1 **Attentive red squirrel mothers have faster-growing pups and higher lifetime reproductive**

2 **success**

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23 **Running head:** Fitness benefits of an attentive mother

24   **Lay Summary**

25   It pays to be attentive to your pups as a squirrel mom. In a long-term study of a wild population

26   of North American red squirrels, we observed repeatable individual variation in maternal

27   attentiveness towards offspring. Mothers who returned faster to pups following a nest intrusion

28   produced faster growing pups and were able to produce larger fast-growing litters. Over their

29   entire lifetime, attentive mothers also had more offspring recruit into the breeding population.

30

31 **Abstract**

32 Parental investment theory predicts that observed levels of parental care afforded to offspring are

33 set by the benefits (to offspring quality and survival) relative to the costs (to parental survival or

34 future reproduction). Although difficult to document in mammals, there is often substantial

35 individual-variation in the amount of parental care within species. We measured the impact of

36 individual variation in maternal care ("attentiveness" towards offspring or maternal motivation)

37 on offspring growth and survival in a wild population of North American red squirrels

38 (*Tamiasciurus hudsonicus*). We used latency to return to pups following a nest intrusion as a

39 measure of maternal attentiveness to pups. We found this behavior to be repeatable within

40 individuals suggesting this behavior is a personality trait or a "maternal style". In this population,

41 postnatal growth rate is important for pup overwinter survival. Pups from large litters grew faster

42 if they had a highly attentive mother, indicating that maternal care behavior can mitigate the

43 trade-off between litter size and offspring growth and potentially improve survival of pups.

44 Additionally, more attentive mothers had slightly higher lifetime reproductive success than less

45 attentive mothers. These results highlight important fitness effects of having a highly attentive

46 mother and show that maternal care behavior can alter a fundamental life history trade-off

47 between offspring quantity and quality.

48   **Introduction**

49   Theory predicts that elevated parental investment will produce more, and/or higher quality,

50   offspring, but this may come at a cost of decreased future fecundity and/or survival of parents

51   (Trivers 1974; Drent and Daan 1980; Stearns 1989; Clutton-Brock 1991). In this context,

52   parental care has been defined to include parental traits, including behavior, that increase fitness

53   of offspring, and is one aspect of parental investment (Clutton-Brock 1991; Royle et al. 2012).

54   The energetic costs of reproduction, which may limit future parental investment (Drent and Daan

55   1980), may be especially high in mammals as offspring are highly dependent on their mother for

56   survival until weaning (Roff 1998; Reinhold 2002; Maestripieri and Mateo 2009). Under the

57   assumption of fixed energy budgets, these energetic costs to parents of parental care likely

58   contribute to the fundamental life history trade-off between offspring number and size (Smith

59   and Fretwell 1974; Charnov and Ernest 2006). This trade-off is reflected in the frequent

60   observation that parents can rarely raise many large offspring (Rogowitz 1996), except when

61   they have a large amount of resources to do so (van Noordwijk and de Jong 1986; Reznick et al.

62   2000). The trade-off for parents between offspring quality and quantity could impact the lifetime

63   trajectory of offspring via differences in developmental rates of individuals (Clutton-Brock 1991;

64   Royle et al. 2012; Klug and Bonsall 2014). For example, offspring growing up in large litters

65   may exhibit slower development and be smaller at the age of independence than those from

66   smaller litters which could in turn influence lifetime reproductive success (Lindström 1999).

67   In mammals, we might expect to see directional positive selection for high maternal care

68   if the benefits afforded to offspring exceed the costs to the mother, yet there is often much

69   individual variation in this behavior (Bales et al. 2002; Champagne et al. 2007; Fairbanks and

70   Ackles 2012). For example, in primates, individual variation in maternal care, or "maternal

71   style", can include protective, rejecting, restrictive, or laissez-faire mothers (Fairbanks and

72   Ackles 2012). Maternal styles can have important consequences for a female's fitness and may

73   be a mechanism for transmitting individual differences across generations (Fairbanks and Ackles

74   2012). Many studies in mammals have investigated the proximate mechanisms behind individual

75   variation in maternal care (Numan and Insel 2006), yet the ultimate mechanisms (i.e. fitness

76   consequences) are rarely addressed, especially in wild rodents, due to the logistical challenges of

77   accurately documenting parental behaviors. Much research in primates has been done to describe

78   individual variation in maternal care (Fairbanks and Ackles 2012), however it is challenging to

79   follow the fitness consequences beyond interbirth interval in such long-lived species.

80   In this study, we used latency to return to pups, a measurement commonly used with

81   laboratory rodents (e.g. Numan and Insel 2006; Champagne et al. 2007), as a measurement of

82   maternal attentiveness following a nest intrusion in wild North American red squirrels

83   (*Tamiasciurus hudsonicus*). In laboratory studies of rodents, latency to retrieve pups after they

84   are moved to a different location in the cage is interpreted as how motivated an individual is to

85   attend to pups, whether they are their own offspring or another's (Mann 1993; Olazábal et al.

86   2013). For example, virgin female laboratory rats can develop maternal motivation to retrieve

87   pups by prolonged exposure to pups (Seip and Morrell 2008). Many neuroendocrine studies

88   measure retrieval behavior when manipulating brain regions to identify neural structures

89   involved in maternal behavior (Numan and Woodside 2010). In wild animals, we cannot

90   distinguish between whether this is how motivated a mother is to defend pups or how motivated

91   she is to exhibit infant-directed behaviors, both important components of motivated maternal

92   care (Olazábal et al. 2013).

