehogs, which excludes them from potentially suitable habitat because of a perceived risk of predation (Laundre et al., 2010). Badgers may affect hedgehog populations not only by direct predation (Doncaster, 1992, 1994; Hof and Bright, 2010; Morris and Warwick, 1994; Neal, 1986), but also by indirectly negatively impacting on their ability to forage, survive and reproduce, i.e. non-lethal predation (Lima, 1998; Valeix et al., 2009). We must consider that this study was constrained to four sites, and further study is required to confirm the impact of badger presence on hedgehog DEE across the UK.

We found a positive relationship between DEE and the mean distance a hedgehog was from buildings. We speculate that this finding arose from lower prey densities and food availability in arable habitats, compared with villages (in which supplementary feeding may take place), requiring hedgehogs to spend more time looking for food in arable habitats. Locomotion accounts for a large proportion of a small mammal's energy budget (Covell et al., 1996; Kenagy and Hoyt, 1989), and increased movement is energetically costly. Additionally, arable lands were approximately 1°C colder than village habitats, which may also contribute to higher energetic costs further from buildings.

We found no evidence that the effect of distance from buildings on DEE varied among sites, suggesting that badgers affected hedgehogs' DEE regardless of the hedgehogs' proximity to buildings. Although hedgehogs may use residential areas as a refuge from badgers, this may not completely mitigate the risk of badger predation. For example, Young et al. (2006) found that

hedgehog numbers were lower on amenity grassland when badger sett density was higher in surrounding areas. Also, when badgers are particularly abundant they may use urban areas, particularly in rural settlements with large gardens (Davison et al., 2009). Finally, when badgers are present hedgehogs may stay closer to buildings (Doncaster, 1994), and so mean distance to buildings in our study may have been unavoidably confounded with badger presence to some extent. This last point notwithstanding, our findings provide an energetic explanation for those findings of previous studies that demonstrate hedgehogs to be attracted to residential areas (Doncaster, 1994; Doncaster et al., 2001; Micol et al., 1994).

Female hedgehogs had a higher DEE than males, despite male hedgehogs travelling further than females during the release period. The energetic costs of reproduction are high for female small mammals, particularly during lactation (Fletcher et al., 2012; Poppitt et al., 1993; Speakman, 2008), which may explain why females in this study had higher rates of energy expenditure than males. We found that the high DEE of pregnant or lactating females strongly influenced the mean DEE for female hedgehogs, which corroborates this hypothesis (Fig. 4).

Hedgehog DEE was higher in 2013 than in 2014. In 2013, energetics experiments went on later into September, and during the autumn hedgehogs forage intensively to increase fat stores for hibernation (Dowding et al., 2010; Haigh et al., 2012). Rates of foraging result in high energy expenditure (Bryce et al., 2001; Humphries et al., 2002) and we surmise that we only captured the effects of intensive autumn foraging in 2013.

Ranging behaviour
Hedgehogs that stayed closer to buildings did not travel as far in the 4 day release period as those further away. An individual will use the minimum area possible to obtain enough food to meet energy needs (Tufto et al., 1996), and this result may suggest that hedgehogs maintain energy intake on arable land by foraging over greater distances. Male hedgehogs travelled further than females in this study. Male hedgehogs are known to have larger home ranges than females as they range further in order to mate with as many females as possible, whereas females are more sedentary (Haigh et al., 2013; Rautio et al., 2013; Reeve, 1994), thus male hedgehogs may require a larger home range than that simply required for foraging.

Hedgehogs on badger-occupied sites travelled the same distance in the release period as hedgehogs on sites without badgers, but had smaller home range sizes over the season. This behaviour may be a result of hedgehogs using rural villages as refuge when badgers are present (Hof et al., 2012) and, as discussed above, hedgehogs that stay closer to buildings do not travel as far. Alternatively, as in the landscape of fear theory described above, hedgehogs may spend more time taking cover when badgers are present, thus reducing their movement and restricting home range size.

