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FITNESS BENEFITS OF A MOTIVATED MOM

A PREPRINT

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ABSTRACT

Parental investment theory predicts that observed levels of parental care afforded to offspring are set by the benefits (to offspring quality and survival), relative to the costs (to parental survival or future reproduction). Although difficult to document, there is often substantial individual-variation in the amount of parental care within species. We measured the impact of individual variation in maternal care on fitness in a wild population of North American red squirrels (*Tamiasciurus hudsonicus*). We used pup retrieval latency following a nest intrusion as a measure of maternal motivation to care for pups. Pups from large litters grew faster if they had a highly motivated mother, indicating that maternal motivation can mitigate the trade-off between litter size and offspring growth. Pups whose mothers who returned to the nest faster were more likely to survive to autumn, a critical life history stage. These results highlight important fitness impacts of having a highly motivated mother and show that maternal motivation can alter a fundamental life history trade-off between offspring quantity and quality.

Keywords fitness · growth rate · maternal behavior · maternal care · North American red squirrel

1 Introduction

Parental investment theory predicts that elevated parental investment will produce more, and/or higher quality, offspring, but this may come at a cost of decreased future fecundity and/or survival of parents [1, 2, 3, 4]. In this context, parental care has been defined to include parental traits, including behaviour, that increase fitness of offspring, and is one aspect of parental investment [3, 5]. The energetic costs of reproduction, which may limit their future parental investment [4], may be especially high in mammals as offspring are typically dependent on their mother for survival until weaning [6, 7, 8]. This energetic cost of parental care contributes to the fundamental life history trade-off between offspring number and size [9, 10], where parents can rarely raise many large offspring [11]. The trade-off for parents between offspring quality and quantity could impact the lifetime trajectory of offspring via differences in developmental rates of individuals [3, 5, 12].

In mammals, we might expect to see directional selection for high maternal care if the benefits afforded to offspring exceed the costs to the parents, yet there is much individual variation in this behaviour [13, 14, 15]. Many studies in mammals have investigated the proximate mechanisms behind variation in maternal care [16], yet the ultimate mechanisms (i.e. fitness consequences) are rarely addressed, due to the logistical challenges of doing so (but see [17, 18]). In this study, we used pup retrieval latency, a measurement commonly used with laboratory rodents [13, 16], as a proxy for maternal motivation following a nest intrusion in wild North American red squirrels (*Tamiasciurus hudsonicus*). In laboratory studies of rodents, latency to retrieve pups after they are moved to a different location in the

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cage is interpreted as how motivated an individual is to care for pups [19, 20]. In wild animals, we cannot distinguish between whether this is how motivated a mother is to defend pups or how motivated she is to exhibit infant-directed behaviours, both important components of motivated maternal care [20]. Pup retrieval latency is also biologically meaningful in our study species. For example, lactating female red squirrels are known to move their pups between nests on their territory as the ambient temperature fluctuates [21]. This behaviour could potentially be useful in other situations, such as reducing flea load on pups [22, 23] or reducing risk of infanticide [24] or predation [25]. Highly motivated moms may move pups immediately following a nest disturbance, despite the inherent risk involved, thereby potentially increasing chances of offspring survival.

We conducted this study as part of a long-term study of red squirrels in Yukon, Canada. Red squirrel pups are altricial and dependent upon their mother until weaning whereupon they typically disperse to nearby territories (mean = 92 m – 102 m from natal territory [26, 27]). Weaned pups experience strong selective pressures with a majority of juvenile mortality (68%, on average) occurring over the summer before mid-August and few surviving through their first winter, depending on food availability [28, 29]. Pups that grow faster early in life are typically more likely to survive their first winter [30], particularly in years with high conspecific density [31]. Despite fitness benefits of fast growth, there is substantial variation in pup growth rates among females and within litters. Some of this variation in pup growth rate is explained by variation in size and birth dates of litters [32] or levels of maternal glucocorticoids during pregnancy [31]e. Here, we tested the hypothesis that maternal behaviour contributes to variation in offspring growth rate. We predicted that mothers who exhibited higher maternal motivation (i.e., fast pup retrieval) would produce faster growing offspring that were more likely to survive. Consistent with life history theory, individual growth rates of pups are typically lower in larger litters, however previous research has shown mothers in a high conspecific density environment can reduce this trade-off between litter size and pup growth rates [31]. Therefore, we also hypothesized that behaviour of mothers could ameliorate this life history trade-off and predicted that pups from litters with several siblings would grow faster if they had a highly motivated mother.