93   We conducted this study as part of a long-term project on red squirrels in Yukon, Canada.

94   Red squirrel pups are altricial and dependent upon their mother until weaning whereupon they

95   typically disperse to nearby territories (mean = 92 m – 102 m from natal territory (Berteaux and

96   Boutin 2000; Cooper et al. 2017)). Weaned pups experience strong selective pressures with a

97   majority of juvenile mortality (68%, on average though this is highly variable among years)

98   occurring over the summer before mid-August and few surviving through their first winter (61%

99   of those alive in August, on average), depending on food availability and adult density (McAdam

100   et al. 2007; Hendrix et al. 2019). Pups that grow faster early in life are typically more likely to

101   survive their first winter (McAdam and Boutin 2003a; Fisher et al. 2017; Hendrix et al. 2019),

102   particularly in years with high conspecific density (Dantzer et al. 2013). Despite the link between

103   increased survival and fast growth in red squirrels, there is substantial variation in pup growth

104   rates among and within litters. Some of this variation in pup growth rate is explained by large

105   maternal effects including variation in litter size and the birth dates of litters (McAdam et al.

106   2002) or levels of maternal glucocorticoids during pregnancy (Dantzer et al. 2013), although

107   much variation among females in the growth rates of their pups remains unexplained (McAdam

108   et al. 2002). Here, we tested the hypothesis that maternal behavior affects offspring growth rate

109   and survival. We also tested the within-individual repeatability of this behavior to identify if red

110   squirrels exhibit a "maternal style" and tested whether more attentive mothers had more pups

111   recruit into the breeding population over their lifetime. We predicted that mothers who exhibited

112   higher maternal attentiveness (i.e., faster return to the nest) would produce faster growing

113   offspring and the pups would be more likely to survive to autumn. Consistent with life history

114   theory, individual growth rates of pups are typically lower in larger litters (Humphries and

115   Boutin 2000), however previous research has shown mothers in a high conspecific density

116   environment or those with supplemental food can reduce this trade-off between litter size and

117   pup growth rates (Dantzer et al. 2013). Therefore, we also hypothesized that the attentiveness of

118   mothers towards their offspring could be one mechanism by which mothers ameliorate this life

119   history trade-off.

120

121   **Methods**

122   *Study population*

123   North American red squirrels are arboreal, solitary, and sexually monomorphic (Boutin and

124   Larsen 1993). Both sexes defend individual year-round territories and have many nests on their

125   territory (Dantzer et al. 2012; Siracusa et al. 2017). Mothers provide all parental care in this

126   species and typically produce one successful litter per year, with the exception of white spruce

127   (*Picea glauca*) mast years when they may produce 2 litters (Boutin et al. 2006). Renesting

128   following a failed litter also occurs (Williams et al. 2014). Our study was conducted within

129   Champagne and Aishihik First Nations traditional territory (with their explicit agreement) in

130   Yukon, Canada (61°N, 138°W). Squirrels in our study population rely mainly on the seeds of

131   white spruce for food (Fletcher et al. 2010; Fletcher et al. 2013), which they cache in an

132   underground larder hoard ("midden") within their territory. White spruce exhibit mast seed

133   production, meaning that trees synchronously produce large numbers of spruce cones in some

134   years followed by years with almost no cones produced (LaMontagne and Boutin 2007). Mast

135   events by white spruce typically occur every 4-6 years (Nienstaedt and Zasada 1990). As their

136   main seed predator in the region, the population density of red squirrels increases following mast

137   seed events (Dantzer et al. 2013; McAdam et al. 2019). Because we have previously documented

138   that spruce cone availability impacts growth and survival of offspring (Humphries and Boutin

139   1996; Boutin et al. 2000; McAdam and Boutin 2003a; Fletcher et al. 2010; Fletcher et al. 2013),

140   we estimated the number of cones available in the study area by using visual cone counts to

141   determine cone index (for details, see LaMontagne et al. 2005).

142   *Maternal behavior observations*

143   In 2008, 2009, 2016 and 2017, we live-trapped (Tomahawk Live Trap, Tomahawk, WI, USA)

144   breeding females (n = 272 unique squirrels across 4 years) at regular intervals to determine

145   reproductive status (see McAdam et al., 2007 for more details). Squirrels in this study were from

146   either a control study area (n = 141 squirrels) or a study area that was provided with

147   supplemental *ad libitum* peanut butter from 2004 to 2017, resulting in a higher density of

148   squirrels (n = 79 squirrels) (described in Dantzer et al. 2013). Squirrels in the high-density study

149   area typically have higher levels of glucocorticoids (Dantzer et al. 2013) and spend less time in

150   the nest (Dantzer et al. 2012). We included these squirrels from the high-density study area

151   because it increased our sample size by 56%. However, in our present study, study area did not

152   predict growth rate (Table 1). Nonetheless, to control for any variation due to this difference in

153   conspecific density and food availability, we included study area as a covariate in all models

154   predicting pup survival or growth rate.

155   As soon as lactation was detected through trapping, we used VHF radio telemetry to locate

156   the nests where VHF collars were put on the mother. We will refer to this as the "first nest entry"

157   (n = 292 litters from 167 females; mean pup age ± SD: 2.75 ± 3.33 days old). We estimated

158   parturition date based on mass of pups, as well as palpation and lactation history of the mother

159   (McAdam et al. 2007). When pups were ~25 days old, we repeated this process for what we will

160   refer to as the "second nest entry" (n = 227 litters from 152 females; mean pup age ± SD: 25.8 ±

161   2.47 days old). Forty-eight females were observed across two years.

