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ORIGINAL ARTICLE

Attentive red squirrel mothers have faster growing pups and higher lifetime reproductive success

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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 in mammals, there is often substantial individual variation in the amount of parental care within species. We measured the impact of individual variation in maternal care ("attentiveness" towards offspring or maternal motivation) on offspring growth and survival in a wild population of North American red squirrels (*Tamiasciurus hudsonicus*). We used latency to return to pups following a nest intrusion as a measure of maternal attentiveness to pups. We found this behavior to be repeatable within individuals suggesting this behavior is a personality trait or a "maternal style." In this population, postnatal growth rate is important for pup overwinter survival. Pups from large litters grew faster if they had a highly attentive mother, indicating that maternal care can mitigate the trade-off between litter size and offspring growth and potentially improve survival of pups. Additionally, more attentive mothers had slightly higher lifetime reproductive success than less attentive mothers. These results highlight important fitness effects of having a highly attentive mother and show that maternal care can alter a fundamental life history trade-off between offspring quantity and quality.

Significance statement

It pays to be attentive to your pups as a squirrel mom. In a long-term study of a wild population of North American red squirrels, we tested whether maternal behavior was predictive of growth rate and survival of offspring. To do this, we observed maternal attentiveness towards offspring by recording the time until the mother returned to her pups following a nest intrusion by researchers. We found repeatable individual variation in maternal attentiveness suggesting consistent "maternal styles" among individuals. Mothers who returned faster to pups following a nest intrusion produced faster growing pups and were able to produce larger fast-growing litters. Over their entire lifetime, attentive mothers also had more offspring survive to adulthood.

Keywords Fitness · Growth rate · Maternal behavior · Maternal care · North American red squirrel · Survival

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Introduction

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 (Trivers 1974; Drent and Daan 1980; Stearns 1989; Clutton-Brock 1991). In this context, parental care has been defined as parental behavior that increases fitness of offspring and is one aspect of parental investment (Clutton-Brock 1991; Royle et al. 2012). The energetic costs of reproduction, which may limit future parental investment (Drent and Daan 1980), may be especially high in mammals as offspring are highly dependent on their mother for survival until weaning (Roff 1998; Reinhold 2002; Maestripieri and Mateo 2009). Under the assumption of fixed energy budgets, these energetic costs to parents of parental care likely contribute to the fundamental life history trade-off between offspring number and size (Smith and Fretwell 1974; Charnov and Ernest 2006). This trade-off is reflected in the frequent observation that parents can rarely raise many large offspring (Rogowitz 1996), except when they have a large amount of resources to do so (van Noordwijk and de Jong 1986; Reznick et al. 2000). The trade-off for parents between offspring quality and quantity could impact the lifetime trajectory of offspring via differences in developmental rates of individuals (Clutton-Brock 1991; Royle et al. 2012; Klug and Bonsall 2014). For example, offspring growing up in large litters may exhibit slower development and be smaller at the age of independence than those from smaller litters which could in turn influence lifetime reproductive success (Lindström 1999).

In mammals, we might expect to see directional positive selection for high maternal care as long as the benefits afforded to offspring consistently exceed the costs to the mother, yet there is often much individual variation in this behavior (Bales et al. 2002; Champagne et al. 2007; Fairbanks and Ackles 2012). For example, in primates, individual variation in maternal care, or "maternal style," can include protective, rejecting, restrictive, or laissez-faire mothers (Fairbanks and Ackles 2012). Maternal styles can have important consequences for a female's fitness and may be a mechanism for transmitting individual differences across generations (Fairbanks and Ackles 2012). Many studies in mammals have investigated the proximate mechanisms behind individual variation in maternal care (Numan and Insel 2006), yet the ultimate mechanisms (i.e., fitness consequences) are rarely addressed, especially in wild rodents, due to the logistical challenges of accurately documenting parental behaviors.

In this study, we used latency to return to pups, a measurement commonly used with laboratory rodents (Numan and Insel 2006; Champagne et al. 2007), as a measurement of maternal attentiveness 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 cage is interpreted as how motivated an individual is to attend to pups (Mann 1993; Olazábal et al. 2013). For example, virgin female laboratory rats can develop maternal motivation to retrieve pups by prolonged exposure to pups (Seip and Morrell 2008). Latency to return to a nest box after manipulation of the brood has also been used as a measure of willingness to provide parental effort in great tits (*Parus major*) (David et al. 2015). Many neuroendocrine studies measure retrieval behavior when manipulating brain regions to identify neural structures involved in maternal behavior (Numan and Woodside 2010). In wild animals, returning to the nest could represent how motivated a mother is to defend pups or how motivated she is to exhibit infant-directed behaviors, both important components of motivated maternal care (Olazábal et al. 2013). In sum, the latency of returning to the pups represents a measure of attentiveness towards the offspring.