2 Methods

2.1 Study Population

North American red squirrels are arboreal, asocial, and sexually monomorphic [33]. Both sexes exhibit year-round territoriality and have many nests on their territory [34, 35]. Mothers provide all parental care in this species and typically produce one successful litter per year, with the exception of mast years [36]. Our study was conducted within Champagne and Aishihik First Nations traditional territory in Yukon, Canada (61N, 138W). Squirrels in our study population rely mainly on the seeds of white spruce (*Picea glauca*) for food [37, 38], which they cache in an underground larder hoard ("midden") located on the centre of their territory. White spruce exhibit masting, meaning all trees in the area synchronously produce large numbers of spruce cones followed by years with almost no cones produced [38]. As their main seed predator in the region, the population density of red squirrels increases following mast seed events [31, 39]. Because we have previously documented that spruce cone availability impacts growth and survival of offspring [30, 37, 38, 40, 41], we estimated the number of cones available in the study area by using visual cone counts to determine cone index [42].

2.2 Maternal behaviour observations

In 2008, 2009, 2016 and 2017, we live-trapped (Tomahawk Live Trap, Tomahawk, WI, USA) breeding females (n = 272 unique squirrels across 4 years) at regular intervals to determine reproductive status (see [28] for more details). Squirrels in this study were from either a control study area (n = 141 squirrels) or a study area that was provided with supplemental ad libitum peanut butter from 2004 to 2017, resulting in a higher density of squirrels (n = 79 squirrels) [31]. As soon as lactation was detected, we used radio telemetry to locate nests. We will refer to this as the "first nest entry" (n = 292 litters from 167 females). We estimated parturition date based on weight of pups, as well as palpation history, and lactation history of the mother [28]. When pups were 25 days old, we repeated this process for what we will refer to as the "second nest entry" (n = 227 litters from 152 females). 48 females were observed across two years. At each nest entry, the litter was processed (details discussed below) and then replaced in the original nest. Not every litter was observed for both first and second nest entries.

After each nest entry, we performed focal behavioural observations on mothers. An observer (n =31 different observers) moved >5 m away from the nest tree and watched the mother's behaviour for 7 minutes following replacement of pups to record the time pups were replaced in the nest and time mother returned to the nest. Observers were blind to any previous maternal behaviour observations of the focal squirrel. Five observations were at underground nests, with the remaining in trees. Pup retrieval latency was determined from these observations and censored to 420 seconds for any observations where the mother did not return within 7 minutes (n = 319 censored observations). With this

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measurement, our goal was to capture individual variation in how motivated a mother was to retrieve her pup following a nest intrusion.

2.3 Offspring measurements: growth rate and survival

At each nest entry, we removed pups from the nest to weigh (to nearest 0.1g), mark, and sex individuals. During the second nest entry, we additionally assigned unique coloured disk combinations and unique alphanumeric stamped ear tags (National Band And Tag Company, Newport, KY, USA) to each pup for identification after emergence. Afterwards, we replaced all pups in the nest we originally found them in. In a sample of nests from 2016, the average time pups spent out of the nest during the first nest entry was 11:56 min:sec [range: 06:19-34:50] (n = 65 litters) and the average time pups spent out of the nest during the second nest entry was 38:32 [range: 14:47-01:31:17] (n = 64 litters). Data on time pups spent out of the nest was not collected in other years but the above data should be representative of all years as data collection protocols were uniform across all years.