162   At each nest entry, we removed pups from the nest to weigh (to nearest 0.1 g), mark, and sex

163   individuals. During the second nest entry, we additionally assigned unique colored disk

164   combinations and unique alphanumeric stamped ear tags (National Band and Tag Company,

165   Newport, KY, USA) to each pup for identification after emergence. In a sample of nests from

166   2016, the average time pups spent out of the nest during the first nest entry was 11:56 min:sec

167   [range: 06:19-34:50] (n = 65 litters) and the average time pups spent out of the nest during the

168   second nest entry was 38:32 [range: 14:47-01:31:17] (n = 64 litters). In general linear models, we

169   found no relationship between the time pups spent out of the nest for processing and the latency

170   to return to pups (ß = -35.37, SE = 110.44, t_{185} = -0.32, p = 0.75) or the number of pups in a litter

171   (ß = -75.27, SE = 144.23, t_{185} = -0.52, p = 0.60). This suggests that the time pups spent outside of

172   the nest for processing or the number of pups in a litter did not influence the latency for a female

173   to return to her nest. Data on time pups spent out of the nest were not collected in other years, but

174   the above data should be representative of all years as data collection protocols were uniform

175   across all years.

176   After processing the litter, we replaced all pups in the original nest. While the pups are being

177   processed, there is high variation in maternal behavior. Some mothers explore the empty nest and

178   stay nearby or approach the researchers. Some vocalize during the entire process and never

179   approach. Mothers may even enter the nest before the researcher has left the nest tree.

180   Alternatively, some mothers will move further away from the researchers or immediately leave

181   and only return once the researchers have left (Westrick, personal observation). Not every litter

182   was observed for both first and second nest entries because some of the litters did not survive

183   from the first to second nest entry and some first nest entries were missed.

184   After each nest entry, we performed focal behavioral observations on mothers. An observer

185   (n = 31 different observers) moved >5 m away from the nest tree and watched the mother's

186   behavior for 7 minutes following replacement of pups in the nest to record the time pups were

187   replaced in the nest, the time mother returned to the nest, and the time mother began moving the

188   pups. Observers were blind to the previous return latencies of the focal squirrel and were blind to

189   the specific growth rates of pups. Because the observers processed the litter prior to behavioral

190   observations, it was impossible to keep them blind to the litter size. Five observations were at

191   underground nests, with the remaining in trees. We determined latency to return to pups as the

192   time between pup replacement in their original nest and the mother's return to the nest and

193   censored any observations where the mother did not return within 7 minutes (n = 319 censored

194   observations). Mothers typically moved their pups to a different nest immediately following their

195   return to the nest after our intrusion as indicated by a strong relationship between the uncensored

196   latency to return and latency to begin moving pups (linear model: adjusted R^2 = 0.81, ß = 0.87,

197   SE = 0.032, t = 27.43, $p < 0.0001$). Among trials where the mother returned, 83% of mothers

198   moved their pups within 7 minutes. By measuring latency to return, our goal was to capture

199   individual variation in how motivated a mother was to retrieve her pups to move them to a safer

200   nest following a nest intrusion.

201   While many studies in the lab measure the time to retrieve all pups, the spatial scale at which

202   wild female red squirrels move their offspring makes this problematic. Females move their pups

203   individually to a new nest that is meters to tens of meters away. As a result, variation in the

204   length of time between initiation and completion of moving pups is likely to be caused mostly by

205   the distance between nests and the number of pups to be moved rather than by maternal

206   motivation. Recording the latency to return to her pups following a standardized nest disturbance

207   allows us to quickly capture the responsivity of a mother to her pups needs in a wild animal.

208   *Offspring measurements: growth rate and survival*

209   Growth between the two nest entries is approximately linear (McAdam and Boutin 2003b),

210   so we calculated growth rate (g/day) of pups (n = 671 pups) as the change in mass from first to

211   second nest entry divided by number of days between nest entries. We monitored survival of

212   juveniles (n = 870 juveniles from 251 litters) for the remainder of the year and following spring.

213   We recorded survival to autumn of the birth year as a binary measure (alive or dead on August

214   15th). As part of our long-term data collection, we censused the entire study population yearly to

215   confirm territory ownership by August 15th and again by May 15th (McAdam et al. 2007).

216   Survival to August 15th captures a key life-history event. In this population, caching of spruce

217   cones typically begins mid-August and ends in September (Fletcher et al. 2010). Territory

218   ownership before this period allows individuals to take advantage of that year's cone crop by

219   providing them with a physical space to cache cones (cones must be cached in a midden for the

220   seed to remain a viable food source (Streubel 1968)). Because offspring disperse from their natal

221   territory around 70-80 days old to compete for their own territory (Nice et al. 1956; McAdam et

222   al. 2007), we limited survival data to litters born ≥ 70 days prior to August 15th. Because

223   squirrels are diurnal and their activity (territorial defense behavior and presence) is conspicuous,

224   we were able to completely enumerate all squirrels inhabiting the study areas through a

225   combination of repeated live trapping and behavioral observations. We are confident our survival

226   observations are not influenced by dispersal outside our study area because, in this population,

227   the apparent survival of juveniles born on the edge of the study areas is not significantly different

228   from those born in the core (Kerr et al. 2007).

