

CROSS-GENERATIONAL EFFECTS OF HABITAT AND DENSITY ON LIFE HISTORY IN RED DEER

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Abstract. We used long-term data on movements, survival, and reproduction of female red deer (*Cervus elaphus* Linnaeus) of the Isle of Rum, Scotland (1970–2001), to explain variation in life history (age at maturity) from a hind's access to habitat resources and exposure to local density, and cross-generational (maternal) effects on observed relationships. We described each hind's use of resources relative to availability in the study area from an individual-based resource selection function (RSF); we defined local density as the total number of hinds aged ≥ 1 year within the subpopulation cluster to which an individual belonged. The likelihood of a hind producing her first calf in the period from birth to the end of the summer in which she turned age 3 was positively related to relative use of *Agrostis/Festuca* grasslands and other low-elevation communities, and inversely related to a hind's mean annual local density. However, when we considered both a daughter's RSF and exposure to local density and her mother's RSF and exposure to local density, maternal data alone most parsimoniously explained variation in age at maturity of daughters. Mothers were able to lower age at maturity in their daughters in two, non-mutually exclusive ways. First, birth mass of daughters was inversely related to age at maturity, and mothers that used relatively less uplands (*Calluna*-dominated heath and heather moorland) and occupied areas of lower density produced larger offspring. Second, mothers could establish a home range that enabled daughters to mature in areas with access to high quality *Agrostis/Festuca* grasslands at low density. Lifetime reproductive success was inversely associated with a hind's age at maturity via extension of the reproductive life span. Longevity did not change in association with age at maturity. Patterns in how animals use available habitat resources may depend on that of previous generations, especially at larger scales of resource selection.

Key words: age at maturity; birth mass; *Cervus elaphus*; density; fitness; habitat; life history; maternal effects; red deer; resource selection function (RSF).

INTRODUCTION

Individual-based research programs in animal ecology have recently allowed us to test relationships between long-term proxies of fitness—including lifetime reproductive success (LRS)—and variables describing large-scale habitat use (e.g., red deer, *Cervus elaphus* Linnaeus [Conradt et al. 1999, McLoughlin et al. 2006]; roe deer, *Capreolus capreolus* Linnaeus [Pettorelli et al. 2003, Nilsen et al. 2004, McLoughlin et al. 2007]; caribou, *Rangifer tarandus* Linnaeus [McLoughlin et al. 2005]; migratory passerines [Fontaine and Martin 2007]). This research raises several new questions about the relationship between individual fitness and an organism's use of habitat resources (the “fitness–habitat association”). For example, how does foraging theory, primarily developed and tested using indirect proxies of fitness such as net energetic gain and short-term use of discrete foods or

feeding patches (Stephens and Krebs 1986), “scale-up” to larger spatial and temporal scales (e.g., the lifetime home range or resources used across a landscape through several breeding seasons)? What components of fitness respond to variation in resource use at different scales? Are there processes important to the fitness–habitat association at the large scale that may have been overlooked by researchers working on problems at smaller scales, processes now evident from long-term observation of individuals in the wild? A case in point regarding the latter may be the potentially important role of cross-generational (maternal) effects in how offspring later use habitat and develop life histories.

Maternal effects describe instances where the phenotype of the mother or the environment she experiences has a phenotypic effect on her offspring, independent of offspring genotype (Bernardo 1996). Most published examples of maternal effects in the context of habitat treat a mother's use of available habitat resources (or resource covariates) as an underlying environmental effect. For example, the temperature of a nest site selected by females of many species of reptiles can

Manuscript received 25 June 2007; accepted 17 January 2008;
final version received 26 April 2008. Corresponding Editor:
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determine the sex of offspring (Roosenburg and Niewiarowski 1998), or maternal resource use might underlie maternal effects important to traits of dominance or life history by enabling mothers to give birth to larger offspring through sequestering more food during gestation (e.g., savannah baboons, *Papio cynocephalus* Linnaeus; Altmann and Alberts 2005). However, it is also possible that maternal use of available resources can influence patterns of resource use later observed in offspring, and therefore the fitness–habitat association in offspring. For example, offspring may copy the way in which their mother uses available resources, or, mothers, through establishing bounds of the home range, may act to restrict the functional availability of resources and thus later resource “selection” patterns of their progeny, especially if offspring show natal philopatry.

Here we demonstrate associations between individual characteristics important to fitness (morphometric and life history traits) and an animal’s relative use of available habitat resources at the landscape level, and ask how relationships in offspring might be influenced by patterns in habitat use expressed first by their mothers. We base our analysis on long-term movements and life histories of female red deer (*Cervus elaphus* Linnaeus) of the Isle of Rum, Scotland (see Plate 1). This population has been the subject of intense, individual-based study since the late 1960s (Clutton-Brock et al. 1982). Previous work has shown that at the landscape level an individual’s multivariable resource selection function (RSF; Manly et al. 2002) and exposure to local density (proximity to conspecifics) can explain significant variation in LRS (McLoughlin et al. 2006). Further, the strength of maternal effects (measured as the variance explained in a trait by maternal identity divided by total phenotypic variance of a trait) has been reported for several morphometric and life history traits of study animals (Kruuk et al. 2000). We take a life history trait (age at maturity) shown by Kruuk et al. (2000) to have a weak maternal effect and demonstrate how it may yet be influenced by maternal identity through a relationship with a life history trait shown by Albon et al. (1987) and Kruuk et al. (2000) to have a strong maternal effect (birth mass). We then include what we suspect to be the underlying environmental basis of the observed maternal effect in birth mass—variables describing maternal habitat use and exposure to local density (“the maternal environment”)—as predictors in a model explaining variation in age at maturity of offspring. We show how the maternal environment explains considerably more variation in age at maturity of daughters than does birth mass. We attribute the extra variation in a daughter’s age at maturity explained by the maternal environment to “inherited” patterns in the RSF expressed by the daughter after she is born (from birth to the population mean age at maturity).

