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Persistent maternal effects on juvenile survival in North American red squirrels

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Maternal effects can have lasting fitness consequences for offspring, but these effects are often difficult to disentangle from associated responses in offspring traits. We studied persistent maternal effects on offspring survival in North American red squirrels (*Tamiasciurus hudsonicus*) by manipulating maternal nutrition without altering the post-emergent nutritional environment experienced by offspring. This was accomplished by providing supplemental food to reproductive females over winter and during reproduction, but removing the supplemental food from the system prior to juvenile emergence. We then monitored juvenile dispersal, settlement and survival from birth to 1 year of age. Juveniles from supplemented mothers experienced persistent and magnifying survival advantages over juveniles from control mothers long after supplemental food was removed. These maternal effects on survival persisted, despite no observable effect on traits normally associated with high offspring quality, such as body size, dispersal distance or territory quality. However, supplemented mothers did provide their juveniles an early start by breeding an average of 18 days earlier than control mothers, which may explain the persistent survival advantages their juveniles experienced.

Keywords: food supplementation; lactation; territory settlement; recruitment; dispersal; territory quality

1. INTRODUCTION

The early environment experienced by offspring can have important fitness consequences that persist across life-history stages (Lindström 1999; Martin-Gronert & Ozanne 2006). For many organisms, much of the early environment is determined by maternal behaviour and reproductive allocation. As such, maternal effects are widespread and can represent a substantial component of variation in many offspring traits (Mousseau & Fox 1998).

In mammals, the transition from nurtured, dependent neonate to free-living, independent recruit is a critical life-history interval with major implications for natural selection and population dynamics (Lee *et al.* 1991; Hayssen 1993). Juvenile mammals feed entirely or almost entirely on their mother's milk prior to weaning, so their early life development is highly influenced by maternal nutrition and energy allocation (e.g. Rogowitz & McClure 1995; McAdam & Boutin 2003*a*). As a result, maternal nutritional support is likely to be a major determinant of the survival of juveniles following nutritional independence. Increased offspring survival in response to parental food supplementation has frequently been documented in birds (Martin 1987; Newton 1998), but has rarely been demonstrated in wild mammals (Gaillard *et al.* 2000; Ylönen *et al.* 2004).

Although maternal influences on juvenile development and post-emergent fate have received much recent attention (Mousseau & Fox 1998; Gorman & Nager 2004; Gendreau *et al.* 2005), it is often unclear whether maternal nutritional effects have ephemeral or persistent effects on offspring traits and fitness. If juveniles provided with a nutritional advantage as neonates consistently outperform their peers at later life-history stages (Lindström 1999; Madsen & Shine 2000), the strength of maternal effects will magnify over time. Conversely, if juveniles can compensate for disadvantages experienced early in life during subsequent life-history stages (Wilson & Osbourn 1960; Sikes 1998; Gurney *et al.* 2003), then the strength of maternal effects will diminish or even disappear over time.

In the present study, we experimentally tested for the occurrence and persistence of maternal nutritional effects on offspring survival in a population of North American red squirrels (*Tamiasciurus hudsonicus*). By removing supplemental food from the system prior to juvenile emergence, we manipulated maternal resources without altering the post-emergent nutritional environment experienced by offspring. This experimental design, combined with the territorial and year-round residency of red squirrels, permitted evaluation of whether neonatal nutritional support had diminishing, persisting or magnifying effects on juvenile survival through sequential life-history stages.

2. MATERIAL AND METHODS

Red squirrels were studied near Kluane National Park, in southwestern Yukon, Canada (61° N, 138° W) from August 2003 to May 2005 during a period of low natural food availability (Boutin *et al.* 2006). All squirrels present on the study grids were marked and monitored for survival and reproduction using standardized methodology (Boutin *et al.* 2006; McAdam *et al.* in press). The territorial nature of red squirrels provided the opportunity to food supplement targeted adult females. We supplemented half with peanut butter and the other half with sunflower seeds from autumn 2003 to spring 2004. These food items are not typically hoarded by red squirrels and food supplements were removed from the study site just prior to juvenile emergence.