229   From our biannual population censuses and behavioral observations, we tracked lifetime

230   reproductive success (LRS) of mothers. We defined LRS as the number of pups borne over the

231   entire lifetime of a dam that survived to recruit into the breeding population (i.e., alive for more

232   than 199 days or roughly to the spring following their year of birth). To accurately calculate

233   LRS, we only included mothers with known birth years before 2011 (n = 45 females) to ensure

234   we captured the number of pups produced over their entire lifespan. We excluded mothers that

235   died of unnatural causes.

236   All work was conducted under animal ethics approvals from Michigan State University

237   (AUF#04/08-046-00), University of Guelph (AUP#09R006), and University of Michigan

238   (PRO00005866).

239

240   *Statistical analyses*

241   We conducted all statistical analyses in R version 3.4.3 (R Core Team, 2016). To estimate

242   within-individual repeatability of maternal attentiveness, we used the R package 'rptR' version

243   0.9.21 (Stoffel et al. 2017). In our linear mixed effects model for repeatability, we included

244   squirrel identity (ID) as a random intercept term, no fixed effects, and used parametric

245   bootstrapping (n = 1000) to estimate the confidence interval.

246   In our models to assess how maternal nest attentiveness affected offspring growth, we

247   included the following predictors: return latency, number of pups in litter, parity of mother (first

248   time mother or not), Julian parturition date of the litter, cone index of the previous autumn, sex

249   of pup, birth year (as a factor), and study area (control or high-density). We used the R package

250   'lme4' version 1.1-19 (Bates et al. 2015) to fit linear mixed-effects models and estimated P-

251   values using the R package 'lmerTest' version 3.0-1 (Kuznetsova et al. 2016). To detect any

252   collinearity in the predictors included in our model, we used R package 'car' version 3.0-2 (Fox

253   and Weisberg 2011) to assess the variance inflation factors. $\text{GVIF}^{(1/(2\times DF))}$ for all predictors was <

254   3, except cone index of the previous autumn ($\text{GVIF}^{(1/(2\times DF))} = 11$) which is colinear with birth

255   year. We decided to still include spruce cone abundance (cone index: LaMontagne et al. 2005) in

256   these models as it is a major influence on offspring survival and growth rate in this study system

257   (McAdam and Boutin 2003a; McAdam and Boutin 2003b; Boutin et al. 2006; Dantzer et al.

258   2013) and we wanted to control for its influence on these traits. We included birth year to control

259   for any additional year effects, e.g. variation in predator abundance or weather effects. Cone

260   index of the previous year is also predictive of conspecific density which also influences growth

261   rate (Dantzer et al. 2013). To assess if maternal nest attentiveness behavior could mitigate effects

262   of increasing litter size on offspring growth rates, we included the interaction between return

263   latency and litter size. We standardized pup growth rates, litter size, and birthdate within each

264   grid-year combination and standardized all other continuous variables across all data (latency to

265   return and cone index). Since multiple pups were measured per litter, we included litter ID as a

266   random effect.

267   To model the relationship between maternal care and offspring survival, a binary value for

268   offspring survival to autumn was predicted by the following fixed effects: return latency, pup

269   growth rate, sex of pup, parity of mother (first time mother or not), Julian birth date, cone index

270   of birth year, cone index of previous year, and study area (control or high-density). We

271   standardized pup growth rate across grid-year combinations and standardized all other

272   continuous variables (latency to return to pups and cone indexes) across all data. Again, we

273   assessed variance inflation factors and found $\text{GVIF}^{(1/(2\times DF))}$ for all predictors was < 2.

274   Due to the count nature of LRS and the high variance of LRS relative to the mean, we used a

275   negative binomial generalized linear model to estimate the relationship between maternal

276   attentiveness and LRS. For each squirrel, we averaged latency to return to pups across all

277   observations of that individual. In addition to latency to return to the pups, the model included

278   fixed effects for lifespan (in days) since lifespan is highly correlated with LRS (McAdam et al.

279   2007). While mothers who experience a spruce cone mast in their lifetime have higher LRS on

280   average (Haines et al. unpublished), in our dataset experiencing a mast year is highly correlated

281   with lifespan (Pearson's correlation R: 0.87, t = 11.78, df = 43, $p < 0.00001$), therefore we left

282   this out of the model. We also fit the same model reducing the dataset to only observed return

283   latencies, excluding any censored data, as a comparison. To fit these models, we used the R

284   package 'MASS' version 7.3-51.1 (Venables and Ripley 2002). We standardized all continuous

285   fixed effects to allow for comparison of effect size. $\text{GVIF}^{(1/(2 \times DF))}$ for all predictors was < 2.

286   We ran all models for growth rate and survival with observations from the two nest entries

287   separately due to the potential for different levels of maternal investment at different times in the

288   breeding season. Specifically, squirrels born earlier in the year generally are more likely to

289   survive until the following year so mothers that lose their litter earlier in the season (e.g. right

290   after birth) have the potential to successfully breed again (McAdam et al. 2007; Williams et al.

291   2014), whereas mothers that lose their litter later in the season (e.g. a month after birth of the

292   first litter) may not have the same potential for a successful second litter in a non-mast year.

293   Additionally, newborn pups are hairless and more dependent on their mother for temperature

294   regulation than ~25-day old pups with fur. Consequently, we might expect behavior observations

295   at the two nest entries to vary due to this difference in maternal investment and pup

296   developmental stage, thus the measurements at the two nest entries may not be equivalent.

297   Additionally, due to natural litter failures and missed observations, not every litter was observed

298   at both the first and second nest entries.