METHODS

Study area and sampling

Data were collected by recorders of Cambridge University in a 14-km² study area on the Isle of Rum, Scotland (57°01′ N, 06°17′ W, NM-402996), from 1970 to 2001. The northern boundary of the study area followed ~3.5 km of coastline from Kilmory Bay to Rubha Shamhnan Insir. Movements of hinds were largely contained along the seashore and a 4-km section of the Kilmory River (Kilmory Glen), which drains the surrounding hills (elevation ~300 m) and empties into Kilmory Bay. We classified vegetation into five types following Clutton-Brock et al. (1982). Grasslands dominated by *Agrostis* and *Festuca* spp. (*Agrostis/Festuca* grassland) occurred near the coast at Kilmory Bay and Shamhnan Insir, and along Kilmory Glen. The community was composed of two subtypes (combined for analysis): G1 grassland (short greens) occurring in well-drained soils and calcareous dunes relatively high in pH, and G2 grassland (long greens), which occurred in more acidic soil along edges of streams and the Kilmory River (Upper and Lower Glen). Other vegetation associations in the study area, supporting lower quality forage compared to G1/G2 grasslands (Clutton-Brock et al. 1982, 1987), included *Juncus*-dominated marshland along the Kilmory River and expanses of *Molinia*-dominated flush and *Calluna*-dominated heath and heather moorland in the glen and surrounding hills. *Eriophorum*-dominated bog (blanket bog) occurred in small patches throughout the study area.

The study area supported between 200 and 400 red deer (50–200 hinds) in a natural state (free range, uncultured since 1972). Through regular, ground-based censuses (47 ± 2.6 censuses/year, mean \pm SD), observations of large-scale resource use (occupancy of 1-ha grids in the study area) and morphometric and life history data were compiled for hinds in the study area. Clutton-Brock et al. (1982) provides a detailed description of the deer population and sampling protocol.

Resource selection functions (RSF)

We quantified landscape-level, multivariable use of habitat features in the study area by computing a series of individual-based resource selection functions (RSFs; Manly et al. 2002). A RSF is calculated by comparing the known distribution of resource use by an animal to that expected from random. At the landscape level, locations used by animals (e.g., points in space or pixels of land) may be conceived as resource units, described by “resource variables” (e.g., patch or vegetation association) or modifying covariates (e.g., elevation, slope, distance to water). A number of techniques are available to estimate the RSF (Manly et al. 2002). A common approach (applied here) assumes an exponential or log-linear structure:

$$\text{RSF} = w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k) \quad (1)$$

for a vector of predictor resource variables or covariates associated with resource units (sites). Sites where an individual is present are coded 1, whereas a random sample (or all possible sites) are coded 0. The model coefficient, β_i , for the i th resource covariate, x_i , is estimated using the corresponding coefficient from logistic regression. Although primarily computed from individual-pooled data sets (Boyce et al. 2002), there is no reason that a RSF cannot be computed for individuals (McLoughlin et al. 2006). For individual-based RSFs, the set of β coefficients, β_j , will describe an animal's unique pattern in relative resource use.

We compiled census observations of red deer into 100 \times 100 m census blocks (resource units) within the study area. Attributes of census blocks included proportions of the main vegetation types occurring on Rum. For each hind, we estimated two RSFs: one RSF that considered the movements of deer up to and including the end of the summer (30 September) in which an animal turned age 3 (38–40 months), which corresponded to the end of summer prior to the population mean age at maturity; and a lifetime RSF (McLoughlin et al. 2006). We defined use of resource units from sightings at census blocks and availability of resource units from a random sample of the totality of census blocks where hinds were observed to occur (1377 blocks [ha]). We used a 1:5 ratio of used:available resource units in estimating RSFs to ensure comparability of model coefficients among hinds (McLoughlin et al. 2006). Proportional availability of vegetation types stabilized after randomly sampling approximately 100 resource units (McLoughlin et al. 2006); hence, the minimum number of locations considered per analysis (per hind) was 20 locations (≤ 4 years, 136 ± 58 sightings/hind; lifetime, 341 ± 208 sightings/hind, mean \pm SD). In specifying equal availability of resource units for all hinds we did not consider individual variation in functional responses in habitat use (Myserud and Ims 1998). By not constraining availabilities of resource units to a hind's home range, interpretation of the strength of individual-based coefficients of RSFs remained comparable among hinds, although this was restricted to interpretation only at the landscape level. Note that in computing individual-based RSFs we used logistic regression as an estimating function and not for statistical inference (Boyce et al. 2002:282). We used only animals for which nonzero use of all vegetation types was recorded, as zero use of a resource results in an extreme negative coefficient in the estimating function (we removed two hinds from analysis).