Growth between these two nest entries is approximately linear [43], so we calculated growth rate (g/day) of pups (n = 671 pups) as the change in mass from first to second nest entry divided by number of days between nest entries. We monitored survival of juveniles (n = 870 juveniles from 251 litters) for the remainder of the year and following spring. We recorded survival to autumn of the birth year as a binary measure (alive or dead on August 15th). In this population, caching of spruce cones typically begins mid-August and ends in September [38]. Territory ownership before this period allows individuals to take advantage of that year's cone crop by providing them with a physical space to cache cones (cones must be cached in a midden for the seed to remain a viable food source [43]). Because offspring disperse from their natal territory around 70-80 days old to compete for their own territory [28, 44], we limited survival data to litters born 70 days prior to August 15th. As part of our long-term data collection, the entire study population was censused yearly to confirm territory ownership by August 15th and again by May 15th [29]. Because squirrels are diurnal and their activity (territorial defense behavior and presence) is conspicuous, we were able to completely enumerate all squirrels inhabiting the study areas through a combination of repeated live trapping and behavioural observations.

2.4 Statistical Analyses

We conducted all statistical analyses in R version 3.4.3 (R Core Team, 2016). We used the R package 'lme4' version 1.1-19 [45] to fit linear mixed-effects models and estimated P-values using the R package 'lmerTest' version 3.0-1 [46].

In our models to assess how maternal motivation affected offspring growth, we included the following predictors: retrieval latency, number of pups in litter, parity of mother (first time mother or not), Julian birth date, cone index of the previous year, sex of pup, birth year, and study area (control or high density). To detect any collinearity in the predictors included in our model, we used R package 'car' version 3.0-2 to assess the variance inflation factors. GVIF(1/(2xDF)) for all predictors was < 5, except cone index of the previous year (GVIF(1/(2xDF)) = 11). We decided to still include spruce cone abundance (cone index: [42]) in these models as it is a major influence on survival and growth rate in this study system [30, 31, 36, 47] and we wanted to control for its influence on offspring growth. Cone index of the previous year is also predictive of conspecific density which also influences growth rate [31]. To assess if maternal motivation could mitigate effects of increasing litter size on offspring growth rates, we included the interaction between retrieval latency and litter size. Since multiple pups were measured per litter, we included litter ID as a random effect.

To model the relationship between maternal care and offspring survival, a binary value for offspring survival to autumn was predicted by the following fixed effects: pup retrieval latency, cone index of birth year, cone index of previous year, study area (control or high density), and Julian birth date. Again, we assessed variance inflation factors and found GVIF(1/(2xDF)) for all predictors was < 2. We ran models with observations from the two nest entries separately due to the potential for different levels of maternal investment at different times in the breeding season. Squirrels born earlier in the year generally are more likely to survive until the following year so mothers that lose their litter earlier in the season (e.g. right after birth) have the potential to successfully breed again [29, 48], whereas mothers that lose their litter later in the season (e.g. a month after birth of the first litter) may not have the same potential for a successful second litter in a non-mast year.

3 Results

In simple linear models, we found no relationship between the number of pups in a litter and the time pups spent out of the nest (ß = -75.27, SE = 144.23, t = -0.52, p = 0.60), as well as the pup retrieval latency and the time pups spent out of the nest (ß = -0.25, SE = 0.77, t = -0.32, p = 0.75).