299

300   **Results**

301   *Variation and repeatability in maternal nest attentiveness*

302   Mothers varied in the time it took them to return to the nest following our temporary

303   removal of their pups (median: 385 s, CI = [333, 420]). Observations were censored at 7 minutes

304   (50% of observations) and the latency to return ranged from 0 s to the maximum observation of

305   420 s. During 16% of observations, mothers returned within 2 minutes. Using Kaplan-Meier

306   survival curves, the median latency to return was slightly faster during the second nest entry

307   compared to the first nest entry, but survival curves do not significantly differ (nest entry 1

308   median = 407 s; nest entry 2 median = 342 s; difference between curves: $\chi^2 = 0.1$, p = 0.7).

309   In our models for within-individual repeatability of latency to return to pups, we found

310   mothers were consistent across observations of maternal nest attentiveness behavior whether we

311   included censored observations (R = 0.22, SE = 0.053, CI = [0.11, 0.32], p = 0.000013), or

312   excluded them (R = 0.36, SE = 0.09, CI = [0.17, 0.52], p = 0.00072).

313   *Maternal nest attentiveness and pup growth rate*

314   We found that the apparent cost for an individual pup of being in a litter with many

315   siblings, in terms of a reduced growth rate, was lessened by having a highly attentive mother. As

316   predicted by life history theory, in both our models of growth rate, pups from larger litters grew

317   more slowly than pups in small litters (nest 1: ß = -0.14, SE = 0.025, $t_{192.53}$ = -5.87, $p < 0.00001$;

318   nest 2: ß = -0.11, SE = 0.024, $t_{175.09}$ = -4.60, $p < 0.00001$). However, pups in large litters with

319   mothers that returned soon after pup replacement (i.e., more attentive mothers) grew faster than

320   those in large litters with mothers that took longer to return to the nest, particularly early in pup

321   development (latency x litter size interaction - nest entry 1: ß = -0.051, SE = 0.023, $t_{196.22}$ = -

322   2.22, *p* = 0.028; nest entry 2: ß = -0.021, SE = 0.023, $t_{170.77}$ = -0.91, *p* = 0.37; **Figure 1**; **Table 1**).

323   In both models for the first and second nest entry, male pups grew faster than female

324   pups (nest entry 1: ß = 0.040, SE = 0.018, $t_{370.67}$ = 2.22, *p* = 0.027; nest entry 2: ß = 0.054, SE =

325   0.020, $t_{338.66}$ = 2.71, *p* = 0.0071; **Table 1**) and pups born later in the year also grew faster than

326   pups born earlier (nest entry 1: ß = -0.10, SE = 0.033 $t_{180.18}$ = -3.07, *p* = 0.0025; nest entry 2: ß =

327   -0.087, SE = 0.037, $t_{164.44}$ = -2.37, *p* = 0.019, **Table 1**).

328   *Maternal nest attentiveness and survival*

329   Faster growing pups in both models were more likely to survive to autumn (nest entry 1:

330   ß = 0.24, SE = 0.11, z = 2.12, *p* = 0.034; nest entry 2: ß = 0.29, SE = 0.12, z = 2.44, *p* = 0.015;

331   **Table 2**). There was no further effect of maternal attentiveness once the direct effect of growth

332   was accounted for (nest entry 1: ß = -0.11, SE = 0.11, z = -1.00, *p* = 0.32; nest entry 2: ß = -0.12,

333   SE = 0.11, z = -1.05, *p* = 0.29; **Table 2**). Overall, females were more likely than males to survive

334   until autumn (nest entry 1: ß = 0.71, SE = 0.22, z = -3.30, *p* < 0.0001; nest entry 2: ß = -0.54, SE

335   = 0.23, z = -2.34, *p* = 0.019; **Table 2**). Pups born earlier in the year (nest entry 1: ß = -0.27, SE =

336   0.12; z = -2.17, *p* = 0.00098; nest 2: ß = -0.19, SE = 0.13, z = -1.47, *p* = 0.14; **Table 2**) and pups

337   born during years where there was high autumn spruce cone production were more likely to

338   survive (nest entry 1: ß = 0.25, SE = 0.11, z = 2.21, *p* = 0.027; nest 2: ß = 0.36, SE = 0.14, z =

339   2.64, *p* = 0.0084; **Table 2**).

340   *Maternal nest attentiveness and lifetime reproductive success*

341   Mothers who on average returned to their pups faster had slightly more pups recruit into

342   the population during their lifetime (ß = -0.35, SE = 0.19, z = -1.89, *p* = 0.059; **Figure 2**; **Table**

343 **3a**). While this relationship is uncertain and therefore not statistically significant, the effect size

344 is quite large. On average, mothers who returned immediately after pups were replaced in the

345 nest had ~1 more pup recruit than mothers who returned at the end of the 7 min observation

346 period. If we only include observed maternal behavior data (n = 32 females, no censored data),

347 this relationship becomes stronger (ß = -0.40, SE = 0.17, z = -2.31, p = 0.021; **Table3b**).

348 Females who lived longer had higher LRS (ß = 0.56, SE = 0.16, z = 3.40, p = 0.00068; **Table**

349 **3a**).