Age at maturity and birth mass

Age at first parturition showed limited variation in red deer (4.05 ± 0.84 years, mean \pm SD, $n = 415$ individuals; Fig. 1), and initial analyses suggested models based on the continuous distribution of age at maturity (as a dependent variable) would be underdispersed. However, it was possible to divide the sample into hinds that

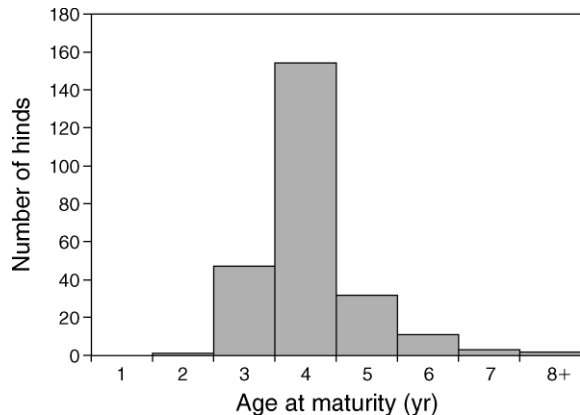


FIG. 1. Distribution of age at maturity (age at first parturition) in red deer hinds ($n = 415$ individuals) of the Isle of Rum, Scotland, 1970–2001.

produced a calf before age 4 and those that failed (Clutton-Brock et al. 1985), including females that failed to produce any calves during their lifetime despite being alive to produce a calf at age 3. Through a relationship with reproductive life span, age at maturity was expected to inversely relate to composite proxies of fitness like LRS (the number of offspring born to a hind that survived at least until age 2). We first tested whether this was the case in red deer by comparing the mean LRS (mean and 95% CI) of individuals producing their first calf before age 4 (whether or not the calf survived to recruitment at age 2) to those that failed, taking into consideration any differences in longevity between the two groups (this was tested for and found not to exist, see *Results*).

We estimated birth mass of offspring from residuals of the relationship between mass (kilograms) at first measurement and hours since birth. Birth mass of red deer on Rum was shown by Albon et al. (1987) and Kruuk et al. (2000) to have a strong maternal effect, but we suspected that variation in age at maturity in daughters, although not shown to have a significant maternal effect by Kruuk et al. (2000), might yet be explained by variation in birth mass. We tested whether birth mass was a significant predictor of the odds of a daughter reproducing prior to age 4 using logistic regression.

Relationships with habitat and density

Kruuk et al. (2000) suggested that a higher frequency of maternal effects in female than male life history traits was the result of females sharing home ranges of differing quality with their mothers, implying an underlying environmental effect associated with higher-order resource selection. To test such an environmental basis for Kruuk et al.'s observed maternal effect in birth mass, we used multiple regression to relate birth mass of an offspring to variables describing the lifetime RSF of its mother (the set of β coefficients, β_j). We knew that



PLATE 1. Hind and calf near Kilmory Bay, Isle of Rum, Scotland. Photo credit: Kelly Moyes.

density might also play an important role as an environmental effect in this population (Clutton-Brock et al. 1982, Coulson et al. 1997, Kruuk et al. 1999, McLoughlin et al. 2006); hence, we also included local density experienced by mothers over their lifetime as a predictor in the model. Further, we suspected that density dependence would operate in different ways depending on observed use of habitat (McLoughlin et al. 2006), and so we included a limited number of interactions between the maternal RSF and density on birth mass (i.e., density \times β coefficients for two opposed vegetation associations: *Calluna*-dominated moorland [β_{Call}] and *Agrostis/Festuca* grassland [$\beta_{A/F}$]). We defined local density of an individual as the total number of hinds aged ≥ 1 year within the coarse-scale, subpopulation cluster to which an individual belonged, determined from spatial hierarchical cluster analysis and averaged over all years of life ("scalar 90" of Coulson et al. 1997). Because we used lifetime means in estimating the maternal environment, predictors in the model described the average state of the environment experienced by an animal. We used Akaike's information criterion adjusted for sample size (AIC_c ; Burnham and Anderson 2002) to discriminate among models of β_j only, density only, $\beta_j +$ density, $\beta_j \times$ density, and the null. Here and throughout this study we did not use AIC_c to distinguish among all possible combinations of variables of resource use (β coefficients of the RSF) to include in a model set, as the number of combinations was unwieldy (some-

times offering exceedingly small differences in ΔAIC_c) and uninformative compared to differences associated with other variables like density.

We then tested whether the maternal environment could explain variation in offspring age at maturity. We used logistic regression to estimate the odds of a daughter producing a calf prior to age 4 (coded 1) or not (coded 0) from the set of β_j coefficients describing the maternal RSF and local density, and interactions of $\beta_{Call} \times$ density and $\beta_{A/F} \times$ density (as before). We used AIC_c to identify the most parsimonious subsets of the most complex model considered.