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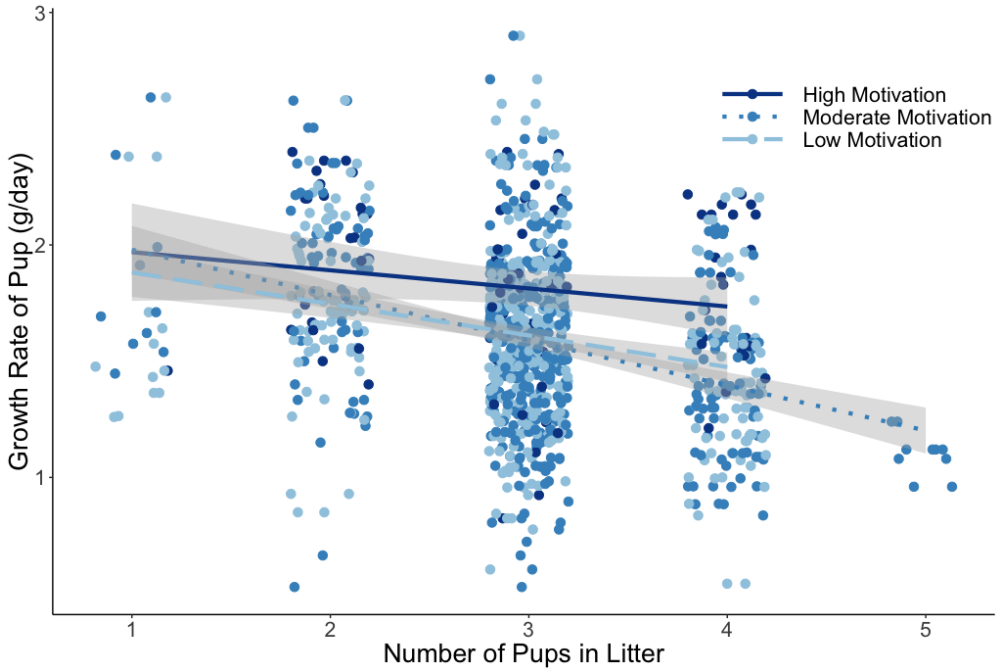

Figure 1: **Relationship between maternal care and growth rates of pups** Pups from larger litters typically grew slower than pups from smaller litters. This relationship was mitigated by highly motivated mothers. Pups in large litters grow faster if their mother was highly motivated. In this graph, pup retrieval latency is broken down into three categories, distinguished by line type and color: high motivation (1 min.; solid line), moderate motivation (>1 min, <7 min.; dotted line), and low motivation (7 min.; dashed line). Darker colors indicate greater motivation.

3.1 Maternal motivation and pup growth rate

We found that the apparent cost for an individual pup of being in a litter with many siblings, in terms of a reduced growth rate, was lessened by having a highly motivated mother. Pups in large litters with mothers that returned soon after pup replacement grew faster than those in large litters with mothers that took longer to return to the nest (latency x litter size interaction - nest entry 1: ß = -0.073, CI = 0.14 – -0.01, t = -2.22, p = 0.028; nest entry 2: ß = -0.057, CI = -0.13 – 0.01, t = -1.61, p = 0.11; Figure 1; Table 1).

3.2 Maternal motivation and survival

We found pups with mothers who retrieved their pups faster following a nest disturbance were more likely to survive until autumn than pups with mothers who returned more slowly (nest entry 1: ß = -0.21, SE = 0.10, t = -2.11, p = 0.035; nest entry 2: ß = -0.23, SE = 0.11, t = -2.17, p = 0.030; Figure 2; Table 2). Pups with mothers who returned immediately after pups were replaced were about twice as likely to survive than pups from mothers who returned at the end of the 7-minute observation period.

4 Conclusions

Female red squirrels that exhibited higher levels of maternal motivation (measured as pup retrieval latency) lessened the fundamental life history trade-off between offspring quantity and quality and produced fast-growing offspring that were more likely to survive a critical life history stage. While overall juvenile survival was low, offspring from highly motivated mothers were more likely to survive post-weaning through summer. Additionally, highly motivated red squirrel mothers are capable of producing more high-quality pups, compared to less motivated mothers, by mitigating the trade-off between litter size and pup growth rates. This amelioration could be one way that maternal behaviour alters offspring lifetime fitness trajectories [12].