We conducted this study as part of a long-term project on 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 = 92–102 m from natal territory (Berteaux and Boutin 2000; Cooper et al. 2017)). Weaned pups experience strong selective pressures with a majority of juvenile mortality (68%, on average though this is highly variable among years) occurring over the summer before mid-August and few surviving through their first winter (61% of those alive in August, on average), depending on food availability and adult density (McAdam et al. 2007; Hendrix et al. 2020). Pups that grow faster early in life are typically more likely to survive their first winter (McAdam and Boutin 2003a; Fisher et al. 2017; Hendrix et al. 2020), particularly in years with high conspecific density (Dantzer et al. 2013). Despite the link between increased survival and fast growth in red squirrels, there is substantial variation in pup growth rates among and within litters. Some of this variation in pup growth rate is explained by large maternal effects including variation in litter size and the birth dates of litters (McAdam et al. 2002) or levels of maternal glucocorticoids during pregnancy (Dantzer et al. 2013), although much variation among females in the growth rates of their pups remains unexplained (McAdam et al. 2002). Here, we tested the hypothesis that maternal behavior predicts offspring growth rate and survival. We also tested the within-individual repeatability of this behavior to identify if red squirrels exhibit a "maternal style" and tested whether more attentive mothers had more pups that recruited into the breeding population over their lifetime. If we find that maternal attentiveness is a consistent individual phenotype (repeatable), this suggests that selection can act upon this behavior. We predicted that mothers who exhibited higher maternal attentiveness (i.e., faster return to the nest) would produce faster growing offspring and the pups would be more likely to survive to autumn. Consistent with life history theory, individual growth rates of red squirrel pups are typically lower in larger litters (Humphries and Boutin 2000). However, previous research has shown pups from mothers in a high conspecific density environment or those with supplemental food show a reduction in the trade-off between litter size and pup growth rates (Dantzer et al. 2013) though the route by which the increase density results in a reduced trade-off is still unclear. Therefore, we also hypothesized that an increase in maternal care could be one way mothers contribute to the reduction in this trade-off.

Methods

Study population

North American red squirrels are arboreal, solitary, and sexually monomorphic (Boutin and Larsen 1993). Both sexes defend individual year-round territories and have many nests on their territory (Dantzer et al. 2012; Siracusa et al. 2017). Our study was conducted within Champagne and Aishihik First Nations traditional territory (with their explicit agreement) in Yukon, Canada (61° N, 138° W). Squirrels in our study population rely mainly on the seeds of white spruce for food (Fletcher et al. 2010, 2013), which they cache in an underground larder hoard (“midden”) within their territory. Mothers provide all parental care in this species and typically produce one successful litter per year (renesting if necessary after a failed litter; Williams et al. 2014), with the exception of producing two litters during a white spruce (*Picea glauca*) mast year (Boutin et al. 2006), a synchronously large production of cones that occurs every 4–6 years (Nienstaedt and Zasada 1990; LaMontagne and Boutin 2007). Due to this boost in reproduction during mast years, the population density of red squirrels increases following mast seed events (Dantzer et al. 2013; McAdam et al. 2019). Because we have previously documented that spruce cone availability impacts growth and survival of offspring (Humphries and Boutin 1996; Boutin et al. 2000; McAdam and Boutin 2003a; Fletcher et al. 2010, 2013), we estimated the number of cones available in the study area by using visual cone counts to determine cone index (LaMontagne et al. 2005).

Maternal behavior observations

In 2008, 2009, 2016, and 2017, we live-trapped (Tomahawk Live Trap, Tomahawk, WI, USA) breeding female squirrels (*n* = 288 unique breeding squirrels across 4 non-mast years) at regular intervals to determine reproductive status (see McAdam et al. 2007 for more details). Squirrels in this study were from either a control study area (*n* = 209 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) (Dantzer et al. 2013). Squirrels in the high-density study area typically have higher levels of glucocorticoids (Dantzer et al. 2013) and spend less time in the nest based on focal observations of male and female squirrels (Dantzer et al. 2012), though we note that we do not currently know whether lactating females in high-density areas spend less time with their pups. We included these squirrels from the high-density study area to increase our sample size by 27%. However, in our present study, the study area did not predict growth rate (Table 1). Nonetheless, to control for any variation due to this difference in conspecific density and food availability, we included the study area as a covariate in all models predicting pup survival or growth rate.

We estimated maternal latency to return to the nest (attentiveness) following two nest entries where we accessed the pups soon after birth (first nest entry) and when the pups were about 25 days of age (second nest entry). We chose these time periods to access the pups as this is when we measure offspring postnatal growth rate, which is a linear period of growth while the pups have never exited the nest on their own and are exclusively fed by their mother. To conduct two nest entries as pups were developing, we used VHF radio collars (Holohil PD-2C, 4-g, Holohil Systems Limited, Carp, ON, Canada) fitted on mothers to locate mothers when they were in the nest with their pups using either an R-1000 radio telemetry receiver (Communications Specialist, Inc., Orange, CA, USA) or a TR-4 radio telemetry receiver (Telonics, Inc., Mesa, AZ, USA). We performed the first nest entry as soon as lactation was detected through trapping (mean pup age ± SD 2.75 ± 3.33 days old). We estimated parturition date based on mass of pups as well as palpation and lactation history of the mother (McAdam et al. 2007). We entered the nest for the second time when pups were ~ 25 days old (mean pup age ± SD 25.8 ± 2.47 days old). Mothers wore the collar for variable lengths of time depending on the trappability of the individual but were typically removed as soon as possible after the nest entry was completed.