350

351 **Discussion**

352 We found that maternal nest attentiveness (measured as latency to return to pups)

353 following a nest intrusion is a repeatable behavior among female red squirrels, which suggests

354 individuals exhibit maternal styles with some mothers being more attentive to the pups and other

355 mothers adopting a more laissez-faire approach. The repeatability of this maternal behavior is

356 near the average repeatability of other behavior studies (R = 0.37; Bell et al. 2009), but lower

357 than the repeatability of other behavioral traits in red squirrels (docility R = 0.41, aggression R =

358 0.44, activity R = 0.51; Taylor et al. 2012). Research in wild deer mice (*Peromyscus*

359 *maniculatus*) also demonstrates low, but significant, repeatability of multiple maternal behaviors

360 with a high degree of seasonal plasticity (Stewart and McAdam 2014). We are limited in

361 assessing the plasticity of return latency behavior in red squirrels as our dataset does not include

362 observations during a mast year, a potential driver of a plastic change in behavior.

363 Variation in maternal behavior in red squirrels has important consequences for offspring.

364 Female red squirrels exhibiting higher levels of maternal nest attentiveness lessened the

365 fundamental life history trade-off between offspring quantity and quality. Red squirrel mothers

366   that were highly attentive at the first nest entry were capable of producing faster growing pups,

367   compared to less attentive mothers, by mitigating the trade-off between litter size and pup

368   growth rates. This amelioration of the negative impact that siblings can have on the growth of

369   each offspring in the litter could be one way that maternal behavior alters offspring lifetime

370   fitness trajectories (Klug and Bonsall 2014). For example, offspring that grow up in large litters

371   may grow nearly as fast as offspring in smaller litters if they have a highly attentive mother.

372   Mothers could potentially decrease the amount of time pups spend in a vulnerable life stage by

373   increasing growth rate or, alternatively, promote slower development in poor environmental

374   conditions (Klug and Bonsall 2014). Studies in other species have found that parents can alter

375   their investment in the quantity or quality of offspring according to environmental conditions.

376   For example, in quacking frogs (*Crinia georgiana*), mothers face a trade-off between egg size

377   and number and can use variable egg provisioning to influence survival of offspring in good and

378   poor-quality environments (Dziminski and Roberts 2006). Similarly, in birds, habitat elevation is

379   an important factor influencing whether parents invest in quantity or quality of offspring

380   (Badyaev and Ghalambor 2001). Our study suggests red squirrels use maternal behavior as one

381   mechanism to adjust the trade-off between offspring size and number, but the ecological cause of

382   variation in maternal behavior is yet to be determined. Mothers may invest heavily in offspring

383   when density is high to increase growth or reduce investment when the benefits no longer exceed

384   the costs during years when growth is less predictive of success, such as mast years (Humphries

385   and Boutin 2000; McAdam and Boutin 2003a; Dantzer et al. 2013). Indeed, we see higher rates

386   of litter loss in mast years potentially suggesting less maternal investment and care (Haines et al.

387   2018).

388   In our study population of red squirrels, faster early life growth rate is associated with an

389   increased probability of pup survival into adulthood, especially when population density is high

390   (McAdam and Boutin 2003a; Dantzer et al. 2013; Hendrix et al. 2019). Because growth rate is

391   predicted by maternal behavior, including these two measurements as predictors in the same

392   model may mask the indirect impact of maternal care on survival. These results suggest growth

393   rate may be the mechanism by which maternal behavior increases survival of pups, but we have

394   no evidence to suggest that maternal attentiveness has any further effect on offspring survival

395   beyond that which is mediated through the increased growth rate of her pups. Additionally, we

396   found that, over their lifetime, mothers that exhibit a more attentive maternal style have more

397   offspring that recruit into the breeding population. Latency to return to pups and subsequently

398   move them to a new nest following a nest disturbance may affect offspring growth and survival

399   through a variety of pathways. Lactating female red squirrels are known to move their pups

400   between nests on their territory as the ambient temperature fluctuates to maintain an optimum

401   temperature for offspring growth (Guillemette et al. 2009). Since latency to return to pups is

402   highly correlated with latency to move pups (see Methods), highly attentive mothers may be

403   better able to move offspring from one nest to another that puts offspring in the optimal thermal

404   environment that maximizes growth. Highly attentive mothers may also increase offspring

405   growth or survival by reducing flea load on pups by reducing their risk of death due to

406   infanticide (Haines et al. 2018) or predation (Studd et al. 2014), or by moving them to nests with

407   lower infestations of ectoparasites (Gooderham and Schulte-Hostedde 2011; Duma 2013). It is

408   also likely that maternal attentiveness, as we measured it here, does not have any direct effects

409   on growth and survival but is simply representative of a suite of maternal behaviors representing

410   maternal style.

411   Despite finding that highly attentive mothers had higher lifetime reproductive success,

412   we found substantial individual variation in maternal nest attentiveness. This begs the question of

413   why is there variation in this highly beneficial behavior? Although, we did not explicitly

414   compare the costs and benefits assumed in parental investment theory, there are likely costs

415   experienced by highly attentive mothers. For example, if the nest was intruded upon by

416   predators, highly attentive mothers that quickly return to the nest could face the cost of

417   potentially being preyed upon themselves. Additionally, there are likely substantial energetic

418   costs associated with moving pups to a new nest; on average one ~25-day old pup weighs ~18%

419   of the body mass of an adult female. We have not yet documented the costs of maternal

420   attentiveness but there are three possible explanations for why there is substantial individual-

421   variation in maternal attentiveness despite the clear fitness benefits we documented in this study.

422   First, high maternal nest attentiveness could be exhibited by high quality mothers who can afford

423   higher investment in current reproduction, and variation we see in maternal behavior is due to

424   limitations on the mother and current environmental conditions, rather than fitness consequences

425   (van Noordwijk and de Jong 1986). For example, highly attentive mothers that produce fast

426   growing offspring with higher survival may be those with larger amounts of cached food.