In many species, we often see parental investment theory linked to this trade-off. For example, in quacking frogs (*Crinia georgiana*), mothers face a trade-off between egg size and number and can use variable egg provisioning to influence

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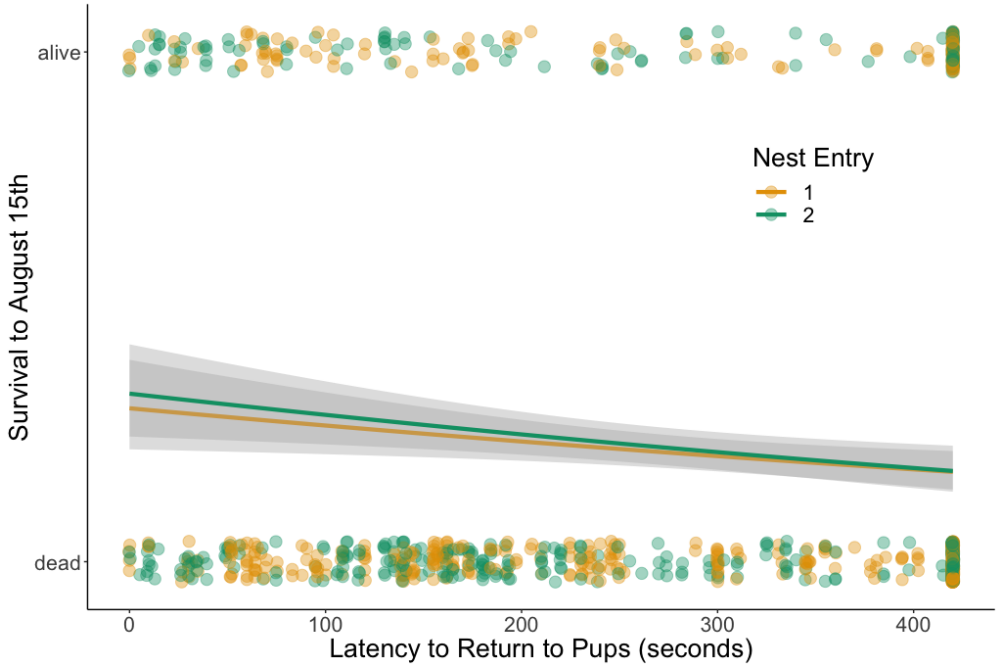

Figure 2: **Logistic relationship between maternal care and survival to autumn** Pups born to a highly motivated mother were more likely to survive to August 15th of their birth year. Orange color indicates a first nest entry observation and green color indicates a second nest entry observation.

survival of offspring in good and poor-quality environments [49]. Similarly, in birds, habitat altitude is an important factor in whether parents invest in quantity or quality of offspring [50]. Our study suggests red squirrels use maternal behaviour as one mechanism to adjust this trade-off between offspring size and number.

Despite finding that highly motivated mothers produced offspring with higher survival, we show individual variation in maternal motivation. Although, we did not explicitly compare the costs and benefits assumed in parental investment theory, the costs to the mother are clear. For example, if the nest was intruded on by predators, mothers could face the cost of potentially being preyed upon herself, or the energetic costs of moving pups to a new nest (on average one 25-day old pup weighs 18% of the body mass of an adult female). In addition, we see annual variation in selection on growth rate [30, 31], so it may be an unreliable strategy for mothers to invest in faster growing offspring if it can result in a high energetic cost with little fitness benefit [30, 31]. In other words, we may see balancing selection where mothers with slow growing pups have an advantage in years when fast growth is not selected for, which is not captured in our limited dataset across 4 years. Similarly, we see balancing selection for other behavioural traits of aggression and activity in mothers [51]. Alternatively, high maternal motivation could be driven by high quality mothers who can afford higher investment in current reproduction and variation we see in maternal behaviour is due to limitations on the mother and current environmental conditions, rather than fitness consequences. Future work should investigate plasticity of this behaviour in response to environmental variables, impact of maternal condition, and costs associated with maternal care to more comprehensively test parental investment theory [52].