Daughters could influence their own age at maturity through interacting with the environment after being born. We used logistic regression to determine the odds of a hind producing a calf prior to age 4 given its RSF computed using data from birth until the end of summer in which a hind turned three years, plus the additive effect of mean local density experienced by hinds during the same period, and second-order effects of $\beta_{Call} \times$ density and $\beta_{A/F} \times$ density (again carrying out model selection using AIC_c).

To help us interpret the relative importance to age at maturity of the maternal environment vs. the environment experienced by a daughter after birth, using AIC_c we compared candidate logistic regression models describing the relationship between age at maturity (< 4 yr, coded 1; ≥ 4 yr, coded 0) and predictor variables of top-ranked models of β_j and density presented in

TABLE 1. Ranks of candidate multiple regression models describing the relationship between birth mass of offspring and predictor variables of the maternal resource selection function (RSF; β_j) and mean local density for red deer of the Isle of Rum, Scotland, 1970–2001 ($n = 875$).

| Model | Model predictors† | k | AIC _c | Δ_i AIC _c | w_i |
|-------|--|-----|------------------|-----------------------------|-------|
| 1 | β_j + density | 7 | 2892.38 | 0.00 | 0.33 |
| 2 | β_j + density + ($\beta_{Agrostis/Festuca}$ × density) | 8 | 2892.85 | 0.46 | 0.26 |
| 3 | β_j + density + ($\beta_{Calluna}$ × density) | 8 | 2893.27 | 0.89 | 0.21 |
| 4 | β_j + density + ($\beta_{Calluna}$ × density) + ($\beta_{Agrostis/Festuca}$ × density) | 9 | 2894.59 | 2.21 | 0.11 |
| 5 | β_j | 6 | 2894.82 | 2.44 | 0.10 |
| 6 | density | 2 | 2910.49 | 18.11 | 0.00 |
| 7 | null | 1 | 2942.94 | 50.55 | 0.00 |

Notes: The number of model parameters is denoted by k . The parameter Δ_i AIC_c refers to the change in AIC_c between model i and the model with lowest AIC_c score. AIC_c weights (w_i) sum to 1.0 over considered models.

† For models with interactions, first-order terms of interacting parameters are included in model subsets.

Tables 3 and 5. These included variables describing RSFs of daughters (D_{β_j}) paired with that of their mothers (M_{β_j}), mean local density of daughters (D_{dens}), and mean local density of mothers (M_{dens}). We did not consider models of D_{β_j} in the presence of maternal density, and vice versa, except in the full model.

At the landscape level, cross-generational effects in habitat use on age at maturity may also be due to factors such as a daughter's fidelity to the maternal home range in the study area. Indeed, in the first year of life daughter–mother movements are expected to be highly correlated. In females, some degree of natal philopatry is expected (Clutton-Brock et al. 1982). To assess the extent of maternal influences on higher-order RSFs in red deer (maternal effects in habitat use), we compared associations between β_j of mothers (lifetime) and daughters (first 38–40 months) using the Pearson product-moment correlation. RSFs of female red deer at this scale have already been shown to have a significant effect on total fitness, measured as LRS (McLoughlin et al. 2006).

Statistical analyses were conducted using SPSS version 13.0 (SPSS, Chicago, Illinois, USA) to develop individual-based resource selection functions and the open-source programming application R, version 2.4.1 for all other analyses (available online).⁵ Relevant R software included that of the MASS library (Venables and Ripley 2002). Tolerances among all additive effects included for analysis were >0.20 .

RESULTS

We were able to determine both LRS and whether a calf was born prior to age 4 for 241 female red deer. Females calving for the first time before age 4 produced 2.09 ± 0.49 offspring (mean and 95% CI) surviving at least to age 2 (recruits) during their lifetime ($n = 44$ females). Females that lived at least to the end of the summer in which they turned three years but failed to produce a calf during that period, raised on average 1.32 ± 0.18 recruits during their lifetime ($n = 197$). This number increased to 1.39 ± 0.18 recruits if we excluded

data from 12 females that failed to produce any calves during their lifetime (despite being alive to produce a calf at least at age 3). Mean lifespan between the two groups (those producing calves before vs. at or after age 4) did not significantly differ (11.61 ± 1.48 vs. 11.32 ± 0.58 [mean and 95% CI], respectively); hence, we can conclude that hinds producing their first calves relatively early in life benefited from a longer reproductive life span with no associated increase in longevity.

Birth mass was a significant predictor of the odds of a female reproducing prior to age 4 ($n = 415$, log-odds = 0.234 ± 0.111 [$b \pm \text{SE}$], odds ratio = 1.264 [e^b], Wald statistic = 4.49 , $P = 0.034$). Mass of 875 offspring at birth was significantly related to their mother's RSF and local density (Table 1). Coefficients of the top three AIC_c models, which were all relatively close to each other, suggested that as mothers used relatively less uplands (*Calluna*-dominated moorland) and were exposed to lower density, birth mass of their offspring increased (Table 2). R^2 of the top model was 0.075. Models 2 and 3 supported interactions between RSF coefficients for *Agrostis/Festuca* grassland and density and *Calluna*-dominated habitat and density on offspring birth mass, although in both cases second-order terms were not significant (Tables 1 and 2).