Ambient temperature
Day in the season, a proxy for increasing ambient temperature, was positively correlated with DEE, opposite to the hypothesis that DEE

would increase in colder temperatures owing to increased costs of endothermy (Shkolnik and Schmidt-Nielsen, 1976; Speakman, 1997b; Wroot, 1984). This relationship has been found in previous studies of intraspecific DEE (Bryce et al., 2001; Fletcher et al., 2012), and Dowding et al. (2010) found that hedgehog activity, and therefore energy expenditure, increased with temperature owing to increased prey activity.

Conclusions

Although these constitute preliminary findings on a complex issue, the observed gradient in hedgehog abundance with increased distance from buildings is at least partially explicable by increasing energetic costs, which may be related to decreasing food abundance and temperatures. Disentangling these effects, however, will require further studies. Our finding of lower hedgehog DEE on sites with badgers suggests that predator presence may alter hedgehog energy budgets, potentially by reducing their ability to forage, which could lower DEE through three mechanisms: (1) limiting intake of food and thus the ability to maintain a high DEE, (2) decreasing hedgehog movement or (3) altering hedgehog body temperature to conserve energy in the face of predation. We speculate that lower energetic costs in villages than on the surrounding arable land may be a constituent factor determining hedgehogs' preference for remaining in close proximity to buildings in arable areas.

These results are of conservation concern for hedgehogs. At present, 25% of the land in the UK is arable land (FAO, 2012), which represents substantial unsuitable areas with low connectivity between rural villages. There has been mass removal of hedgerows since the 1950s (Robinson and Sutherland, 2002; Stoate et al., 2001), and less than 10% of remaining hedgerows on arable land are in good structural condition (Carey et al., 2008). Such lack of habitat structure can impact negatively on intraguild prey, in this case the hedgehog, because of a lack of cover from predation (Janssen et al., 2007). Increasing suitability of arable land for hedgehogs may require increasing macroinvertebrate prey densities, increasing the abundance of grassy field margins (Hof and Bright, 2010) and reducing pesticide use. All three may decrease foraging costs for hedgehogs and also provide alternative prey for badgers. Likewise, reinstating hedgerow cover and habitat complexity on arable land may mitigate the effect of badgers, and also potentially provide warmer locations for hedgehogs (arable hedgerows were a mean of 0.7°C warmer than the fields). While badger numbers have increased on arable land in the past 30 years (Judge et al., 2014), there is evidence that species in an intraguild relationship can co-exist (Holt and Polis, 1997; Kamler et al., 2012; Polis and Holt, 1992). Further investigation is warranted to assess the feasibility of these conservation proposals, particularly in respect to the level of hedgerow cover required to mitigate the negative effects of badgers on arable land.

In a broader context, our results show that for non-fleeing prey, DEE may be lowered in the face of predation, and our data support the hypothesis that individuals may be forced to alter habitat use, or restrict foraging to avoid predators. Our study highlights that variations in habitat productivity, coupled with predator presence, can have an impact on the energy budgets of individuals, giving us insight into the physiological constraints underpinning habitat selection in a patchily distributed and declining species.

Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.150359.supplemental

References

Aebischer, N. J., Davey, P. D. Kingdon, N. G. (2011). National Gamebag Census: Mammal Trends to 2009. Game & Wildlife Conservation Trust. http://www.gwct. org.uk/research/long-term-monitoring/national-gamebag-census/mammal-bags-comprehensive-overviews/hedgehog/.

Anderson, D. R. (2008). *Model Based Inference in the Life Sciences: A Primer on Evidence*. New York: Springer.

Banks, P. B., Hume, I. D. and Crowe, O. (1999). Behavioural, morphological and dietary response of rabbits to predation risk from foxes. *Oikos* **85**, 247-256.

Berteaux, D., Masseboeuf, F., Bonzom, J.-M., Bergeron, J.-M., Thomas, D. W. and Lapierre, H. (1996a). Effect of carrying a radiocollar on expenditure of energy by meadow voles. *J. Mammal.* **77**, 359-363.