We used nest entries, visual surveys and live trapping to document the survival of marked juveniles arising from 12 food-supplemented mothers and 47 control mothers between birth, emergence, territory settlement and 1 year of age. To evaluate whether maternal supplementation resulted in differential bequeathal (Price & Boutin 1993; Berteaux & Boutin 2000) or variation in offspring traits frequently associated with fitness, we also quantified juvenile dispersal and settlement distance, territory quality and body mass. We treated data collected on littermates prior to and during territory settlement as non-independent and tested them as litter means or proportions, but following territory

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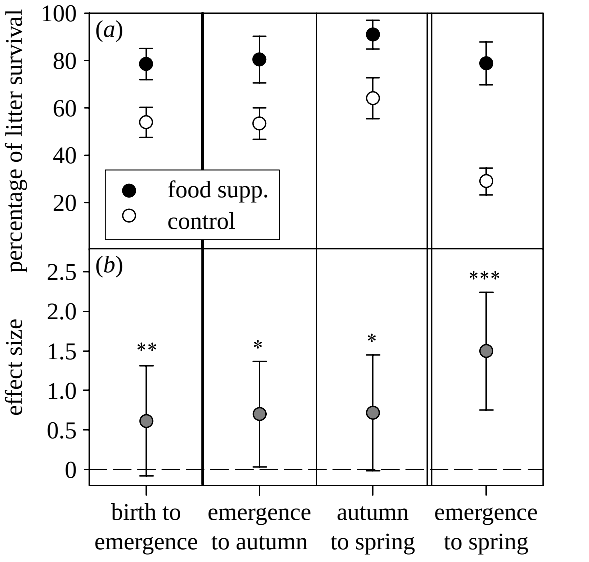

Figure 1. Effects of maternal food supplementation on juvenile survival from birth to emergence and, following removal of the supplemental food (right of the thick vertical line), from emergence to autumn, autumn to spring and (right of the double line) cumulative survival from emergence to 1 year of age. (*a*) Mean proportion of litter surviving ±1 s.e. (*b*) Effect sizes (Cohen's *d*) and 95% confidence intervals of differences between juveniles from supplemented mothers and control mothers ($^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$).

settlement assumed independence of littermates and included the fates of individual juveniles in our analyses (see electronic supplementary material for a more detailed description of methodology).

3. RESULTS

Survival of juveniles through sequential life-history stages was strongly influenced by maternal food supplementation. On average, 78% of juveniles from food-supplemented mothers survived from birth to emergence, whereas only 54% of juveniles from control mothers survived the same interval ($n=50$ litters; $t_{47.4}=-2.854$, $p=0.006$). Following removal of the food supplement, survival of offspring between emergence and territory settlement continued to be significantly higher for juveniles from previously supplemented mothers (80%) than control mothers (53%; $n=48$ litters, $U=297.5$, $p=0.042$). Of the 17 juveniles from food-supplemented mothers that settled a territory, 16 (94%) survived over winter to the following spring, whereas only 23 of the 37 (62%) successfully settled juveniles from control mothers survived to spring ($\chi_1^2=5.929$, $p=0.015$). Thus, the overall survival of litters from emergence (when food was removed) to 1 year of age was nearly threefold higher for food supplemented (79%) than control mothers (29%; $n=45$ litters, $U=314.500$, $p<0.001$; figure 1).

(a) *Potential correlates of juvenile survival*

Supplemented females gave birth, on average, 18 days earlier than control females (April 20±4 days, $n=10$ food supplemented versus May 8±2 days, $n=50$ control; $t_{58}=-3.941$, $p<0.001$). Litter sizes were not significantly different between food-supplemented and control females (3.20±0.42, $n=10$ food supplemented versus 2.88±0.09, $n=50$ control; $t_{9.9}=0.75$, $p=0.47$). Body masses of juveniles (days of age included as a covariate) raised by food-supplemented and control mothers did not differ during pre-emergent tagging ($F_{1,38}=0.38$, $p=0.54$), first capture following emergence ($F_{1,38}=2.72$, $p=0.11$), autumn ($F_{1,23}=0.09$, $p=0.77$) or the following spring ($F_{1,32}=0.32$, $p=0.57$).