At each nest entry, we removed pups from the nest to weigh (to nearest 0.1 g), mark, and sex individuals. During the second nest entry, we additionally assigned unique colored disk combinations and unique alphanumeric stamped ear tags (National Band and Tag Company, Newport, KY, USA) to each pup for identification after emergence. In a sample of nests from 2016, the average time pups spent out of the nest during the first nest entry was 11:07 min:s (range 06:33–28:53) (*n* = 41 litters) and the average time pups spent out of the nest during the second nest entry was 43:05 (range 14:47–01:33:01) (*n* = 36 litters). The second nest entry was longer due to the time spent ear-tagging individuals, which is not performed at the first nest entry. In general linear models, we found no relationship between the time pups

Table 1 Results from our linear mixed-effects models on the relationship between growth rate and maternal attentiveness. 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). We standardized litter size by study area-year each combination and standardized all other continuous variables (latency to return to pups and cone indices) across all data. Italicized values indicate statistical significance of $p < 0.05$

Response variable	Fixed effect	β	SE	df	t	p
a) Latency observations at first nest entry (pups ~ 1 day old)						
Growth rate (g/day)						
n = 524 pups	Intercept	1.15	0.94	180.78	1.23	0.22
n = 193 litters	Latency to return to pups	− 0.036	0.024	259.71	− 1.49	0.14
n = 167 mothers	Litter size	*− 0.14*	*0.025*	*192.53*	*− 5.87*	*0.0001*
	Parity of mother					
	Primiparous	− 0.09	0.10	181.42	− 0.86	0.39
	Year					
	2009	0.075	0.61	179.87	0.12	0.90
	2016	0.46	0.94	180.72	0.49	0.63
	2017	0.22	0.77	180.78	0.29	0.77
	Birth date	*− 0.10*	*0.033*	*180.18*	*− 3.07*	*0.0025*
	Cone index of previous year	0.34	0.72	180.62	0.72	0.47
	Study area					
	Food addition + high density	0.081	0.071	180.97	1.14	0.26
	Sex of pup					
	Male	*0.040*	*0.018*	*370.67*	*2.22*	*0.027*
	Latency to return × litter size	*− 0.051*	*0.023*	*196.22*	*− 2.22*	*0.028*
	Random effect	**Variance**	**SD**			
	Litter ID	0.10	0.32			
	Residual	0.027	0.16			
Response variable	**Fixed effect**	**β**	**SE**	**df**	**t**	**p**
b) Latency observations at second nest entry (pups ~ 25 days old)						
Growth rate (g/day)						
n = 480 pups	Intercept	0.82	1.00	164.21	0.83	0.41
n = 178 litters	Latency to return to pups	*− 0.06*	*0.028*	*160.96*	*− 2.19*	*0.030*
n = 152 mothers	Litter size	*− 0.11*	*0.024*	*175.09*	*− 4.60*	*0.0001*
	Parity of mother					
	Primiparous	− 0.061	0.11	164.15	− 0.57	0.57
	Year					
	2009	0.32	0.65	163.47	0.49	0.62
	2016	0.81	1.00	164.14	0.81	0.42
	2017	0.45	0.82	164.23	0.56	0.58
	Birth date	*− 0.087*	*0.037*	*164.44*	*− 2.37*	*0.019*
	Cone index of previous year	0.45	0.51	164.08	0.89	0.37
	Study area					
	Food addition + high density	0.10	0.078	165.31	1.35	0.18
	Sex of pup					
	Male	*0.054*	*0.020*	*338.66*	*2.71*	*0.0071*
	Latency to return × litter size	− 0.021	0.023	170.77	− 0.91	0.37
	Random effect	**Variance**	**SD**			
	Litter ID	0.11	0.34			
	Residual	0.029	0.17			

spent out of the nest for processing and the latency of mothers to return to pups (β = 11.98, SE = 178.37, t_{76} = − 0.06, p = 0.94) or the number of pups in a litter (β = − 113.4, SE = 214, t_{76} = − 0.53, p = 0.60). This suggests that the time pups spent outside of the nest for processing or the number of pups in a litter did not influence the latency for a mother to return to her nest. Data on time pups spent out of the nest were not collected in other years, but the above data should be representative of all years as data collection protocols were uniform across all years.

After processing the litter, we returned all pups to the original nest. While the pups are being processed, there is high variation in maternal behavior. Some mothers explore the empty nest and stay nearby or approach the researchers. Some vocalize during the entire process and never approach. Mothers may even enter the nest before the researcher has left the nest tree. Alternatively, some mothers will move further away from the researchers or immediately leave and only return once the researchers have left (Westrick, personal observation). Not every litter was observed for both first and second nest entries because some of the litters did not survive from the first to second nest entry ($n = 47$ litters), some first nest entries were missed, and maternal behavior observation was skipped at some nest entries due to logistics.

After each nest entry, we performed focal behavioral observations on mothers. An observer (n = 31 different observers) moved > 5 m away from the nest tree and watched the mother's behavior for 7 min following returning the pups to the nest to record the time pups were replaced in the nest, the time mother returned to the nest, and the time mother began moving the pups. Because we were tracking many litters and often performed multiple nest entries on the same day, we were constrained logistically in the length of time we could watch the nest after placing the pups back in the nest. We chose 7 min to be consistent with previous behavioral focal observation protocols completed with this study population (Dantzer et al. 2012; Siracusa et al. 2019). Observers were blind to the previous return latencies of the focal squirrel and were blind to the specific growth rates of pups. Because the observers processed the litter prior to behavioral observations, it was impossible to keep them blind to the litter size. Five observations were at underground nests, with the remaining in trees. We determined latency to return to pups as the time between pup replacement in their original nest and the mother's return to the nest and censored any observations where the mother did not return within 7 min (n = 218 censored observations). Mothers typically moved their pups to a different nest immediately following their return to the nest after our intrusion as indicated by a strong relationship between the uncensored latency to return and latency to begin moving pups (linear model: adjusted $R^2 = 0.81$, $\beta = 0.87$, SE = 0.032, $t = 27.43$, $p < 0.0001$). Among trials where the mother returned, 83% of mothers moved their pups within 7 min. By measuring latency to return, our goal was to capture individual variation in how motivated a mother was to retrieve her pups to move them to a safer nest following a nest intrusion.