Berteaux, D., Thomas, D. W., Bergeron, J.-M. and Lapierre, H. (1996b). Repeatability of daily field metabolic rate in female meadow voles (*Microtus pennsylvanicus*). *Funct. Ecol.* **10**, 751-759.

Boonstra, R., Hik, D., Singleton, G. R. and Tinnikov, A. (1998). The impact of predator-induced stress on the snowshoe hare cycle. *Ecol. Monogr.* **68**, 371-394.

Bozinovic, F., Muñoz, J. L. P. and Cruz-Neto, A. P. (2007). Intraspecific variability in the Basal metabolic rate: testing the food habits hypothesis. *Physiol. Biochem. Zool.* **80**, 452-460.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* **85**, 1771-1789.

Bryce, J. M., Speakman, J. R., Johnson, P. J. and Macdonald, D. W. (2001). Competition between Eurasian red and introduced eastern grey squirrels: the energetic significance of body-mass differences. *Proc. R. Soc. B Biol. Sci.* **268**, 1731-1736.

Burton, T., Killen, S. S., Armstrong, J. D. and Metcalfe, N. B. (2011). What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proc. R. Soc. B Biol. Sci.* **278**, 3465-3473.

Butler, P. J., Green, J. A., Boyd, I. L. and Speakman, J. R. (2004). Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. *Funct. Ecol.* **18**, 168-183.

Carey, P. D., Wallis, S., Chamberlain, P. M., Cooper, A., Emmett, B. A., Maskell, L. C., McCann, T., Murphy, J., Norton, L. R., Reynolds, B., et al. (2008). *Countryside Survey: UK Results from 2007*. NERC: Centre for Ecology & Hydrology.

Covell, D. F., Miller, D. S. and Karasov, W. H. (1996). Cost of locomotion and daily energy expenditure by free-living swift foxes (*Vulpes velox*): a seasonal comparison. *Can. J. Zool.* **74**, 283-290.

Davison, J., Huck, M., Delahay, R. J. and Roper, T. J. (2009). Restricted ranging behaviour in a high-density population of urban badgers. *J. Zool.* **277**, 45-53.

Doncaster, C. P. (1992). Testing the role of intraguild predation in regulating hedgehog populations. *Proc. R. Soc. B Biol. Sci.* **249**, 113-117.

Doncaster, C. P. (1994). Factors regulating local variations in abundance: field tests on hedgehogs, *Erinaceus europaeus*. *Oikos* **69**, 182-192.

Doncaster, C., Rondinini, C. and Johnson, P. C. D. (2001). Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. *J. Anim. Ecol.* **70**, 33-46.

Dowding, C. V., Harris, S., Poulton, S. and Baker, P. J. (2010). Nocturnal ranging behaviour of urban hedgehogs, *Erinaceus europaeus*, in relation to risk and reward. *Anim. Behav.* **80**, 13-21.

Ergon, T., Speakman, J. R., Scantlebury, M., Cavanagh, R. and Lambin, X. (2004). Optimal body size and energy expenditure during winter: why are voles smaller in declining populations? *Am. Nat.* **163**, 442-457.

FAO (2012). Land-use database. Rome: FAO. http://faostat.fao.org/

Fletcher, Q. E., Speakman, J. R., Boutin, S., McAdam, A. G., Woods, S. B. and Humphries, M. M. (2012). Seasonal stage differences overwhelm environmental and individual factors as determinants of energy expenditure in free-ranging red squirrels. *Funct. Ecol.* **26**, 677-687.

Ford, R. G. (1983). Home range in a patchy environment: optimal foraging predictions. *Am. Zool.* **23**, 315-326.

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27**, 2865-2873.

Haigh, A., O'Riordan, R. M. and Butler, F. (2012). Nesting behaviour and seasonal body mass changes in a rural Irish population of the western hedgehog (*Erinaceus europaeus*). *Acta Theriol.* **57**, 321-331.

