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Territory acquisition mediates the influence of predators and climate on juvenile red squirrel survival

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32 **Abstract**

33 1) Juvenile survival to first breeding is a key life history stage for all taxa. Survival through
34 this period can be particularly challenging when it can coincide with harsh environmental
35 conditions such as a winter climate or food scarcity, leading to highly variable cohort
36 survival. However, the small size and dispersive nature of juveniles generally makes
37 studying their survival more difficult.

38 2) In territorial species, a key life history event is the acquisition of a territory. A territory is
39 expected to enhance survival, but how it does so is not often identified. We tested how
40 the timing of territory acquisition influenced the winter survival of juvenile North
41 American red squirrels *Tamiasciurus hudsonicus*, hereafter red squirrels, and how the
42 timing of this event mediated sources of mortality. We hypothesized that securing a
43 territory prior to when food resources become available would reduce juvenile
44 susceptibility to predation and climatic factors over winter.

45 3) Using 27 years of data on the survival of individually-marked juvenile red squirrels, we
46 tested how the timing of territory acquisition influenced survival, whether the population
47 density of red squirrel predators and mean temperature over winter were related to
48 individual survival probability, and if territory ownership mediated these effects.

49 4) Juvenile red squirrel survival was lower in years of high predator abundance and in
50 colder winters. Autumn territory owners were less susceptible to lynx *Lynx canadensis*,
51 and possibly mustelid *Mustela* and *Martes* spp., predation. Autumn territory owners had
52 lower survival in colder winters, but surprisingly non-owners had higher survival in cold
53 winters.

54 5) Our results show how the timing of a life history event like territory acquisition can
55 directly affect survival and also mediate the effects of biotic and abiotic factors later in
56 life. This engenders a better understanding of the fitness consequences of the timing of
57 key life history events.

58
59 **Key words:** juvenile survival, life history timing, lynx, mustelid, predation, red squirrel,
60 *Tamiasciurus*, territory

61

62 **Introduction**

63 The juvenile age class, when individuals are no longer completely dependent on the parent but
64 not yet sexually mature, is a crucial life history stage for all taxa (Ferguson & Fox, 1984;
65 Gaillard, Festa-Bianchet, & Yoccoz, 1998; Searcy & Sponaugle, 2001). A large component of
66 reproductive success is surviving to sexual maturity, hence juvenile survival can be a key
67 determinant of lifetime fitness, and so variation in survival can dictate population dynamics
68 (McAdam, Boutin, Sykes, & Humphries, 2007; Oli & Dobson, 2003). For example, rates of
69 juvenile survival in mammals can be highly variable year-to-year and may be the key
70 determinant of population dynamics (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000;
71 Millar & McAdam, 2001; Morrison & Hik, 2007). Understanding the causes of variation in
72 juvenile survival and the selection such variability facilitates therefore shapes how we expect
73 populations to change over time.

74 The time period between juvenile independence and first breeding poses novel challenges
75 to survival, as individuals at this stage must survive in the absence of the parental care on which
76 they were previously dependent (Galef, 1981). Climatic factors can have strong effects on
77 survival of juveniles (Fuller, Stebbins, & Dyke, 1969; Schorr, Lukacs, & Florant, 2009) through
78 a combination of limited food availability and increased thermoregulatory costs (Jackson,
79 Trayhurn, & Speakman, 2001; Rödel et al., 2004), particularly over winter. Due to their small
80 size and lack of experience, as well as their dispersive nature, juveniles can also be particularly
81 vulnerable to predation (Garrett & Franklin, 1988; Rödel et al., 2015). Various behavioural and
82 physiological responses such as adjusting metabolic rate (Wunder, Dobkin, & Gettinger, 1977),
83 activity (Merritt, 1986), or food caching (Morrison, Pelchat, Donahue, & Hik, 2009) can mitigate
84 this risk. Understanding how these mediating traits alter juvenile survival is necessary to
85 understand how selection has resulted in the phenotypes we observe in the wild.

86 The acquisition of a territory is a key life history event that can mediate sources of
87 mortality in some species, by providing access to space, refuges and food stores. Timing of life
88 history stages, such as birth or hatching (Rodríguez, van Noordwijk, Álvarez, & Barba, 2016), or
89 developmental rate (van der Jeugd & Larsson, 1998) can have strong effects on survival at later
90 life stages (O'Connor, Norris, Crossin, & Cooke, 2014). Territory acquisition is one such event:
91 predation risk is elevated while searching for territories (Larsen & Boutin, 1994), and territory

92 ownership also leads to increased food availability, particularly in food caching species. Earlier
93 acquisition of a territory should, therefore, improve the probability of survival by reducing these
94 risks earlier in life. It is well known that acquiring a territory provides benefits (reviewed in:
95 Carpenter, 1987; e.g. Whitham, 1986). However, despite the potential importance of
96 understanding how the timing of territory acquisition modifies juvenile survival and mediates
97 sources of mortality, this has not yet occurred, in part due to the difficulty in collecting such data.