While many studies in the lab measure the time to retrieve all pups, the spatial scale at which wild female red squirrels move their offspring makes this problematic. Females move their pups individually to a new nest that is meters to tens of meters away. As a result, variation in the length of time between initiation and completion of moving pups is likely to be caused mostly by the distance between nests and the number of pups to be moved rather than by maternal motivation. Recording the latency to return to her pups following a standardized nest disturbance allows us to quickly capture the responsivity of a mother to her pups' needs in a wild animal.

Offspring measurements: growth rate and survival

Growth between the two nest entries is approximately linear (McAdam and Boutin 2003b) so we calculated growth rate (g/day) of pups ($n = 763$ 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 ($n = 541$ juveniles from 206 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 15). As part of our long-term data collection, we censused the entire study population yearly to confirm territory ownership by August 15 and again by May 15 (McAdam et al. 2007). Survival to August 15 captures a key life history event. In this population, caching of spruce cones typically begins mid-August and ends in September (Fletcher et al. 2010). 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 (Streubel 1968)). Because offspring disperse from their natal territory around 70–80 days old to compete for their own territory (Nice et al. 1956; McAdam et al. 2007), we limited survival data to litters born ≥ 70 days prior to August 15. 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 behavioral observations.

From our biannual population censuses and behavioral observations, we tracked lifetime reproductive success (LRS) of mothers. We defined LRS as the number of pups born over the entire lifetime of a dam that recruited into the breeding population (i.e., alive for more than 199 days or roughly to the spring following their year of birth). To accurately calculate LRS, we only included mothers with known birth years before 2011 (n = 40 females) to ensure we captured the number of pups produced over their entire lifespan. We excluded mothers that died of unnatural causes. It is possible that there may be biases in offspring survival estimates, but our past work suggests that this is unlikely. First, our study areas are surrounded by unsuitable habitat for red squirrels and natal dispersal is usually about 100 m away from the site of birth (Berteaux and Boutin 2000; Cooper et al. 2017). Second, if our estimates of juvenile survival (and therefore maternal LRS) were biased due to offspring dispersal, we would expect that females on the edge of the study area have lower LRS than those on the center of the study area. However, we have not found this (Kerr et al. 2007; McAdam et al. 2007; Martinig et al. 2020) suggesting that our measures of maternal LRS are not affected by juvenile dispersal.

Statistical analyses

We conducted all statistical analyses in R version 3.4.3 (R Core Team 2016). With censored data, the mean event time is an underestimation of the true mean (Datta 2005; Zhong and Hess 2009). With 30% or more censoring, the Kaplan-Meier estimator of the median is less biased than the mean (Datta 2005; Zhong and Hess 2009). Therefore, instead of comparing means to test for a difference between the first and second nest entries, we compared Kaplan-Meier survival curves using the R package “survival” version 2.43-3. To estimate within-individual repeatability of maternal attentiveness, we used the R package “rptR” version 0.9.21 (Stoffel et al. 2017). In our linear mixed-effects model for repeatability, we included squirrel identity (ID; $n = 104$ mothers observed twice, $n = 24$ mothers observed three times, $n = 20$ mothers observed four times, and $n = 1$ mother observed five times [three litters across 2 years]) as a random intercept term, no fixed effects, and used parametric bootstrapping ($n = 1000$) to estimate the confidence interval.

In our models to assess how maternal nest attentiveness affected offspring growth, we included the following predictors: return latency, number of pups in litter, parity of mother (first time mother or not), parturition date of the litter, cone index of the previous autumn, sex of pup, birth year (as a factor), and study area (control or high density). We used the R package “lme4” version 1.1-19 (Bates et al. 2015) to fit linear mixed-effects models and estimated p values using the R package “lmerTest” version 3.0-1 (Kuznetsova et al. 2016). To detect any collinearity in the predictors included in our model, we used R package “car” version 3.0-2 (Fox and Weisberg 2011) to assess the variance inflation factors. $\mathrm{GVIF}^{(1/(2\mathrm{xDF}))}$ for all predictors was < 3, except cone index of the previous autumn ($\mathrm{GVIF}^{(1/(2\mathrm{xDF}))} = 11$) which is colinear with birth year. We decided to still include spruce cone abundance (cone index: LaMontagne et al. 2005) in these models as it is a major influence on offspring survival and growth rate in this study system (McAdam and Boutin 2003a, 2003b; Boutin et al. 2006; Dantzer et al. 2013), and we wanted to control for its influence on these traits. We included birth year as a fixed effect to control for any additional year effects, e.g., variation in predator abundance or weather effects. In this population, female squirrels typically breed their first year and each subsequent year; thus, maternal age and parity are closely correlated across our long-term database ($R = 0.89$, CI = [0.89–0.90], $t = 170.68$, df = 7571, $p < 0.001$). We included parity as a binary variable to account of the initial experience of a nest disturbance by researchers. Cone index of the previous year is also predictive of conspecific density which also influences growth rate (Dantzer et al. 2013). To assess if maternal nest attentiveness behavior could mitigate effects of increasing litter size on offspring growth rates, we included the interaction between return latency and litter size. We standardized pup growth rates, litter size, and birthdate within each study area-year combination and standardized all other continuous variables across all data (latency to return and cone index). In our data set, we had 13 one-pup litters, 46 two-pup litters, 128 three-pup litters, 28 four-pup litters, and 1 five-pup litter. 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: return latency, pup growth rate, sex of pup, parity of mother (first time mother or not), birth date, cone index of birth year, cone index of previous year, and study area (control or high density). We standardized pup growth rate across study area-year combinations and standardized all other continuous variables (latency to return to pups and cone indices) across all data. Again, we assessed variance inflation factors and found $\mathrm{GVIF}^{(1/(2\mathrm{xDF}))}$ for all predictors was < 2.