Haigh, A., O'Riordan, R. M. and Butler, F. (2013). Habitat selection, philopatry and spatial segregation in rural Irish hedgehogs (*Erinaceus europaeus*). *Mammalia* **77**, 163-172.

Hik, D. S. (1995). Does risk of predation influence population dynamics? Evidence from cyclic decline of snowshoe hares. *Wildl. Res.* **22**, 115.

Hof, A. R. (2009). A study of the current status of the hedgehog (*Erinaceus europaeus*), and its decline in Great Britain since 1960. *PhD Thesis*, University of London, Royal Holloway.

Hof, A. R. and Bright, P. W. (2010). The value of agri-environment schemes for macro-invertebrate feeders: hedgehogs on arable farms in Britain. *Anim. Conserv.* **13**, 467-473.

Hof, A. R., Snellenberg, J. and Bright, P. W. (2012). Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. *Anim. Behav.* **83**, 1099-1106.

Holt, R. D. and Polis, G. A. (1997). A theoretical framework for intraguild predation. *Am. Nat.* **149**, 745-764.

Hubert, P., Julliard, R., Biagianti, S. and Poulle, M.-L. (2011). Ecological factors driving the higher hedgehog (*Erinaceus europaeus*) density in an urban area compared to the adjacent rural area. *Landsc. Urban Plan.* **103**, 34-43.

Humphries, M. M., Thomas, D. W., Hall, C. L., Speakman, J. R. and Kramer, D. L. (2002). The energetics of autumn mast hoarding in eastern chipmunks. *Oecologia* **133**, 30-37.

Janssen, A., Sabelis, M. W., Magalhães, S., Montserrat, M. and van der Hammen, T. (2007). Habitat structure affects intraguild predation. *Ecology* **88**, 2713-2719.

JNCC (2010). *UK Priority Species Pages– Hedgehog (Erinaceus Europaeus).* Peterborough, UK: Joint Nature Conservation Committee.

Judge, J., Wilson, G. J., Macarthur, R., Delahay, R. J. and McDonald, R. A. (2014). Density and abundance of badger social groups in England and Wales in 2011–2013. *Sci. Rep.* **4**, 3809.

Kamler, J. F., Stenkewitz, U., Klare, U., Jacobsen, N. F. and MacDonald, D. W. (2012). Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. *J. Wildl. Manage.* **76**, 1241-1253.

Kenagy, A. G. J. and Hoyt, D. F. (1989). Speed and time-energy budget for locomotion in golden-mantled ground squirrels. *Cal. State J. Med.* **7**, 150.

Kenagy, G. J., Sharbaugh, S. M. and Nagy, K. A. (1989). Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologia* **78**, 269-282.

Key, C. and Ross, C. (1999). Sex differences in energy expenditure in non-human primates. *Proc. R. Soc. B Biol. Sci.* **266**, 2479-2485.

Kotler, B. P., Brown, J. S. and Hasson, O. (1991). Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* **72**, 2249-2260.

Kruuk, H., Parish, T., Brown, C. A. J. and Carrera, J. (1979). The use of pasture by the European Badger (*Meles meles*). *J. Appl. Ecol.* **16**, 453-459.

Laundre, J. W., Hernandez, L. and Ripple, W. J. (2010). The landscape of fear: ecological implications of being afraid. *Open Ecol. J.* **3**, 1-7.

Lifson, N., Gordon, G. B. and McClintock, R. (1955). Measurement of total carbon dioxide production by means of D2O18. *J. Appl. Physiol.* **7**, 704-710.

Lima, S. L. (1998). Nonlethal effects in the ecology of predator–prey interactions: what are the ecological effects of anti-predator decision-making? *BioScience* **48**, 25-34.

Macdonald, D. W. and Feber, R. E. (2015a). *Wildlife Conservation on Farmland Volume 1: Managing for Nature in Lowland Farms.* Oxford, UK: Oxford University Press.

Macdonald, D. W. and Feber, R. E. (2015b). *Wildlife Conservation on Farmland Volume 2: Conflict in the Countryside.* Oxford, UK: Oxford University Press.