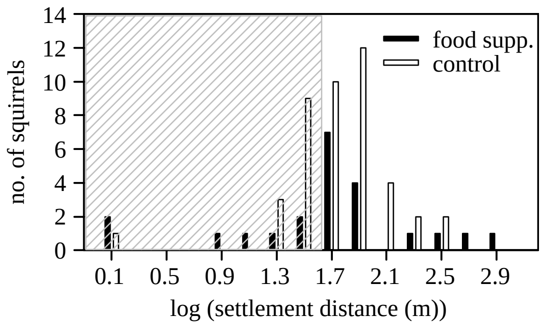

Figure 2. Frequency distribution of individual juvenile settlement distances from the natal area of control and food supplemented mothers. Hatched area indicates distances within estimated mean boundary of natal territory.

There were no significant differences in dispersal and settlement distances of juveniles from food-supplemented and control mothers. Between emergence and settlement, 88% of all juvenile captures were within 160 m (three territory widths based on 53.3±2.2 m diameter of 27 measured juvenile territories in 2004) of their natal territory. Litter average settlement distances did not differ between treatments ($t_{30}=0.24$, $p=0.81$), with 85% of control juveniles and 76% of food-supplemented juveniles settling within three territory widths of their natal territory (figure 2). Food-supplemented mothers (6 of 12) were just as likely to bequeath their territory as control mothers (15 of 26; $\chi_1^2=0.20$, $p=0.66$).

Maternal food supplementation did not enhance juvenile territory quality. Juveniles from food-supplemented and control mothers were not characterized by significantly different territory sizes (0.25±0.02 versus 0.22±0.03 ha; $t_{19}=1.03$, $p=0.32$) or the number of high-quality middens within their territories (1.36±0.20 versus 1.27±0.19; $U=25.5$, $p=0.95$). Territories settled by juveniles from control mothers were estimated to contain more current year cones (8472±4943) than those settled by juveniles from food supplemented mothers (708±247; $U=12.0$, $p=0.004$), but estimates from both treatments were very low owing to overall poor cone production in the year of study.

4. DISCUSSION

Maternal food supplementation had a clear and persistent effect on juvenile red squirrel survival throughout successive life-history stages from birth to recruitment. Across three life-history stages, survival was significantly higher for juveniles raised by food supplemented mothers than for juveniles from unsupplemented mothers. As a result, the consequences of our experimental manipulation of the maternal environment prior to offspring emergence magnified over time, long after supplemental food was removed and offspring were weaned. Thus, although offspring of supplemented mothers were only 1.5 times more likely to emerge from the nest than offspring of non-supplemented mothers (when supplemental food was last available in the system), they were 2.7 times more likely to be still alive the following spring.

Offspring traits, such as body size, dispersal distance and territory quality, did not differ between food-supplemented and control treatments (or, in the case of estimated current year cones, did not differ in the direction favouring juveniles from food supplemented mothers) and thus cannot explain the persistent effects of maternal food supplementation on juvenile survival. Clearly, there are additional traits that we did not measure that could be influenced by maternal nutrition and affect post-emergent juvenile survival. Recent literature has identified immunocompetence, metabolism and stress axis hormones as excellent candidates (Saino *et al.* 1997; Lindström 1999; Steyermark 2002; Reeder & Kramer 2005), and current research on this population is examining their respective roles. The importance of parturition date to offspring fitness has been documented previously in this system (McAdam & Boutin 2003*b*; Réale *et al.* 2003), suggesting that the advanced parturition date of food-supplemented mothers probably enhanced the survival of their juveniles. As a result of their significantly advanced birth dates, juveniles from food-supplemented mothers had an earlier start than controls in emerging from the nest, locating vacant territories, settling and defending these territories and creating autumn food hoards. Birds also consistently advance breeding in response to food supplementation (Martin 1987; Newton 1998), but the subsequent survival effects on offspring are rarely quantified. Additional experiments are required to resolve whether the fitness benefits created by maternal supplementation result primarily from phenological or as-yet-unidentified phenotypic advantages that mothers transfer to their offspring. Nevertheless, the results of the present experiment reveal a surprising magnitude and persistence of maternal effects on offspring survival in a wild population.

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