98 North American red squirrels *Tamiasciurus hudsonicus* are an ideal organism to study
99 how the timing of territory acquisition influences survival and mediates sources of juvenile
100 mortality. Red squirrels in Yukon, Canada defend exclusive individual territories with a central
101 cache of white spruce *Picea glauca* cones, their primary food source (Smith, 1968). Holding a
102 territory with a cache of food is considered necessary for red squirrels in these populations to
103 survive over winter (Larsen & Boutin, 1994; Smith, 1968), as cached resources are essential for
104 annual survival and reproduction (Fletcher et al., 2013; LaMontagne et al., 2013). White spruce
105 cones ripen in early August, when caching begins and finishes once snow falls (Archibald et al.,
106 2013; Fletcher et al., 2010), typically at the end of September. We hereafter refer to this period
107 of time (mid-August to snowfall) as “autumn”. Those juveniles with territories before this cone
108 ripening occurs are able to take advantage of that year’s cone crop and increase their hoard size,
109 whereas those that settle on territories later in the season will acquire what is left from the
110 previous owner but have no opportunity to secure further resources before winter (Fisher et al.,
111 2019). Red squirrels may take advantage of periods of super abundant white spruce cones
112 (“mast” years) to create new territories (LaMontagne & Boutin, 2007; Kelly, 1994; Silvertown,
113 1980), in which case they only have access to what they can cache before snowfall. Vacant
114 territories are typically rare, hence many juveniles cannot acquire one early or even at all (Fisher
115 et al., 2017; Larsen & Boutin, 1994).

116 Juvenile annual winter survival is low, with an average of 26.4 % of all juveniles born
117 surviving their first winter (McAdam et al., 2007), but this is highly variable annually (3-43 %)
118 (McAdam & Boutin, 2003). Annual adult survival in this population is high (80 % for two year
119 old females; steadily decreasing with age; Descamps, Boutin, Berteaux, & Gaillard, 2008), thus
120 much of the variation in lifetime reproductive success is linked to juvenile over winter mortality
121 (McAdam et al., 2007). Acquiring a territory is therefore a key life history event. However, the

122 main causes of juvenile mortality, and how they are influenced by the timing of territory
123 acquisition, remain unknown.

124 Observational studies, while relatively limited, have identified lynx *Lynx canadensis*
125 (Stuart-Smith & Boutin, 1995), goshawks *Accipiter gentilis* (Larsen & Boutin, 1994), and
126 mustelids (Kerr & Descamps, 2008; O'Donoghue, Boutin, Hofer, & Boonstra, 2001) as predators
127 of juvenile red squirrels (Goheen & Swihart, 2005; Haines et al., 2018; Smith, 1968; Steele,
128 1998). Owning a territory, and thus having access to nests or tunnels, could act as spatial refugia
129 and reduce vulnerability to predators (Cowlshaw, 1997; Everett & Ruiz, 1993). Furthermore, red
130 squirrels with smaller caches have lower winter survival (LaMontagne et al., 2013; Larivée,
131 Boutin, Speakman, McAdam, & Humphries, 2010), suggesting that resource limitation is a
132 source of over winter mortality. Owning a territory, and so regular use of nests, would provide
133 thermal refugia during low temperatures (Greenwood & Harvey, 1982; Studd, Boutin, McAdam,
134 Krebs, & Humphries, 2015). It therefore seems that a territory could both directly influence
135 survival and change the suite of selection pressures that act on a juvenile red squirrel.

136 We aimed to better understand how the timing of territory acquisition affects juvenile
137 over winter survival and mediates sources of mortality. To do so we used 27 years of
138 longitudinal data to assess how holding a territory before autumn influences survival and the
139 susceptibility of a juvenile to predation or low temperatures over winter.

140 Our first hypothesis was that earlier territory acquisition would result in higher over
141 winter survival compared to later territory acquisition (Berteaux & Boutin, 2000). We further
142 hypothesized that cold temperatures and predators pose a mortality risk, so that over winter
143 survival of juveniles would be lower in colder winters and when predators are abundant. Our key
144 hypothesis is that timing of territory acquisition would moderate these effects, so that juveniles
145 obtaining territories before autumn would be less susceptible to predators (e.g. Cowlshaw 1997)
146 and adverse weather (e.g. Greenwood and Harvey 1982) over winter.