Due to the count nature of LRS and the high variance of LRS relative to the mean, we used a negative binomial generalized linear model to estimate the relationship between maternal attentiveness and LRS. For each squirrel, we averaged latency to return to pups across all observations of that individual. In addition to latency to return to the pups, the model included fixed effects for lifespan (in days) since lifespan is highly correlated with LRS (McAdam et al. 2007) and study area type (control or high density). While mothers who experience a spruce cone mast in their lifetime have higher LRS on average (J.A. Haines et al. unpublished), in our dataset, experiencing a mast year is highly correlated with lifespan (Pearson’s correlation R 0.87, $t = 11.78$, df = 43, $p < 0.00001$); therefore, we left this out of the model. We also fit the same model reducing the dataset to only observed return latencies, excluding any censored data, as a comparison. To fit these models, we used the R package “MASS” version 7.3-51.1 (Venables and Ripley 2002). We standardized all continuous fixed effects to allow for comparison of effect size. $\mathrm{GVIF}^{(1/(2\mathrm{xDF}))}$ for all predictors was < 2.

We ran all models for growth rate and survival 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. Specifically, 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 (McAdam et al. 2007; Williams et al. 2014), 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. Additionally, newborn pups are hairless and more dependent on their mother for temperature regulation than ~ 25-day-old pups with fur. Consequently, we might expect behavior observations at the two nest entries to vary due to this difference in maternal investment and pup developmental stage; thus, the measurements at the two nest entries may not be equivalent. Additionally, due to natural litter failures and missed observations, not every litter was observed at both the first and second nest entries.

Results

Variation and repeatability in maternal nest attentiveness

Mothers varied in the time it took them to return to the nest following our temporary removal of their pups (median 394 s, CI = [335, 420]). Observations were censored at 7 min (49% of observations) and the latency to return ranged from 0 s to the maximum observation of 420 s. During 16% of observations, mothers returned within 2 min. Using Kaplan-Meier survival curves, the median latency to return was slightly faster during the second nest entry compared with the first nest entry, but the survival curves do not significantly differ (nest entry 1 median = 420 s; nest entry 2 median = 350 s; difference between curves: $\chi^2 = 0.7$, $p = 0.4$; Fig. S1).

In our models for within-individual repeatability of latency to return to pups, we found mothers were consistent across observations of maternal nest attentiveness behavior whether we included censored observations ($R = 0.25$, SE = 0.061, CI = [0.13, 0.36], $p < 0.0001$), or excluded them ($R = 0.32$, SE = 0.10, CI = [0.11, 0.51], $p = 0.0045$).

Maternal nest attentiveness 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 attentive mother. As predicted by life history theory, in both our models of growth rate, pups from larger litters grew more slowly than pups in small litters (nest 1 $\beta = -0.14$, SE = 0.025, $t_{192.53} = -5.87$, $p < 0.00001$; nest 2 $\beta = -0.11$, SE = 0.024, $t_{175.09} = -4.60$, $p < 0.00001$; Table 1). However, pups in large litters with mothers that returned soon after the pups were returned (i.e., more attentive mothers) grew faster than those in large litters with mothers that took longer to return to the nest, particularly early in pup development (latency × litter size interaction—nest entry 1 $\beta = -0.051$, SE = 0.023, $t_{196.22} = -2.22$, $p = 0.028$; nest entry 2 $\beta = -0.021$, SE = 0.023, $t_{170.77} = -0.91$, $p = 0.37$; Fig. 1; Table 1).

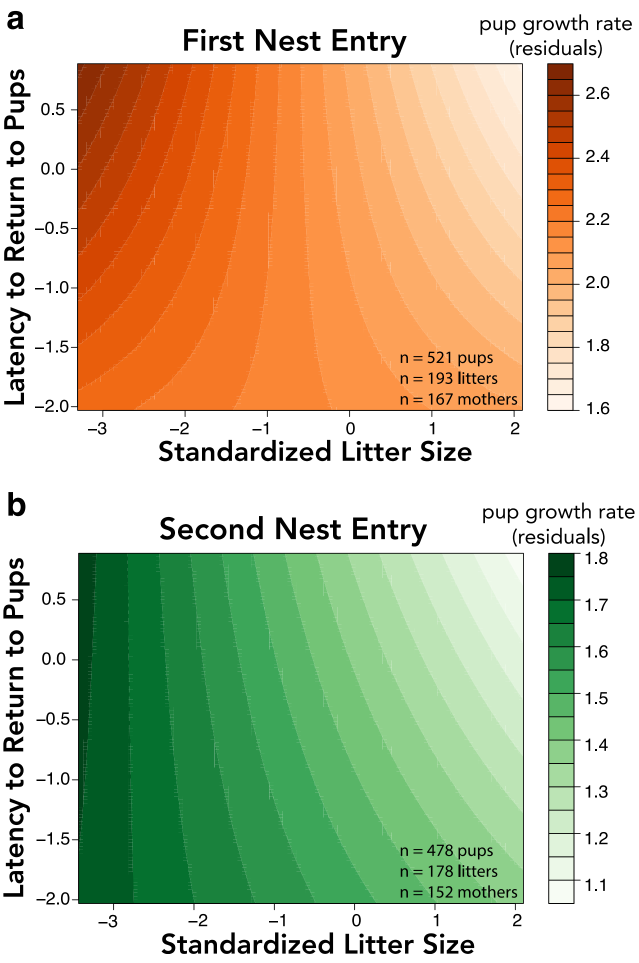

Fig. 1 Both heatmap panels depict the effect of the interaction between litter size and maternal attentiveness on pup growth rate. Panel **a** shows data from first nest entry (pups ~ 1 day old) observations and panel **b** shows data from second nest entry (pups ~ 25 days old) observations. More saturated, darker colors indicate a faster growth rate. Partial residuals of growth rate are plotted. Both litter size and latency to return to pups are standardized