McNab, B. K. (1983). Energetics, body size, and the limits to endothermy. *J. Zool.* **199**, 1-29.

McNab, B. K. (1986). The influence of food habits on the energetics of eutherian mammals. *Ecol. Monogr.* **56**, 1-19.

Micol, T., Doncaster, C. P. and Mackinlay, L. A. (1994). Correlates of local variation in the abundance of hedgehogs *Erinaceus europaeus*. *J. Anim. Ecol.* **63**, 851-860.

Molony, S. E., Dowding, C. V., Baker, P. J., Cuthill, I. C. and Harris, S. (2006). The effect of translocation and temporary captivity on wildlife rehabilitation success: an experimental study using European hedgehogs (*Erinaceus europaeus*). *Biol. Conserv.* **130**, 530-537.

Monarca, R. I., da Luz Mathias, M., Wang, D. H. and Speakman, J. R. (2015a). Predation risk modulates diet-induced obesity in male C57BL/6 mice. *Obesity* **23**, 2059-2065.

Monarca, R. I., Mathias, M. L. and Speakman, J. R. (2015b). Behavioural and physiological responses of wood mice (*Apodemus sylvaticus*) to experimental manipulations of predation and starvation risk. *Physiol. Behav.* **149**, 331-339.

Moreby, S. J. and Southway, S. E. (1999). Influence of autumn applied herbicides on summer and autumn food available to birds in winter wheat fields in southern England. *Agric. Ecosyst. Environ.* **72**, 285-297.

Morris, P. A. (1985). The effects of supplementary feeding on movements of hedgehogs (*Erinaceus europaeus*). *Mamm. Rev.* **15**, 23-33.

Morris, P. A. and Warwick, H. (1994). A study of rehabilitated juvenile hedgehogs after release into the wild. *Anim. Welf.* **3**, 163-177.

Nagy, K. A. (1980). CO_2 production in animals: analysis of potential errors in the doubly labeled water method. *Am. J. Physiol.* **238**, R466-R473.

Nagy, K. A. (1983). *The Doubly Labeled Water ($^{3}HH^{18}O$) Method: A Guide to Its Use.* Los Angeles, CA: Laboratory of Biomedical and Environmental Sciences, University of California Los Angeles.

Nagy, K. A. (1987). Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* **57**, 111-128.

Neal, E. (1986). *The Natural History of Badgers.* London, UK: Croom Helm Ltd.

Neal, E. and Cheeseman, C. (1996). *Badgers.* London, UK: Poyser.

Nowack, J., Cooper, C. E. and Geiser, F. (2016). Cool echidnas survive the fire. *Proc. R. Soc. B Biol. Sci.* **283**, 20160382. The Royal Society.

Polis, G. A. and Holt, R. D. (1992). Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol. Evol.* **7**, 151-154.

Polis, G. A., Myers, C. A. and Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* **20**, 297-330.

Poppitt, S. D., Speakman, J. R. and Racey, P. A. (1993). The energetics of reproduction in the common shrew (*Sorex araneus*): a comparison of indirect calorimetry and the doubly labeled water method. *Physiol. Zool.* **66**, 964-982.

Poppitt, S. D., Speakman, J. R. and Racey, P. A. (1994). Energetics of reproduction in the lesser hedgehog tenrec, *Echinops telfairi* (Martin). *Physiol. Zool.* **67**, 976-994.

Rautio, A., Valtonen, A. and Kunnasranta, M. (2013). The effects of sex and season on home range in European Hedgehogs at the northern edge of the species range. *Ann. Zool. Fennici* **50**, 107-123.

Reeve, N. (1994). *Hedgehogs.* London, UK: Poyser.

Robinson, R. A. and Sutherland, W. J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.* **39**, 157-176.

Roos, S., Johnston, A. and Noble, D. (2012). *UK Hedgehog Datasets and their Potential for Long-Term Monitoring.* Norfolk, UK: The British Trust for Ornithology.