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Response Variable	Fixed Effect	b	CI	t	p-value
a) Growth rate (g/day)					
n = 526 pups	Intercept	1.26	-0.58 – 3.09	1.34	0.18
n = 193 litters	*Latency to return to pups (scaled)*	*0.19*	*-0.01 – 0.38*	*1.89*	*0.061*
	Litter size	**-0.22**	**-0.29 – -0.15**	**-5.98**	**< 0.0001**
	Parity of mother (categorical):				
	primiparous	-0.077	-0.28 – 0.12	-0.75	0.46
	Year:				
	2009	0.74	-0.45 – 1.93	1.22	0.22
	2016	0.82	-1.04 – 2.67	0.86	0.39
	2017	0.68	-0.83 – 2.19	0.89	0.38
	Julian birth date (scaled)	**-0.13**	**-0.22 – -0.04**	**-2.97**	**0.0034**
	Cone index of previous year	0.60	-0.34 – 1.55	1.26	0.21
	Grid type:				
	Food addition + higher density	*0.13*	*-0.01 – 0.27*	*1.82*	*0.07*
	Sex of pup:				
	male	**0.040**	**0.00 – 0.08**	**2.22**	**0.027**
	Latency to return x litter size	**-0.073**	**-0.14 – -0.01**	**-2.22**	**0.028**
	Random effect:	**Variance**	**SD**		
	litter ID	0.10	0.32		
	residual	0.027	0.16		

Response Variable	Fixed Effect	b	CI	t	p-value
b) Growth rate (g/day)					
n = 480 pups	Intercept	0.78	-1.18 – 2.73	0.78	0.44
n = 178 litters	Latency to return to pups (scaled)	0.10	-0.09 – 0.30	1.03	0.30
	Litter size	**-0.16**	**-0.24 – -0.30**	**-4.58**	**< 0.0001**
	Parity of mother (categorical):				
	primiparous	-0.053	-0.26 – 0.12	-0.50	0.62
	Year:				
	2009	0.91	-0.36 – 2.18	1.41	0.16
	2016	1.20	-0.79 – 3.19	1.18	0.24
	2017	0.90	-0.71 – 2.51	1.09	0.28
	Julian birth date (scaled)	**-0.098**	**-0.19 – -0.00**	**-2.05**	**0.042**
	Cone index of previous year	0.72	-0.29 – 1.73	1.40	0.16
	Grid type:				
	Food addition + higher density	*0.15*	*-0.00 – 0.30*	*1.94*	*0.054*
	Sex of pup:				
	male	**0.054**	**0.02 – 0.09**	**2.74**	**0.0064**
	Latency to return x litter size	-0.057	-0.13 – 0.01	-1.61	0.11
	Random effect:	**Variance**	**SD**		
	litter ID	0.11	0.34		
	residual	0.029	0.17		

Table 1: **Full model results for growth rate** Results from our linear mixed effects models on the relationship between growth rate and maternal motivation. We ran two distinct models for observations from the (a) first and (b) second nest entries (at 1 day post-parturition and 25 days post-parturition, respectively).

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Response Variable	Fixed Effect	b	SE	z	p-value
a) Alive in August?					
n = 639 pups	**Intercept**	**-1.87**	**0.31**	**-6.00**	**<0.0001**
n = 223 litters	**Latency to return to pups (scaled)**	**-0.21**	**0.10**	**-2.11**	*0.035*
	Julian birth date (scaled)	**-0.23**	**0.12**	**-1.90**	**0.050**
	Cone index of the birth year	**0.43**	**0.17**	**2.57**	**0.010**
	Cone index of previous year	-0.028	0.19	-0.15	0.88
	Grid type:				
	Food addition + higher density	-0.28	0.26	-1.09	0.28

Response Variable	Fixed Effect	b	SE	z	p-value
b) Alive in August?					
n = 506 pups	**Intercept**	**-2.05**	**0.36**	**-5.69**	**<0.0001**
n = 176 litters	**Latency to return to pups (scaled)**	**-0.23**	**0.11**	**-2.17**	*0.030*
	Julian birth date (scaled)	**-0.23**	**0.11**	**-2.21**	**0.027**
	Cone index of the birth year	**0.47**	**0.20**	**2.43**	**0.015**
	Cone index of previous year	0.18	0.20	0.93	0.35
	Grid type:				
	Food addition + higher density	-0.17	0.28	-0.61	0.54

Table 2: **Full model results for survival** Results from our binomial linear models on the relationship between survival and maternal motivation. We ran two distinct models for observations from the (a) first and (b) second nest entries (at 1 day post-parturition and 25 days post-parturition, respectively).