In both models for the first and second nest entry, male pups grew faster than female pups (nest entry 1 $\beta = 0.040$, SE = 0.018, $t_{370.67} = 2.22$, $p = 0.027$; nest entry 2 $\beta = 0.054$, SE = 0.020, $t_{338.66} = 2.71$, $p = 0.0071$; Table 1) and pups born later in the year also grew faster than pups born earlier (nest entry 1 $\beta = -0.10$, SE = 0.033, $t_{180.18} = -3.07$, $p = 0.0025$; nest entry 2 $\beta = -0.087$, SE = 0.037, $t_{164.44} = -2.37$, $p = 0.019$, Table 1).

Maternal nest attentiveness and survival

Faster growing pups in both models were more likely to survive their first summer to autumn (nest entry 1 $\beta = 0.24$, SE = 0.11, $z = 2.12$, $p = 0.034$; nest entry 2 $\beta = 0.29$, SE = 0.12, $z = 2.44$, $p = 0.015$; Table 2). There was no further effect of maternal attentiveness once the direct effect of growth was accounted for (nest entry 1 $\beta = -0.11$, SE = 0.11, $z = -$

Table 2 Results from our binomial linear models on the relationship between survival to autumn and maternal attentiveness. 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). We standardized growth rate (g/day) and birth date within study area-year combination. We standardized all other continuous variables (latency to return to pups and cone indices) across all data. Italicized values indicate statistical significance of $p < 0.05$

Response variable	Fixed effect	β	SE	z	p
a) Latency observations at first nest entry (pups ~ 1 day old)					
Alive in August (Y/N)					
n = 489 pups	Intercept	*− 0.74*	*0.17*	*− 4.42*	*< 0.0001*
n = 183 litters	Latency to return to pups	− 0.11	0.11	− 1.00	0.32
n = 160 mothers	Growth rate	*0.24*	*0.11*	*2.12*	*0.034*
	Parity of mother				
	Primiparous	0.040	0.48	0.080	0.94
	Sex of pup				
	Male	*− 0.71*	*0.22*	*− 3.30*	*0.00098*
	Birth date	*− 0.27*	*0.12*	*− 2.17*	*0.030*
	Cone index of current year	*0.25*	*0.11*	*2.21*	*0.027*
	Cone index of previous year	0.096	0.13	0.75	0.45
	Study area				
	Food addition + high density	− 0.090	0.23	− 0.39	0.70
Response variable	**Fixed effect**	β	**SE**	z	p
b) Latency observations at second nest entry (pups ~ 25 days old)					
Alive in August (Y/N)					
n = 446 pups	Intercept	*− 0.99*	*0.19*	*− 5.19*	*< 0.0001*
n = 168 litters	Latency to return to pups	− 0.12	0.11	− 1.05	0.29
n = 145 mothers	Growth rate	*0.29*	*0.12*	*2.44*	*0.015*
	Parity of mother				
	Primiparous	− 0.18	0.49	− 0.36	0.72
	Sex of pup				
	Male	*− 0.54*	*0.23*	*− 2.34*	*0.019*
	Birth date	*− 0.19*	*0.13*	*− 1.47*	*0.14*
	Cone index of current year	*0.36*	*0.14*	*2.64*	*0.0084*
	Cone index of previous year	0.22	0.13	1.67	0.095
	Study area				
	Food addition + high density	0.0085	0.25	− 2.34	0.97

1.00, $p = 0.32$; nest entry 2 $\beta = -0.12$, SE = 0.11, $z = -1.05$, $p = 0.29$; Table 2). Overall, females were more likely than males to survive until autumn (nest entry 1 $\beta = 0.71$, SE = 0.22, $z = -3.30$, $p < 0.0001$; nest entry 2 $\beta = -0.54$, SE = 0.23, $z = -2.34$, $p = 0.019$; Table 2). Pups born earlier in the year (nest entry 1 $\beta = -0.27$, SE = 0.12; $z = -2.17$, $p = 0.00098$; nest 2 $\beta = -0.19$, SE = 0.13, $z = -1.47$, $p = 0.14$; Table 2) and pups born during years where there was high autumn spruce cone production were more likely to survive (nest entry 1 $\beta = 0.25$, SE = 0.11, $z = 2.21$, $p = 0.027$; nest 2 $\beta = 0.36$, SE = 0.14, $z = 2.64$, $p = 0.0084$; Table 2).