427   Secondly, it is entirely possible that the survival costs to females of increased

428   attentiveness are underrepresented in our data due to the 'invisible fraction', or individuals that

429   do not survive to express this behavior (Grafen 1988; Hadfield 2008). We are not able to

430   measure maternal attentiveness on all squirrels and many squirrels die prior to even reproducing

431   so we are unable to collect data on them. We are more likely to have sampled older individuals

432   for maternal attentiveness which means the survival costs to females with increased attentiveness

433   are likely to be underrepresented in our data. Essentially, a cost associated with increased

434   attentiveness could have already been paid prior to us being able to measure attentiveness.

435   Lastly, there may also be years when the fitness benefits associated with maternal

436   attentiveness are reduced. Red squirrels in Yukon experience large fluctuations in their major

437   food resource and there is substantial inter-annual variation in directional selection on offspring

438   growth rate (McAdam and Boutin 2003a; Dantzer et al. 2013). In some years, there is strong

439   positive selection favoring fast growth whereas it is reduced or non-significant in other years.

440   Consequently, it may be an unreliable strategy for mothers to invest in faster growing offspring if

441   it can result in a high energetic cost with little fitness benefit (McAdam and Boutin 2003a;

442   Dantzer et al. 2013). This should result in balancing selection on maternal attentiveness where

443   less attentive mothers with slow growing pups have an advantage in years when fast growth is

444   not under positive selection, thereby maintaining individual-variation in maternal attentiveness.

445   While we are limited in testing these predictions with our current dataset, we have already

446   observed balancing selection for other repeatable behavioral traits in female red squirrels such as

447   the aggression and activity of mothers (Taylor et al. 2014). Given that individual variation in

448   maternal behavior has also been documented in other species (e.g. Rachlow and Bowyer 1994;

449   Fairbanks 1996; Dahle and Swenson 2003; Ringsby et al. 2009), it is possible that the variable

450   fitness benefits associated with maternal care depending upon ecological conditions is likely to

451   maintain variation in this important behavior that is closely linked to fitness.

452

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637

638   **Figure 1.**

639   Pups from larger litters typically grew slower than pups from smaller litters. This relationship

640   was mitigated by highly attentive mothers, at both the (A) first nest entry and (B) second nest

641   entry, though the relationship was not statistically significant for the second nest entry (Table 1).

642   Pups in large litters grow faster if their mother was highly attentive for latency to return to the

643   nest at the first nest entry. More saturated, darker colors indicate a faster growth rate. Partial

644   residuals of growth rate are plotted. Both litter size and latency to return to pups are
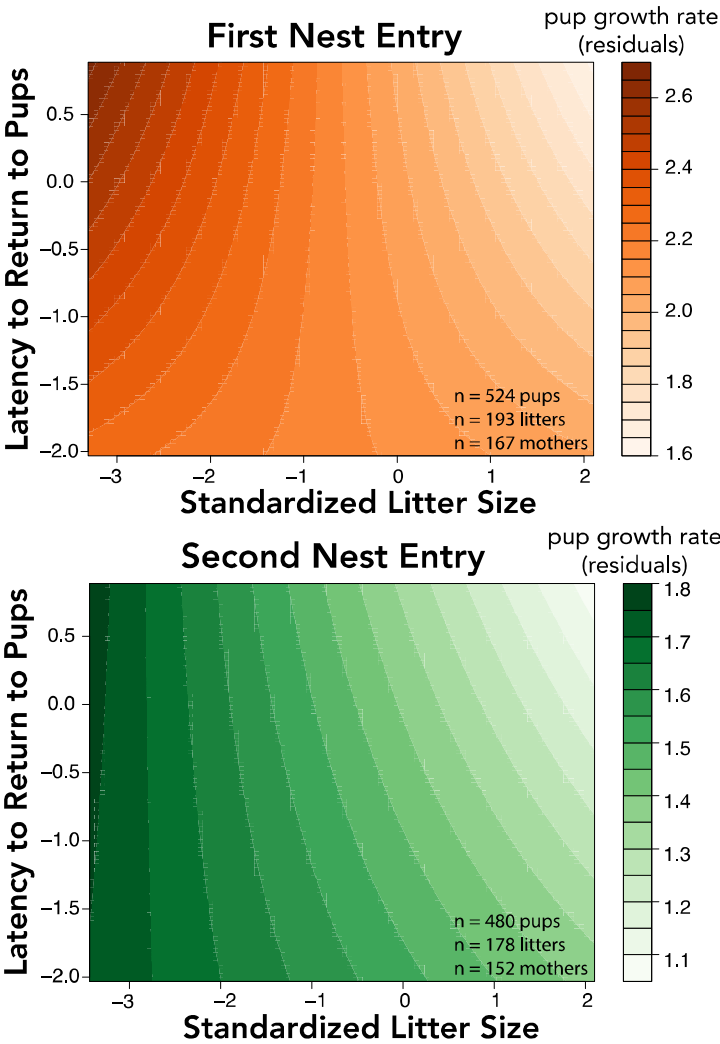
645   standardized.