Like birth mass, a daughter's age at maturity also related to the maternal environment (Table 3). We identified 128 offspring with known age at maturity having mothers for which we could compute a RSF and estimate local density. The top-ranked model, which was twice as likely as that of the next best model (Table 3), indicated that odds of a daughter producing her first calf prior to age 4 was related to a mother's increased relative use of *Agrostis/Festuca* grasslands (with a particularly strong effect size), *Juncus* marsh, and *Molinia* flush; by relatively less use of *Calluna*-dominated heath and heather moorland by mothers; and by maternal exposure to local density (Table 4). R^2 of this model was 0.551 (Nagelkerke R^2 ; Nagelkerke [1991]). The interaction contained in the second-ranked model suggested some dependency of RSF coefficients for *Agrostis/Festuca* grassland on density in terms of reducing age at maturity (Table 3), although this term was nonsignificant ($P > 0.10$).

⁵ (<http://www.R-project.org>)

TABLE 2. Estimates (b) \pm SE, and significance of parameters describing the relationship between birth mass of hinds and predictor variables of their mother's RSF (β_j) and mean local density.

| Parameter | Model 1 | Model 2 | Model 3 |
|---|----------------------|----------------------|---------------------|
| Intercept | 0.334 \pm 0.417 | 0.421 \pm 0.423 | 0.929 \pm 0.694 |
| $\beta_{Calluna}$ | -0.183 \pm 0.069** | -0.197 \pm 0.070** | -0.003 \pm 0.181 |
| $\beta_{Eriophorum}$ | 0.0004 \pm 0.002 | 0.001 \pm 0.002 | 0.001 \pm 0.002 |
| $\beta_{Agrostis/Festuca}$ | -0.024 \pm 0.109 | 0.343 \pm 0.312 | -0.080 \pm 0.121 |
| $\beta_{Molinia}$ | 0.073 \pm 0.065 | 0.037 \pm 0.071 | 0.058 \pm 0.066 |
| β_{Juncus} | 0.016 \pm 0.016 | 0.008 \pm 0.017 | 0.008 \pm 0.018 |
| Density | -0.009 \pm 0.004* | -0.010 \pm 0.004* | -0.016 \pm 0.008* |
| $\beta_{Agrostis/Festuca} \times$ density | | -0.005 \pm 0.004 | |
| $\beta_{Calluna} \times$ density | | | -0.002 \pm 0.002 |

Note: Estimates correspond to the top three models in Table 1.
 * $P < 0.05$; ** $P < 0.01$.

A daughter's own RSF and exposure to local density both related to the timing of her age at maturity (Table 5). A hind was significantly more likely to produce a calf before age 4 if, during the period up to and including the end of the summer in which she turned three years, she had high values of $\beta_{A/F}$ (Table 6). Likelihood of producing a calf before age 4 was also significantly enhanced by use of vegetation communities associated with the lower elevations of Kilmory Glen, including *Juncus*-dominated marsh and *Molinia*-dominated grasslands (Table 6). As a hind's exposure to high local density increased, the likelihood of her reproducing for the first time before age 4 significantly decreased (Table 6). R^2 of the best model was 0.277 (Nagelkerke R^2 ; Nagelkerke [1991]). There was some support for an interaction between a daughter's $\beta_{A/F}$ and density on her age at maturity (Table 5), but again this interaction term was nonsignificant ($P > 0.10$).

When we considered mother–daughter pairings (a daughter's RSF and exposure to local density and her mother's RSF and exposure to local density on daughter's age at maturity), maternal data alone most parsimoniously explained variation in whether or not a daughter would produce her first calf before age 4 (Table 7). Competing models were restricted to additive effects based on results presented in Tables 3 and 5. Lifetime patterns in the maternal RSF were highly correlated with that of their daughters during the first four years of life (main diagonal in Table 8).

DISCUSSION

Interrelationships observed in this study remind us of the importance of habitat and modifying processes like competition in ecology. As reflected in patterns of the RSF, female red deer were able to affect their own and their offspring's fitness in two, non-mutually exclusive ways. First, birth mass of daughters inversely related to age at maturity, and mothers that used relatively less upland habitat (*Calluna*-dominated heath and heather moorland) and occupied areas of less density produced larger offspring (a maternal effect in birth mass). Second, mothers could establish a home range that enabled daughters to mature in areas with access to high quality *Agrostis/Festuca* grasslands at low density (a maternal effect in habitat use). Our analyses also suggest that there is some evidence that benefits of habitat use on offspring traits interacted with density, which is consistent with McLoughlin et al.'s (2006) observation of density dependence in the relationship between fitness and habitat selection. Further, we showed that LRS was inversely associated with a hind's age at maturity through extension of the reproductive life span. Individual-based RSFs examined in this study have already been shown to directly relate to LRS (McLoughlin et al. 2006).

