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Anticipatory parental care: acquiring resources for offspring prior to conception

Stan Boutin[1*], Karl W. Larsen[2] and Dominique Berteaux[3]

[1]*Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9*
[2]*Department of Forestry and Natural Resource Sciences, University College of the Cariboo, Box 3010, Kamloops, British Columbia, Canada V2C 5N3*
[3]*Department of Natural Resource Sciences, McGill University, Macdonald Campus, 21 111 Lakeshore, Ste-Anne-de-Bellevue, Quebec, Canada H9X 3V9*

Many organisms acquire and defend resources outside the breeding season and this is thought to be for immediate survival and reproductive benefits. Female red squirrels (*Tamiasciurus hudsonicus*) acquire traditional food cache sites up to four months prior to the presence of any physiological or behavioural cues associated with mating or offspring dependency. They subsequently relinquish these resources to one of their offspring at independence (ten months later). We experimentally show that acquisition of these cache sites cannot be explained by conventional arguments such as enhanced survival of the parent or increased reproductive output. Instead this behaviour functions as a form of parental care.

Keywords: parental care; parental investment; red squirrel; parent–offspring conflict; *Tamiasciurus hudsonicus*

1. INTRODUCTION

Parental care is 'any form of parental behaviour that appears likely to increase the fitness of a parent's offspring' (Clutton-Brock 1991, p. 8) and parental investment is the cost associated with this behaviour as measured by the reduction in the parent's residual reproductive value (Trivers 1972; Clutton-Brock 1991). The relative costs and benefits of parental care have important implications for the evolution of mating systems, sex ratios and parent–offspring conflict. However, measuring these costs and benefits can be challenging and most researchers interested in the evolution of parental care have concentrated on the period immediately prior to, during and following offspring dependency (Clutton-Brock 1991).

Many species maintain access to resources such as food caches or territories outside the period of offspring dependency. It has been assumed that these resources are secured for the direct benefit of the resource holder and that the amount is sufficient for maintenance and breeding (Brown 1964). However, there has also been discussion about possible instances where the amounts of resources defended are over and above basic requirements. Verner (1977) advanced the hypothesis that individuals may defend more resources than required as a form of spiteful behaviour. This hypothesis has been rejected on the basis that spiteful behaviour is unlikely to evolve in a population because of the potential for 'cheaters' (Getty 1979; Rothstein 1979). Others have pointed out that, under variable conditions, the need for adequate resource levels in low years could make it appear that, in average years, individuals are defending more resources than required (Pitelka *et al.* 1974; MacLean & Seastedt 1979).

An alternative hypothesis for why some organisms might defend more resources than they require is that the additional resources may be used as a form of anticipatory parental care whereby the resources will be held until they can be relinquished to offspring when the offspring gain independence. For this hypothesis to be supported, it will be necessary to show that the additional resources (i) do not lead to immediate fitness benefits such as increased parent survival or reproduction, and (ii) result in survival benefits for offspring.

Individual red squirrels (*Tamiasciurus hudsonicus*) defend exclusive territories containing a traditional food cache site (midden) that is necessary for survival (Smith 1968). Juveniles must establish their own independent territory by winter (Larsen & Boutin 1994) and some females appear to assist their offspring by bequeathing their midden to their offspring and relocating to vacant middens nearby (Smith 1968; Price *et al.* 1986; Boutin *et al.* 1993; Price & Boutin 1993). This 'bequeathal' behaviour is advantageous to offspring because they cannot displace territory owners (S. Boutin, unpublished data), are subordinate to adult squirrels when competing for vacant middens (Boutin *et al.* 1993) and are more likely to be killed by predators when away from their natal territory (Larsen & Boutin 1994). Because red squirrels have evolved very advanced forms of both parental care (territory bequeathal) (Berteaux & Boutin 2000) and investment for the future (traditional food caches), they are good candidates for an investigation of the existence of anticipatory parental care.

In this study we provide experimental evidence that female red squirrels incorporate additional middens into their territory well in advance of conception of offspring and later bequeath these middens to their offspring. We also present evidence suggesting that this behaviour persists in the absence of direct benefits to the parent and

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[*]Author for correspondence (stan.boutin@ualberta.ca).