646

647   **Figure 2.**

648   Highly attentive mothers have more pups survive to recruit into the breeding population than less

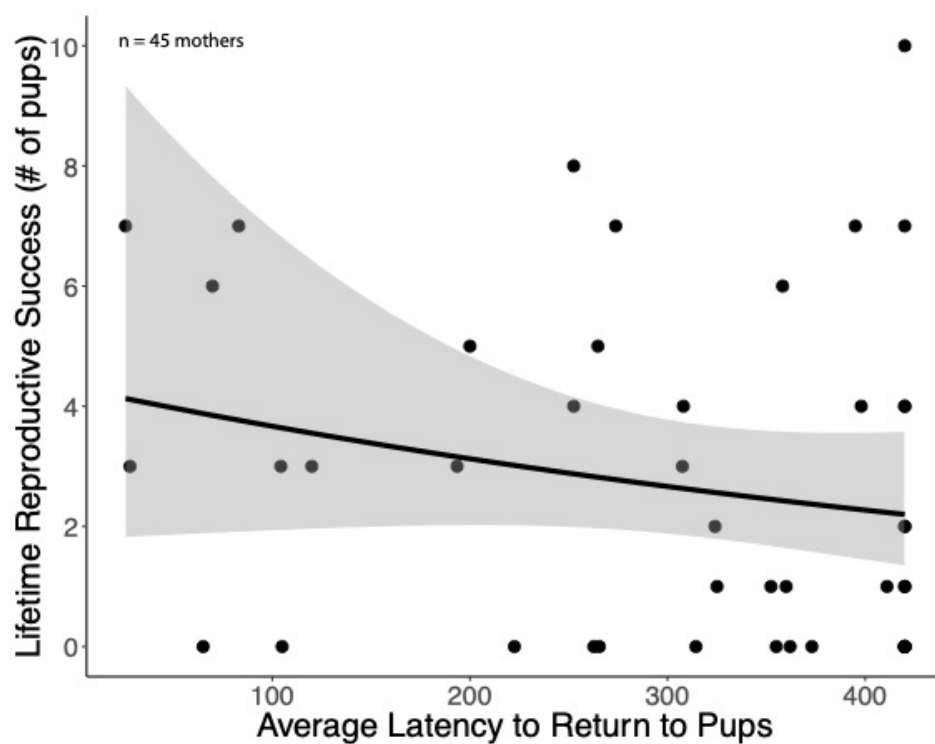649   attentive mothers.

650

651

652

653   **Table 1.**

654   Results from our linear mixed-effects models on the relationship between growth rate and

655   maternal attentiveness. We ran two distinct models for observations from the (a) first and (b)

656   second nest entries (at ~1 day post-parturition and ~25 days post-parturition, respectively). We

657   standardized litter size by grid type-year each combination and standardized all other continuous

658   variables (latency to return to pups and cone indexes) across all data. Bold font indicates

659   statistical significance of $p < 0.05$.

660   a) **Latency observations at first nest entry (pups ~1 day old):**

Response Variable	Fixed Effect	b	SE	df	t	*p*-value
Growth rate (g/day)						
n = 524 individuals	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**	**p < 0.0001**
	Parity of mother					
	primiparous	-0.14	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
	Julian 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
	Grid type					
	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 x 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			

661

662   b) **Latency observations at second nest entry (pups ~25 days old):**

Response Variable	Fixed Effect	b	SE	df	t	*p*-value
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**	**p < 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

Julian 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
Grid type					
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 x 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			

663

664

665   **Table 2.**

666   Results from our binomial linear models on the relationship between survival to autumn and

667   maternal attentiveness. We ran two distinct models for observations from the (a) first and (b)

668   second nest entries (at ~1 day post-parturition and ~25 days post-parturition, respectively). We

669   standardized growth rate (g/day) and Julian birth date within grid-year combination. We

670   standardized all other continuous variables (latency to return to pups and cone indexes) across all

671   data. Bold font indicates statistical significance of $p < 0.05$.

672   **a) Latency observations at first nest entry (pups ~1 day old):**

Response Variable	Fixed Effect	b	SE	z	*p*-value
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**
	Julian 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
	Grid type				
	Food-addition + high-density	-0.090	0.23	-0.39	0.70

673

674   **b) Latency observations at second nest entry (pups ~25 days old):**

Response Variable	Fixed Effect	b	SE	z	*p*-value
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**
	Julian 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
	Grid type				
	Food-addition + high-density	0.0085	0.25	-2.34	0.97

675

676 **Table 3.**

677 Results from our negative binomial linear models on the relationship between lifetime

678 reproductive success of females and maternal motivation. We defined lifetime reproductive

679 success as the number of pups born surviving over winter to recruit into the breeding population.

680 For each squirrel, we averaged latency to return to pups across all observations of that individual,

681 including censored observations as 420 s for (a) and removing any censored observations for (b).

682 We standardized both continuous fixed effects. We included squirrels with known birth years

683 prior to 2011 (range: 2004 to 2010). Bold font indicates statistical significance of $p < 0.05$.

684   a) **Latency to return to pups (censored at 7 min)**

Response Variable	Fixed Effect	b	SE	z	*p*-value
Lifetime reproductive success (# of pups)					
n = 45 mothers	**Intercept**	**0.87**	**0.17**	**5.23**	**< 0.0001**
	Average latency to return to pups	-0.35	0.19	-1.89	0.059
	Lifespan (days)	**0.56**	**0.16**	**3.40**	**0.00068**

685

686   b) **Latency to return to pups (within 7 minutes)**

Response Variable	Fixed Effect	b	SE	z	*p*-value
Lifetime reproductive success (# of pups)					
n = 32 mothers	**Intercept**	**0.97**	**0.17**	**5.57**	**< 0.0001**
	Average latency to return to pups	**-0.40**	**0.17**	**-2.31**	**0.021**
	Lifespan (days)	**0.44**	**0.16**	**2.68**	**0.0074**

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