Several authors have proposed that the maternal environment is likely to underlie observed maternal effects in morphometric traits like birth mass (Reinhold 2002). Clear identification of variables associated with

TABLE 3. Ranks of models of candidate logistic regression models describing the relationship between a daughter's age at first parturition (<4 yr, coded 1; ≥ 4 yr, coded 0) and predictor variables of the maternal RSF (β_j) and mean local density for female red deer ($n = 128$) of the Isle of Rum, Scotland, 1970–2001.

| Model | Model predictors† | k | AIC _c | Δ_i AIC _c | w_i |
|-------|--|-----|------------------|-----------------------------|-------|
| 1 | $\beta_j +$ density | 7 | 62.19 | 0.00 | 0.49 |
| 2 | $\beta_j +$ density + ($\beta_{Agrostis/Festuca} \times$ density) | 8 | 63.44 | 1.24 | 0.26 |
| 3 | $\beta_j +$ density + ($\beta_{Calluna} \times$ density) | 8 | 64.47 | 2.27 | 0.16 |
| 4 | $\beta_j +$ density + ($\beta_{Calluna} \times$ density) + ($\beta_{Agrostis/Festuca} \times$ density) | 9 | 65.75 | 3.56 | 0.08 |
| 5 | β_j | 6 | 76.15 | 13.96 | 0.00 |
| 6 | density | 2 | 87.11 | 24.92 | 0.00 |
| 7 | null | 1 | 90.40 | 28.21 | 0.00 |

Notes: The number of model parameters is denoted by k . The parameter Δ_i AIC_c refers to the change in AIC_c between model i and the model with lowest AIC_c score. AIC_c weights (w_i) sum to 1.0 over considered models.

† For models with interactions, first-order terms of interacting parameters are included in model subsets.

TABLE 4. Log-odds (b), SE, significance of parameters, and odds ratios (e^b) of the selected logistic regression model (Model 1) in Table 3.

| Parameter | b | SE | Wald | P | e^b |
|----------------------------|--------|-------|-------|--------|--------|
| Intercept | -7.098 | 3.856 | 3.39 | 0.066 | 0.00 |
| $\beta_{Calluna}$ | -2.793 | 0.929 | 9.03 | 0.003 | 0.06 |
| $\beta_{Eriophorum}$ | -0.025 | 0.134 | 0.04 | 0.851 | 0.98 |
| $\beta_{Agrostis/Festuca}$ | 5.797 | 1.875 | 9.56 | 0.002 | 329.28 |
| $\beta_{Molinia}$ | 1.385 | 0.598 | 5.36 | 0.021 | 3.99 |
| β_{Juncus} | 1.572 | 0.453 | 12.06 | <0.001 | 4.81 |
| Density | -0.170 | 0.053 | 10.50 | 0.001 | 0.84 |

Note: The model describes the relationship between a daughter's age at maturity (<4 yr, coded 1; ≥ 4 yr, coded 0) and predictor variables of her mother's large-scale RSF (β_j) and mean local density (Nagelkerke $R^2 = 0.551$ [Nagelkerke 1991]).

environmental effects (i.e., variables other than maternal identity), however, has not been common. In wild ungulates, Mech et al. (1991) showed that maternal and grandmaternal nutrition affected mass of white-tailed deer (*Odocoileus virginianus* Zimmerman [Mech et al. 1991]). And Nilsen et al. (2004) suggested that composition of the maternal home range of roe deer (*Capreolus capreolus* Linnaeus) in winter affected a fawn's mass in August, perhaps by influencing the timing of a mother's birth. Further, Sæther and Heim (1993) showed that winter calf mass in moose (*Alces alces* Linnaeus) was related to biomass of herb species in the mother's summer home range. Our results agree with these studies by suggesting the condition of a mother's home range (landscape-level RSF) is likely to influence the size of her offspring, although the small R^2 associated with the observed relationship suggests that the main factor(s) of variation in birth mass were not included in the model (e.g., among-year effects due to climatic variation [Clutton-Brock and Albon 1989]). Our results differ from previous analyses by suggesting that maternal use of habitat can also influence other traits of offspring life history, like age at maturity (which relates to offspring LRS), and by clearly outlining the mechanisms by which this is likely to occur (i.e., via relationships with birth mass but also through con-

TABLE 6. Log-odds (b), SE, significance of parameters, and odds ratios (e^b) of the selected logistic regression model (Model 1) in Table 5.

| Parameter | b | SE | Wald | P | e^b |
|----------------------------|--------|-------|-------|---------|-------|
| Intercept | 3.035 | 1.243 | 5.96 | 0.015 | 20.79 |
| $\beta_{Calluna}$ | 0.325 | 0.202 | 2.59 | 0.107 | 1.38 |
| $\beta_{Eriophorum}$ | -0.001 | 0.001 | 0.58 | 0.445 | 1.00 |
| $\beta_{Agrostis/Festuca}$ | 1.376 | 0.391 | 12.36 | 0.0004 | 3.96 |
| $\beta_{Molinia}$ | 0.726 | 0.242 | 9.01 | 0.003 | 2.07 |
| β_{Juncus} | 0.332 | 0.070 | 22.65 | <0.0001 | 1.39 |
| Density | -0.060 | 0.015 | 14.81 | 0.0001 | 0.94 |

Note: The model describes the relationship between age at maturity (<4 yr, coded 1; ≥ 4 yr, coded 0) and predictor variables of the large-scale RSF (β_j) and mean local density (from birth to end of summer in which a hind turned age 3) of red deer ($n = 241$) of the Isle of Rum, Scotland, 1970–2001 (Nagelkerke $R^2 = 0.277$ [Nagelkerke 1991]).

straints imposed on an offspring's future access to resources by the maternal RSF).