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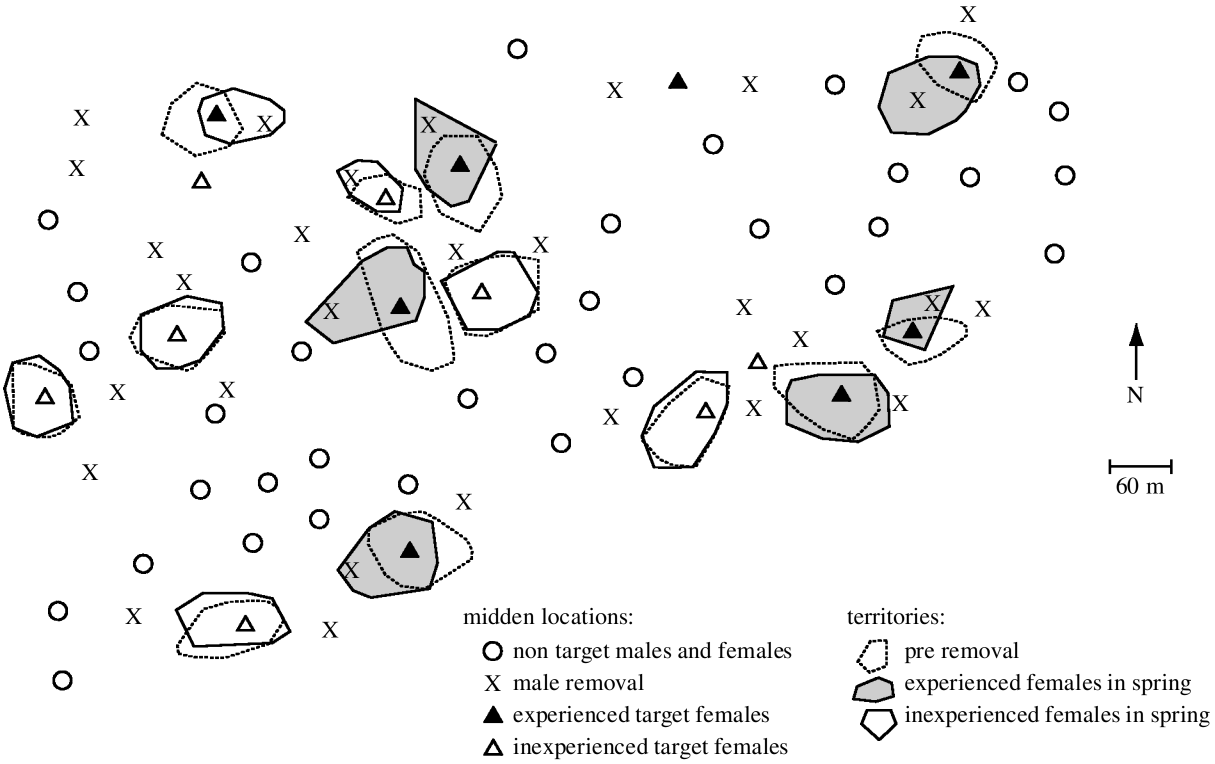

Figure 1. Midden locations for 77 resident red squirrels in one site (75 ha) in autumn 1990. Changes in the territory boundaries of experimental experienced and inexperienced females following the creation of vacant cache sites (middens) by removal of neighbouring males on 15 and 16 October 1990 are also shown.

must accordingly be considered as a form of parental care.

2. METHODS

(a) *Study site and general data collection*

We studied red squirrels on two blocks of jackpine (*Pinus banksiana*) habitat located 3 km apart in central Alberta, Canada (54°20′ N, 114°45′ W) from 1988 through to 1991 (see Larsen & Boutin 1994). All residents were individually marked and the ownership of all middens was determined by repeated live trapping and recording who produced territorial calls and chased away intruders (Smith 1968; Lair 1990). The reproductive history and territory boundaries of most females were also known (for details, see Boutin & Larsen 1993; Larsen 1993; Larsen & Boutin 1994).

(b) *Removal experiment*

We conducted an experiment in October 1990 which was designed for determining whether territory quality was a factor in determining whether or not females bred in a given year (see Larsen & Boutin 1995). The rationale was that adult females that had not bred previously would be more likely to relocate to experimentally vacated territories than reproductively active females. In other words, given the opportunity, non-breeding females would be more likely to attempt to 'improve' their territory by moving to a vacated site. We classified adult females (more than two years old) as experienced (had previously produced young) and inexperienced (had never produced young). Eight experienced and eight inexperienced females were randomly selected in one site. Females with offspring who were still in search of a territory were excluded from the selection process. All females selected were two to four years old and their average age did not differ between the experienced (mean ± s.e. 2.75 ± 0.31 years) and inexperienced (2.37 ± 0.18 years) groups. Two males adjacent to each female were live trapped on 15 and 16 October and permanently removed from the site by transporting and releasing them across a river 10 km away. Logistical constraints in two cases required that one male serve as a removal for both an experienced and an inexperienced female. The average (s.e.) distances from target female middens to vacated middens were 84.5 ± 22.2 and 83.4 ± 22.4 m for experienced and inexperienced females, respectively. We also monitored an additional 11 experienced and ten inexperienced females which we called controls. These individuals were located in the second study site.