Maternal nest attentiveness and lifetime reproductive success

Mothers with a more attentive maternal style had more pups that recruited into the population during their lifetime ($\beta = -0.31$, SE = 0.15, $z = -2.09$, $p = 0.037$; Fig. 2; Table 3). Given

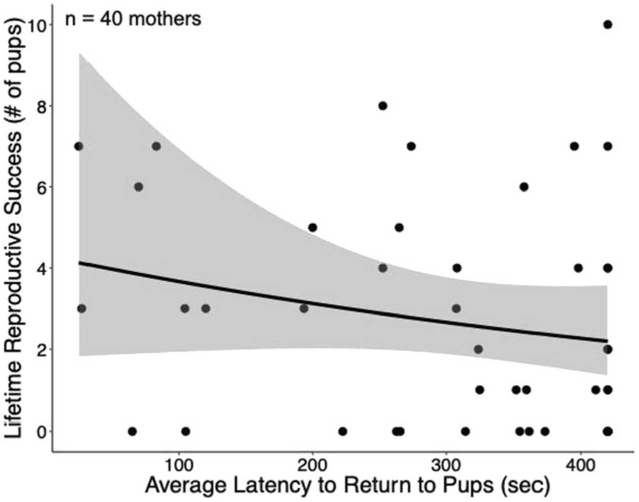

Fig. 2 The scatterplot depicts the relationship between average latency for a mother to return to the nest after pups are returned following a nest entry and lifetime reproductive success. Points represent individual mothers. The solid line with gray shaded area represents the linear regression line with 95% confidence intervals

Table 3 Results from our negative binomial linear models on the relationship between lifetime reproductive success of females and maternal motivation. We defined lifetime reproductive success as the number of pups born surviving over winter to recruit into the breeding population. For each squirrel, we averaged latency to return to pups across all observations of that individual, including censored observations as 420 s. We standardized both continuous fixed effects. We included squirrels with known birth years prior to 2011 (range 2004 to 2010). Italicized values indicate statistical significance of $p < 0.05$

Response variable	Fixed effect	β	SE	z	p
Lifetime reproductive success (# of pups)					
$n = 40$ mothers	Intercept	*1.04*	*0.14*	*7.51*	*< 0.0001*
	Average latency to return to pups	*− 0.31*	*0.15*	*− 2.09*	*0.037*
	Lifespan (days)	*0.69*	*0.14*	*4.91*	*< 0.0001*
	Study area				
	Food addition + high density	− 0.22	0.41	− 0.54	0.59

the mean LRS for females who survive to potentially breed is 1.54 pups (McAdam et al. 2007), this effect size is substantial. On average, mothers who returned immediately after pups were replaced in the nest had ~ 1 more pup that recruited than mothers who returned at the end of the 7-min observation period. Female squirrels who lived longer had higher LRS ($\beta = 0.69$, SE = 0.14, $z = 4.91$, $p < 0.0001$; Table 3). Female squirrels from the high-density food addition study area did not have more pups that recruited than control mothers ($\beta = -0.22$, SE = 0.41, $z = -0.54$, $p = 0.59$; Table 3).

Discussion

Maternal styles

We found that maternal nest attentiveness following a nest intrusion is a repeatable behavior among female red squirrels, which suggests individuals exhibit maternal styles with some mothers being more attentive to the pups and other mothers adopting a more laissez-faire approach. The repeatability of this maternal behavior is near the average repeatability of other behavior studies ($R = 0.37$; Bell et al. 2009), but lower than the repeatability of other behavioral traits in red squirrels (docility $R = 0.41$, aggression $R = 0.44$, activity $R = 0.51$; Taylor et al. 2012). Individual repeatability in parental behavior has been documented in other species as well. For example, the average amount of time a Goeldi's monkey (*Callimico goeldii*) spent carrying infants from their first litter was positively correlated with the amount of time infant carrying for subsequent litters (Schradin and Anzenberger 2001). Research in wild deer mice (*Peromyscus maniculatus*) also demonstrates low, but significant, repeatability of multiple maternal behaviors with a high degree of seasonal plasticity (Stewart and McAdam 2014). Although we and these other studies document significant repeatability in maternal behaviors measured in different ways, it is likely that maternal attentiveness in red squirrels is impacted by environmental factors. For example, maternal attentiveness in red squirrels may be plastic in response to variation in spruce cone availability, but our dataset does not include observations during a white spruce mast year. Future studies should not only attempt to identify whether parental behaviors exhibit repeatability but also document the environmental drivers of plasticity in these behaviors.

Our study interprets the latency to return to the nest following a nest disturbance as a measure of maternal attentiveness. However, maternal attentiveness could simply reflect "boldness" or be one trait in a behavioral syndrome that includes boldness. For example, in great tits, fast exploring parents return faster to the nest box following a nest disturbance by researchers (David et al. 2015). We may predict that more bold squirrels are more likely to return to the nest quickly despite recent human intrusion. The latency to return to the pups following an intrusion may be a similar measurement to the latency to resume normal behavior after a startling event which is often used to describe "boldness" of an individual (e.g., van Oers et al. 2004; Martins et al. 2007; Wilson and Krause 2012). In the lab, rodent mothers show increased boldness or decreased "fear" after giving birth (Hard and Hansen 1985; Wartella et al. 2003). Thus, it is possible that mothers with higher levels of maternal attentiveness are also bolder and that bold and attentive mothers have higher lifetime reproductive success, but we unfortunately do not have adequate data to address this.

Maternal behavior and pup growth rate

Red squirrel mothers that were highly attentive at the first nest entry had faster growing pups and their litters exhibited a reduction in the trade-off between litter size and pup growth rates. This amelioration of the negative impact that siblings can have on the growth of each offspring in the litter could be one way that maternal behavior alters offspring lifetime fitness trajectories (Klug and Bonsall 2014). This indicates that there could be large fitness benefits for highly attentive mothers as offspring that grow up in large litters may grow nearly as fast as offspring in smaller litters if they have a highly attentive mother. However, there was substantial variation in the attentiveness of mothers and the ecological cause of this variation in maternal behavior is yet to be determined.