Female red deer show high natal philopatry (Clutton-Brock et al. 1982); hence, large-scale patterns in maternal RSFs were expected to influence those of their daughters. This type of maternal environmental effect has only recently been proposed as a mechanism to explain variation in spatial heterogeneity in a long-term proxy of fitness. Maternal influences on daughter habitat use were suggested by McLoughlin et al. (2007) to explain recent observations of heterogeneity in LRS of roe deer associated with variation in composition of the home range. McLoughlin et al. showed that roe deer occupying home ranges containing forest openings (meadows) produced more than twice as many recruits as those that did not. The sedentary nature of roe deer (Strandgaard 1972) may have influenced results by increasing among-individual variation in resource selection patterns. Higher-order resource selection in roe deer was likely constrained by factors independent of individual behavior, with the obvious maternal contributing factor of where an individual was born. We probably observed a similar phenomenon here, suggesting an important role for natal philopatry on the relationship between life history parameters and habitat use at larger scales.

TABLE 5. Ranks of models of candidate logistic regression models describing the relationship between age at first parturition (<4 yr, coded 1; ≥ 4 yr, coded 0) and predictor variables of the RSF (β_j) and mean local density for female red deer ($n = 241$) of the Isle of Rum, Scotland, 1970–2001.

| Model | Model predictor \dagger | k | AIC $_c$ | Δ_i AIC $_c$ | w_i |
|-------|--|-----|----------|---------------------|-------|
| 1 | β_j + density | 7 | 198.63 | 0.00 | 0.55 |
| 2 | β_j + density + ($\beta_{Agrostis/Festuca} \times$ density) | 8 | 200.67 | 2.05 | 0.20 |
| 3 | β_j + density + ($\beta_{Calluna} \times$ density) | 8 | 200.75 | 2.12 | 0.19 |
| 4 | β_j + density + ($\beta_{Calluna} \times$ density) + ($\beta_{Agrostis/Festuca} \times$ density) | 9 | 202.82 | 4.19 | 0.07 |
| 5 | β_j | 6 | 215.23 | 16.60 | 0.00 |
| 6 | density | 2 | 226.54 | 27.91 | 0.00 |
| 7 | null | 1 | 231.10 | 32.47 | 0.00 |

Notes: Data are relevant from birth to the end of the summer in which a hind turns age 3. The number of model parameters is denoted by k . The parameter Δ_i AIC $_c$ refers to the change in AIC $_c$ between model i and the model with lowest AIC $_c$ score. AIC $_c$ weights (w_i) sum to 1.0 over considered models.

\dagger For models with interactions, first-order terms of interacting parameters are included in model subsets.

TABLE 7. Ranks of models of candidate logistic regression models describing the relationship between age at first parturition (<4 yr, coded 1; ≥4 yr, coded 0) and predictor variables of RSFs of daughters (D_{β_j}) paired with those of their mothers (M_{β_j}), mean local density of daughters (D_{dens}), and mean local density of mothers (M_{dens}) for red deer of the Isle of Rum, Scotland, 1970–2001.

| Model | Model predictors | k | AIC _c | Δ_i AIC _c | w_i |
|-------|---|-----|------------------|-----------------------------|-------|
| 1 | $M_{\beta_j} + M_{\text{density}}$ | 7 | 62.19 | 0.00 | 0.77 |
| 2 | $D_{\beta_j} + M_{\beta_j} + D_{\text{density}} + M_{\text{density}}$ | 13 | 64.63 | 2.44 | 0.23 |
| 3 | M_{β_j} | 6 | 76.15 | 13.96 | 0.00 |
| 4 | $D_{\beta_j} + D_{\text{density}}$ | 7 | 85.47 | 23.27 | 0.00 |
| 5 | D_{β_j} | 6 | 85.63 | 23.43 | 0.00 |
| 6 | null | 1 | 90.40 | 28.21 | 0.00 |

Notes: Competing models were restricted to parameters contained in the top-ranked models of Tables 3 and 5. There were 128 mother–daughter pairings used in this analysis. The number of model parameters is denoted by k . The parameter Δ_i AIC_c refers to the change in AIC_c between model i and the model with lowest AIC_c score. AIC_c weights (w_i) sum to 1.0 over considered models. Parameters of Model 1 are presented in Table 4.

What is not known about maternal effects and habitat use is the extent to which patterns in RSFs might be conferred to offspring from their mothers based on learning, as opposed to simple natal philopatry. This question speaks to the concepts of natal habitat preference induction (Davis and Stamps 2004) and “learning the ecological niche” (Slagsvold and Wiebe 2007). At the very finest scales of resource selection (e.g., selection of foods to eat or microsites to occupy), it is easy to imagine that through learning by offspring, maternal resource use might influence the later selection patterns of offspring, and thus life history and fitness of the next generation. Foraging cultures and social learning in primates provide good examples of this potential (e.g., chimpanzees [*Pan troglodytes* Blumenbach], Whiten et al. 1999; orang-utans [*Pongo pygmaeus* Linnaeus], van Schaik and Knott 2001). Learning to use resources from others is not limited to primates (Box and Gibson 1999, Slagsvold and Wiebe 2007); nor is it necessary that this occur only at the finest scales of resource selection. For roe deer examined by McLoughlin et al. (2007), for example, it is possible that fawns born to females possessing home ranges with openings in the forest dispersed to seek out similarly structured home ranges to occupy as adults. Generational transfer of information at the large scale is also possible in red deer of this study; however, it is more likely that factors such as where or to what group an animal was born were more important.