(c) *Territory boundaries and reproductive success of females*

The females' boundaries were mapped from late June to 13 October 1990 using behavioural observations and telemetry (Price *et al.* 1986; Larsen & Boutin 1994). We visited the experimental females on the day following removals in order to record any changes in midden ownership as evidenced by squirrels calling on the midden. Territories of experimental females that had survived winter were mapped the following May and the ownership of all middens in the study areas was determined.

Body mass measurements were obtained for each female by live trapping in October and March (just prior to conception). The reproductive success of each female, including the survival and location of settlement of all offspring, was followed in summer 1991 (Larsen & Boutin 1994).

Table 1. *Comparison of the number of experienced (had produced young in 1990) and inexperienced (had never produced young) females at various stages of the experiment*

(The p-values are from Fisher's exact tests.)

	experienced females	inexperienced females	p
number of females that participated in the experiment	8	8	—
number of females that immediately took over an additional midden	5	0	0.026
number of females that survived through the winter	7 (87.5%)	6 (75.0%)	—
number of females that owned an additional midden in spring	6 (85.7%)	1 (16.7%)	0.029
number of females that reproduced and had one or no juveniles to weaning	5	4	—
number of females that bequeathed the additional midden to a juvenile	5	1	—

3. RESULTS

(a) *Midden acquisition and changes in territory boundaries*

Five experienced and no inexperienced females were observed producing territorial calls on or near an adjacent, vacated midden the day following the removals (table 1). Take-over of experimentally vacated middens occurred within hours (Price *et al.* 1986; Boutin & Schweiger 1988) and, in April of the following spring, vacated middens were owned by the same squirrels that had made calls there in October. However, contrary to our expectations, none of the experimental females that had survived winter abandoned their original territory in order to occupy a vacant midden. Instead, seven out of the 13 females that had survived to spring shifted their territory boundaries so as to encompass their original midden plus a midden from a removal territory (figure 1). Despite these shifts, the territory size of these females in spring (0.65 ha) was not significantly different from that in autumn (0.62 ha) (paired t-test = 0.40, $p = 0.35$ and d.f. = 6). An additional 13 vacated middens were owned by adult males and subadults in spring but none of these individuals adjusted their territory boundaries in order to include two middens.

There was one other key result. Experienced females were much more likely than inexperienced females to own two middens (six out of seven experienced females versus one out of six inexperienced females) (table 1 and figure 1) (Fisher's exact test, $p = 0.029$). In the case of control females, of seven experienced and eight inexperienced females present in spring, two experienced and no inexperienced females had acquired a second midden through the natural disappearance of a neighbour.

To summarize, adult females did not relocate to vacated middens, but some did shift their territory boundaries in order to incorporate a vacated midden so as to own two middens in spring. With one exception, only experienced females showed this behaviour.

(b) *Fates of acquired middens and offspring*

We then followed the fates of the middens acquired through to autumn when juveniles were establishing territories. An offspring settled on an acquired midden in each case in 1991 where experimental females had acquired a midden and had offspring survive to weaning (five experienced females and one inexperienced female) (table 1). The one remaining female that had acquired a second midden had no offspring survive to emergence and she subsequently lost the acquired midden to an adult male in July. Only one of those females that owned a single midden and that weaned offspring (control and experimental combined) ($n = 15$) had an offspring settle on their territory. Finally, females that had acquired a second midden were also more likely to have at least one young acquire a midden (six out of six versus seven out of 15) (Fisher's exact test, $p = 0.046$).

(c) *Were females who acquired a second midden different from females with a single midden?*

Experienced females with two middens in spring 1991 did not differ from experienced females with a single midden or from inexperienced females in their average age, autumn mass, spring mass, date of conception or litter size (table 2) (t-tests, all p-values > 0.3). There was no difference in the overwinter survival of experimental experienced (seven out of eight) and inexperienced (six out of eight) females and all of these survivors produced offspring in 1991.

4. DISCUSSION

(a) *Why did experienced females acquire a second midden?*

Our experiment revealed that some females acquired and defended a second midden which they subsequently relinquished to their offspring at weaning. It is clear that the acquired midden was beneficial to offspring as it increased the probability that they could secure their own midden, a key prerequisite for overwinter survival (Larsen & Boutin 1994). Given the benefit to offspring, acquisition of a second midden by adult females could be considered a form of parental care (Clutton-Brock 1991; Berteaux & Boutin 2000). However, the question remains as to whether this was the primary function of the behaviour or simply an offshoot of the more immediate function of providing resources for the female.