Maternal behavior and pup survival

In our study population of red squirrels, faster early life growth rate is associated with an increased probability of pup survival into adulthood, especially when population density is high (McAdam and Boutin 2003a; Dantzer et al. 2013; Hendrix et al. 2020). Because growth rate is predicted by maternal behavior, including these two measurements as predictors in the same model may mask the indirect impact of maternal care on survival. These results suggest growth rate may be the mechanism by which maternal behavior increases survival of pups. Additionally, we found that, over their lifetime, mothers that exhibited a more attentive maternal style had more offspring that recruited into the breeding population. Latency to return to pups and subsequently move them to a new nest following a nest disturbance may affect offspring growth and survival through a variety of pathways.

It is also likely that maternal attentiveness, as we measured it here, does not have any direct effects on growth and survival but is simply representative of a suite of maternal behaviors representing maternal style. For example, lactating female red squirrels are known to move their pups between nests on their territory as the ambient temperature fluctuates to maintain an optimum temperature for offspring growth (Guillemette et al. 2009). Since latency to return to pups is highly correlated with latency to move pups (see Methods), highly attentive mothers may be better able to move offspring from one nest to another that puts offspring in the optimal thermal environment that maximizes growth. Since our current data set is limited to one observed behavior, future work should dissect our findings further to address the specific mechanism by which maternal attentiveness increases growth rate and reproductive success.

Maintaining individual variation in maternal behavior

The fact that highly attentive mothers had higher lifetime reproductive success begs the question of why substantial individual variation in this highly beneficial behavior is maintained in the population. There are likely costs experienced by highly attentive mothers which may contribute to the persistence of alternative maternal styles in the population. For example, if the nest was intruded upon by predators, highly attentive mothers that quickly return to the nest could face the cost of potentially being preyed upon themselves. Additionally, there are likely substantial energetic costs associated with moving pups to a new nest; on average, one ~ 25-day-old pup weighs ~ 18% of the body mass of an adult female. We have not yet documented the costs of maternal attentiveness but there are three possible explanations for why there is substantial individual variation in maternal attentiveness despite the clear fitness benefits we documented in this study. First, high maternal nest attentiveness could be exhibited by high-quality mothers who can afford higher investment in current reproduction, and variation we see in maternal behavior is due to limitations on the mother and current environmental conditions, rather than fitness consequences (van Noordwijk and de Jong 1986). However, individual "quality" is not easily defined (Wilson and Nussey 2010; Bergeron et al. 2011) and can even be considered dynamic across contexts, rather than a static trait (Lailvaux and Kasumovic 2011). If we consider high-quality squirrels as those with the most food resources, maternal attentiveness may be one mechanism by which higher quality female squirrels covert their larger energy stores into increased fitness. Though this explanation seems unlikely to explain the entirety of our results given, we do not see a significant benefit, in terms of pup growth rate or LRS, of increased food availability for squirrels living on the food addition study area, although this result for LRS is expected given that food-supplementation increases conspecific density which should lower the number of offspring that can recruit into the population.

Secondly, it is possible that the survival costs to females of increased attentiveness are underrepresented in our data due to the "invisible fraction," or individuals that do not survive to reproduce and express this behavior (Grafen 1988; Hadfield 2008). We were not able to measure maternal attentiveness on all squirrels, and many squirrels die prior to even reproducing so we are unable to collect data on them. We are more likely to have sampled older individuals for maternal attentiveness which means the survival costs to females with increased attentiveness are likely to be underrepresented in our data. Essentially, a cost associated with increased attentiveness or a related trait of boldness could have already been paid prior to us being able to measure attentiveness.

Lastly, there may also be years when the fitness benefits associated with maternal attentiveness are reduced. Red squirrels in Yukon experience large fluctuations in their major food resource (white spruce seeds) and population density and therefore substantial inter-annual variation in directional selection on offspring growth rate (Humphries and Boutin 2000; McAdam and Boutin 2003a; Dantzer et al. 2013). In some years, there is strong positive selection favoring fast growth whereas it is reduced or non-significant in other years (Dantzer et al. 2013). Consequently, 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 (McAdam and Boutin 2003a; Dantzer et al. 2013). This should result in balancing selection on maternal style where less attentive mothers with slow growing pups have an advantage in years when fast growth is not under positive selection, thereby maintaining individual variation in maternal style. While we are limited in testing these predictions with our current dataset, we have already observed balancing selection for other repeatable behavioral traits in female red squirrels such as the aggression and activity of mothers (Taylor et al. 2014). It is possible that the fitness benefits associated with maternal care depending upon ecological conditions are likely to maintain variation in this important behavior that is closely linked to fitness. The relatively small effect size of maternal behavior predicting lifetime reproductive success suggests environmental shifts may change this relationship, thus maintaining variation in this behavior through fluctuation in fitness benefits.

Conclusions

Here we provide empirical evidence that maternal styles with increased attentiveness correspond to increased offspring growth rate and higher lifetime reproductive success. We propose future studies investigate the causes of individual variation maternal styles in more detail, including the effects of age or breeding experience, heritability, and plasticity of maternal style. Our current study highlights how individual variation in maternal behavior can be linked to variation in developmental trajectories in a wild animal.

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Data availability The datasets generated for the current study are available in a figshare repository after April 13, 2022: https://doi.org/10.6084/m9.figshare.12118704. The datasets analyzed during the current study are available earlier than this date from the corresponding author on reasonable request.

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Ethics approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. All work was conducted under animal ethics approvals from Michigan State University (AUF#04/08-046-00), University of Guelph (AUP#09R006), and University of Michigan (PRO00005866).

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