Our results raise questions about why hinds with inferior ranges remain in those ranges. Female red deer on Rum exist in very stable matrilineal groups, and dominance relationships have been mapped for a large proportion of females observed in this study (Clutton-Brock et al. 1984, Thouless and Guinness 1986, Thouless 1990). Dominance relationships established early in life appear to be perpetuated regardless of differences in body size later in life, with the result that among hinds known to each other, full-scale and dangerous conflicts are few (Thouless 1990). This is not the case for interacting hinds that have not previously met (Thouless 1990). The relative costs to hinds of remaining in a home range of inferior quality may thus be lower than moving to a new area where dominance relationships are not known and risks of dangerous conflict is higher.

Similar to other maternal effects (e.g., McAdam et al. 2002, Wilson et al. 2005), maternal effects related to habitat are likely to be composed of both environmental and genetic components. For instance, maternal exposure to conspecific or predator density (aspects of the maternal environment) may influence a mother’s expression of the RSF (e.g., density dependence in resource selection [review in Rosenzweig 1991] or predation-sensitive foraging [reviews in Sinclair and Arcese 1995, Miller 2002]). Further, animals are likely to be selected for on the basis of having the ability to adapt their resource selection to maximize fitness when confronted by processes like competition or predation

TABLE 8. Pearson product-moment correlation matrix between coefficients of the RSF (β_j) of mothers (lifetime) vs. daughters (from birth to end of summer in which a hind turned age 3) for red deer of the Isle of Rum, Scotland, 1970–2001 ($n = 128$ mother–daughter pairings).

| Daughter RSF | Maternal RSF | | | | |
|-----------------------------------|--------------------------|-----------------------------|-----------------------------------|--------------------------|-------------------------|
| | β_{Calluna} | $\beta_{\text{Eriophorum}}$ | $\beta_{\text{Agrostis/Festuca}}$ | β_{Molinia} | β_{Juncus} |
| β_{Calluna} | 0.91 | −0.37 | 0.22 | 0.66 | −0.72 |
| $\beta_{\text{Eriophorum}}$ | −0.24 | 0.52 | (0.09) | −0.17 | 0.20 |
| $\beta_{\text{Agrostis/Festuca}}$ | 0.33 | (−0.02) | 0.90 | 0.42 | −0.41 |
| β_{Molinia} | 0.72 | −0.19 | 0.31 | 0.93 | −0.63 |
| β_{Juncus} | −0.72 | 0.52 | −0.29 | −0.60 | 0.87 |

Note: All correlations are significant at $P < 0.05$ except those in parentheses.

(e.g., adaptive animal behavior [review in Dall et al. 2005]). Separating environmental and genetic components of maternal effects in habitat use presents an intriguing line of future research.

Our observation of cross-generational effects on the link between life history traits and landscape-level patterns in habitat use is novel. It may be that the importance of these maternal effects is scale dependent, but regardless, our results have implications for how we currently define and think about “resource selection.” The consensus definition of resource selection describes the process as a series of innate and learned behavioral decisions (Johnson 1980, Hall et al. 1997, Manly et al. 2002, Morris 2003). Our results expand this definition to include inherited patterns of use of available resources from parents, which may be particularly relevant to understanding the basis of higher-order resource selection. We contend that the link between fitness and habitat does not depend solely on the innate and learned responses of animals to conditions of habitat and density, but rather that this link is also a function of the responses of previous generations to resource availability and ecological processes like competition or predation. The effect of this inertia on the fundamental link between individual performance and resource selection requires further research.

Questions about maternal effects and the link between fitness and habitat have come about because of the recent use of individual-based models in ecology. Following individuals over long periods of time, in addition to providing information on higher-order resource selection (temporal and spatial scales of habitat selection are linked; Senft et al. 1987), allows us to consider generational proxies of fitness like LRS or its components in how individuals respond to their biotic and abiotic environment. Yet, individual-based research on the fitness–habitat link suffers from a lack of theory specific to larger ecological scales. Despite recent research in this area, it remains to be seen how foraging theory might scale-up to higher orders of resource selection. At the very least, the multivariable complexity of large-scale habitat use and the importance of factors like cross-generational effects on observed patterns will need to be considered.

ACKNOWLEDGMENTS

We thank the Director of Scottish Natural Heritage (SNH) for permission to work on Rum, and to SNH staff for their support and assistance. Many assistants have helped with fieldwork over the several years of study; we thank them all. Our research was supported by grants from the Natural Environmental Research Council (NERC), the Science and Engineering Research Council, and the Royal Society. P. D. McLoughlin was supported by a Natural Sciences and Engineering Research Council (Canada) grant to F. Messier. This work was made possible by NERC sponsorship of the Centre for Population Biology (Imperial College London at Silwood Park) and its Visitor Programme. We thank M. S. Boyce and the Stochastic Demography Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant no. DEB-94-21535),

the University of California–Santa Barbara, and the State of California, for helping to initiate this research.

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