Two lines of evidence suggest that females acquired the middens as a form of parental care rather than for immediate benefits. First, if middens were acquired for immediate benefits, experienced females with two middens relative to those owning a single midden should have shown immediate fitness benefits such as reduced overwinter weight loss or increased reproductive output. We found no evidence of this (table 2).

Table 2. *Comparison of physical and reproductive parameters in 1990–1991 of experienced females (had produced young in 1990) that had acquired a second midden from removal territories, experienced females with a single midden and inexperienced females (had never produced young prior to 1991)*

	experienced females with two middens			experienced females with one midden			inexperienced females		
	mean	s.e.	*n*	mean	s.e.	*n*	mean	s.e.	*n*
age (years)	2.8	0.40	6	3.8	0.31	6	2.4	0.19	8
autumn mass (g)	209.7	7.43	6	215.0	4.82	6	201.7	3.34	8
spring mass (g)	232.1	9.77	6	239.5	4.89	6	223.5	6.75	6
date of conception	19 April	7.90	6	20 April	5.39	6	21 April	9.79	6
litter size	3.3	0.33	6	3.0	0.55	5	3.1	0.40	6
weaned	2.0	0.45	6	1.4	0.67	5	2.3	0.76	6

Second, we obtained the surprising result that experienced females were much more likely to acquire a second midden than inexperienced females. We do not think this was due to differences in dominance status or competitive abilities as the two groups were similar in age and body weight (table 2). Instead, we think the difference could be explained by the fact that this expression of parental care carries differential potential fitness benefits for members of each group. In the population of squirrels we studied, females begin to breed at one to four years of age and they breed every year thereafter for the rest of their lives (Larsen 1993). The probability that nulliparous females will breed in their next year is lower than for experienced females and is highly variable (7–100%) (Becker 1992; Larsen 1993; Becker *et al.* 1998). The proportion of nulliparous females that breed in a given year seems to depend on the food and weather conditions in spring (Becker 1992; Becker *et al.* 1998) which are probably not predictable by females in autumn. Given the difference in the predictability of reproduction by experienced and inexperienced females, the probability of gaining fitness benefits through relinquishing an acquired midden to a weaned offspring is higher for an experienced versus inexperienced female and this could explain why the propensity to show the behaviour differs between these groups.

(b) *Parental care or parental investment?*

The answer to this question depends on whether or not females incurred additional costs by acquiring a second midden and defending it during the whole winter. We could detect no cost as indicated by increased overwinter mass change, delayed date of conception or reduced litter size (table 2). However, there were three indications that females may have incurred some costs. First, we showed that females who acquired a second midden shifted their territory boundaries substantially more than females who did not (figure 1) and we know that any changes in territory boundaries involve increased calling and disputes between neighbours (Boutin *et al.* 1993). Second, the costs of defence of a territory with middens at either end (figure 1) are greater than for a territory having a single central cache (Smith 1981). Third, if females had to re-establish their old territory boundaries after bequeathal of the acquired midden in order to maintain territory size and access to trees from which to harvest cones, additional costs would be expected. It is our perception of the field reality that these costs are far from trivial, but more work is needed in order to demonstrate their existence in our study population definitely. This will be a necessary step before we can rank the behaviour that we observed as parental investment instead of merely parental care.

(c) *Implications*

Our findings suggest that parental investment can occur in the absence of reproductive cues, mating benefits or the presence of offspring. We call this anticipatory parental care and, as a consequence of these findings, researchers studying the evolution of parental care must look beyond the traditional period of breeding and offspring dependency when assessing the true costs and benefits of parental care. In addition, those studying the causes and consequences of resource acquisition must consider the possibility that resources may be acquired for reasons other than immediate benefit for the owner. Future models of territory defence and the evolution of parental care should consider intergenerational costs and benefits.

We do not believe that anticipatory parental care is unique to red squirrels. Kangaroo rats (*Dipodomys spectabilis*) (Waser 1988) and ground squirrels abdicate burrow systems to their offspring (Harris & Murie 1984). Breeding dispersal is known to exist in a wide range of birds and mammals (Petersen & Best 1987; Cockburn 1988; Lambin 1997) and there is growing evidence that this behaviour functions as a form of parental investment (Berteaux & Boutin 2000). These species may also show anticipatory parental care. However, it is not unreasonable to hypothesize that any species that defends resources necessary for long-term survival may show anticipatory parental care.

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