147

148 **Materials and Methods**

149 *Data collection*

150 Our study was part of the Kluane Red Squirrel Project, an ongoing long-term study of a wild
151 population of North American red squirrels within Champagne and Aishihik First Nations
152 traditional territory along the Alaska Highway in southwestern Yukon, Canada (61° N, 138° W).

153 We collected data from two study areas (~ 40 hectares each) separated by the Alaska Highway
154 from 1989 to 2015. We conducted population censuses biannually in May (spring) and August
155 (autumn) to identify all individuals and assign territory ownership. The latter census roughly
156 corresponds to the timing of caching; individuals can acquire territories after the August census,
157 but these individuals would not be able to store cones from that year's production (Larivée et al.
158 2010). We assigned territory ownership based on territorial vocalisations ("rattling"; Lair, 1990)
159 and behavioural observations. We also identified red squirrels that did not own territories in
160 autumn through trapping and behavioural observations. Adult red squirrels rarely relocate, other
161 than through bequeathals by mothers where all or a part of her territory is given to offspring
162 (Berteaux & Boutin, 2000; around 19 % of females do this each year; Lane et al., 2015; Larsen
163 & Boutin, 1994a). Average juvenile dispersal distance is short (mean = 92 to 102 m; Berteaux &
164 Boutin, 2000; Cooper et al., 2017) relative to the size of our study areas. Some juveniles do
165 disperse off our study areas, and would not be included as survivors in our analysis. If this
166 dispersal were skewing our estimates of survival, we would expect to see lower apparent survival
167 of juveniles born at the edge of the study area compared to those born in the core. This is not the
168 case: juveniles born on the edge have equivalent survival to those born in the core (26% vs 27%;
169 McAdam et al., 2007). However, we cannot completely discern between mortality and long-
170 distance dispersal as some long-distance dispersal has been documented (Martinig, A. R.,
171 unpublished data).

172 We used Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, U.S.A.)
173 baited with peanut butter on each individual's territory or that of its mother to trap them. When
174 handled for the first time, we gave each individual numbered ear tags (Monel #1; 5 digits) with a
175 unique combination of coloured wires or pipe cleaners to facilitate future identification without
176 handling. We recorded body mass, sex, and reproductive status at each capture. We radio-
177 collared reproductive females (model PD-2C, 4 g, Holohil Systems Limited, Carp, Ontario,
178 Canada) to find nests. Females typically give birth to three pups (range: one – seven; Humphries
179 & Boutin, 2000) in the spring (median birth date: 23 April). We removed juveniles from the nest
180 after birth, and a second time at ~25 days old, to record litter size, pup mass, and sex, and to tag
181 them. We calculated growth rate (g/day) as the linear increase in mass between the nest entries.
182 We calculated growth rates only for juveniles that weighed less than 50 g at the first nest entry
183 and less than 100 g at the second nest entry (to ensure approximate linearity of the growth curve;

184 McAdam & Boutin, 2003), and only for juveniles where the two weight measures were >5 days
185 apart. Juvenile red squirrels emerge from the nest around 42-50 days old (Martinig, A. R.,
186 unpublished data) and wean around 70 days (Larsen & Boutin, 1994). We considered juveniles
187 surviving to the spring following the year of their birth to have recruited into the population, as
188 we have done previously (McAdam & Boutin, 2003). This research was approved by the
189 University of Guelph Animal Care Committee (AUP 1807), the University of Alberta Animal
190 Care and Use Committee for Biosciences and the University of Michigan Institutional Animal
191 Care and Use Committee (PRO00007805).

192

193 *Predator and temperature data collection*

194 Our available temperature and predator data are annual, regional measures, so for this analysis
195 we considered all juveniles born in the same year to be experiencing the same conditions. We
196 obtained monthly temperature records from Environment Canada's online historical weather
197 database for the Haines Junction weather station (Climate ID 2100630, 60.77° N, 137.57° W),
198 approximately 35 km SE of our study area. We used mean temperature over winter, as we
199 expected that climate would primarily influence over winter survival by increasing
200 thermoregulatory costs as opposed to extreme weather events or precipitation. We averaged the
201 monthly temperatures from October of a juvenile's birth year to the following March to obtain an
202 annual average winter temperature.