Rutkowska, J., Koskela, E., Mappes, T. and Speakman, J. R. (2011). A trade-off between current and future sex allocation revealed by maternal energy budget in a small mammal. *Proc. R. Soc. B Biol. Sci.* **278**, 2962-2969.

Shkolnik, A. and Schmidt-Nielsen, K. (1976). Temperature regulation in hedgehogs from temperate and desert environments. *Physiol. Zool.* **49**, 56-64.

Speakman, J. (1997a). *Doubly Labelled Water: Theory and Practice.* London: Chapman & Hall.

Speakman, J. (1997b). Factors influencing the daily energy expenditure of small mammals. *Proc. Nutr. Soc.* **56**, 1119-1136.

Speakman, J. R. (2008). The physiological costs of reproduction in small mammals. *Philos. Trans. R. Soc. B Biol. Sci.* **363**, 375-398.

Speakman, J. R. and Król, E. (2005). Comparison of different approaches for the calculation of energy expenditure using doubly labeled water in a small mammal. *Physiol. Biochem. Zool.* **78**, 650-667.

Speakman, J. R., Racey, P. A., Haim, A., Webb, P. I., Ellison, G. T. H. and Skinner, J. D. (1994). Inter- and intraindividual variation in daily energy expenditure of the pouched mouse (*Saccostomus campestris*). *Funct. Ecol.* **8**, 336-342.

Speakman, J. R., Ergon, T., Cavanagh, R., Reid, K., Scantlebury, D. M. and Lambin, X. (2003). Resting and daily energy expenditures of free-living field voles are positively correlated but reflect extrinsic rather than intrinsic effects. *Proc. Natl. Acad. Sci. USA* **100**, 14057-14062.

Stawski, C., Körtner, G., Nowack, J. and Geiser, F. (2015). The importance of mammalian torpor for survival in a post-fire landscape. *Biol. Lett.* **11**, 20150134.

Stoate, C., Boatman, N. D., Borralho, R. J., Carvalho, C. R., de Snoo, G. R. and Eden, P. (2001). Ecological impacts of arable intensification in Europe. *J. Environ. Manage.* **63**, 337-365.

Tidhar, W. L., Bonier, F. and Speakman, J. R. (2007). Sex- and concentration-dependent effects of predator feces on seasonal regulation of body mass in the bank vole *Clethrionomys glareolus*. *Horm. Behav.* **52**, 436-444.

Tufto, J., Andersen, R. and Linnell, J. (1996). Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *J. Anim. Ecol.* **65**, 715-724.

Valeix, M., Loveridge, A. J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. and Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* **90**, 23-30.

Ward, J. F., MacDonald, D. W., Doncaster, C. P. and Mauget, C. (1996). Physiological response of the European hedgehog to predator and nonpredator odour. *Physiol. Behav.* **60**, 1469-1472.

Ward, J. F., Macdonald, D. W. and Doncaster, C. P. (1997). Responses of foraging hedgehogs to badger odour. *Anim. Behav.* **53**, 709-720.

Wilson, J. D., Morris, A. J., Arroyo, B. E., Clark, S. C. and Bradbury, R. B. (1999). A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agric. Ecosyst. Environ.* **75**, 13-30.

Wroot, A. J. (1984). *Feeding Ecology of the European Hedgehog. PhD Thesis*, University of London: Royal Holloway College.

Yalden, D. W. (1976). The food of the hedgehog in England. *Acta Theriol.* **21**, 401-424.

Young, R. P., Davison, J., Trewby, I. D., Wilson, G. J., Delahay, R. J. and Doncaster, C. P. (2006). Abundance of hedgehogs (*Erinaceus europaeus*) in relation to the density and distribution of badgers (*Meles meles*). *J. Zool.* **269**, 349-356.

Zub, K., Szafrańska, P. A., Konarzewski, M. and Speakman, J. R. (2011). Effect of energetic constraints on distribution and winter survival of weasel males. *J. Anim. Ecol.* **80**, 259-269.