203 We considered potential mammalian predators: mustelids (short-tailed weasel *Mustela*
204 *erminea*, least weasel *M. nivalis*, and marten *Martes americana*) and lynx. We obtained
205 abundance data for predators and their alternate prey from population monitoring in our region,
206 first as part of the Kluane Boreal Forest Ecosystem Project (Krebs, 2001), and after 1996 as part
207 of the Community Ecological Monitoring Program (data available at
208 <http://www.zoology.ubc.ca/~krebs/kluane.html>). Repeated snow track counts along set transects
209 during winter provided an index of species abundance as the mean number of snow tracks per
210 100 km of transect for each year. We do not estimate population sizes from these track counts,
211 but instead use them as indices for relative comparisons between years. As the monitoring
212 protocol was consistent throughout the study, we do not expect a directional bias in these
213 estimates. We used the sum of short-tailed weasel, least weasel, and marten tracks as an index of
214 the total mustelid abundance for each year. The population densities of snowshoe hares *Lepus*

215 *americanus* and red-backed voles *Myodes rutilus* were estimated with live trapping and mark-
216 recapture (Krebs, Boonstra, Kenney, & Gilbert, 2018), providing measures of alternate prey
217 availability for these predators. We chose these combinations as lynx are known snowshoe hare
218 specialists (O'Donoghue, Boutin, Krebs, Murray, & Hofer, 1998), while weasels (the majority of
219 the mustelids) are known vole specialists (Boonstra & Krebs, 2006), and both populations follow
220 the cycles of their preferred prey (Boutin et al. 1995). While birds of prey such as goshawks and
221 great horned owls *Bubo virginianus* are known predators of red squirrels (Larsen & Boutin,
222 1994), we were not able to include them in our analysis because density indices were not
223 available. Such birds of prey primarily prey on snowshoe hares, and so their populations
224 typically track those of snowshoe hares, as lynx populations do (Boutin et al. 1995). Therefore,
225 the effect of lynx abundance may somewhat represent the overall effect of snowshoe hare
226 predators on red squirrels.

227

228 *Statistical analyses of survival*

229 We used a binomial mixed effects model to test how predation and temperature interacted with
230 autumn territory ownership to affect juvenile survival over winter. From 1989 to 2015, our
231 analysis considered whether those juveniles that survived to the beginning of autumn (n = 1305
232 squirrels) were still alive the following spring.

233 For our main question – does territory ownership mediate how predators and climate
234 affect over winter survival – we included territory ownership in autumn as a binary predictor
235 with temperature and predator abundance as numeric predictors, and fit interactions between
236 autumn ownership and each of temperature, lynx, and mustelid abundances separately. We
237 included separate interactions between the abundance of lynx and snowshoe hares, and mustelids
238 and voles, so the effect of predators on red squirrels depended on the availability of preferred
239 prey. Temperature and species abundances were standardized as z-scores across years. This
240 improves model convergence and interpretability of regression coefficients (Schielzeth, 2010).
241 We included random effects of litter identity and year to account for variation in survival due to
242 sibling and maternal interactions, as well as otherwise unaccounted for annual variation.

243 We also included several factors previously shown to affect juvenile survival in our
244 system (Descamps, Boutin, Berteaux, & Gaillard, 2008): these included adult population density
245 (number of adults within a set 38 ha area that remained consistent over the entire study period),

246 white spruce cone availability (annual index of cones produced on a consistent subset of trees on
247 each study area; see: LaMontagne et al., 2005), a fixed effect of study area to account for any
248 differences between the two study areas, birth date, growth rate, and sex. Growth rate, birth date,
249 adult population density, and cone availability were standardized as z-scores for each study area
250 in each year.

251 We also fitted a separate model with interactions of juvenile birth date and growth rate
252 with predators and temperature, to determine whether these traits influence these sources of
253 mortality. We used a different model in order to avoid overfitting due to too many terms in our
254 initial model. We present these results in the supporting information (Table S1); we found no
255 evidence of predator abundance or temperature over winter acting as agents of selection on either
256 of these traits.

257 We have provided the correlations between predictor variables (Table S2) and variance
258 inflation factors (Table 2). We note here that correlations between predictor variables and the
259 resulting larger standard error for an estimate are not necessarily problematic (see Morrissey &
260 Ruxton, 2018). We interpret each of our estimates in light of the fact that they are estimated
261 given the other effects in the model. As each continuous variable was mean centred, estimates
262 are effectively given for the mean value of all other variables.

263 We conducted all statistical analyses using R version 3.3.3 (R Core Team 2017), with the
264 packages lme4 (version 1.1-19; Bates et al., 2015), and lmerTest (version 2.0-33; Kuznetsova,
265 Brockhoff, & Christensen 2016). Reported estimates are means \pm SE.

266

267 **Results**

268 *Over winter survival*

269 We found that an average of 60 % of juveniles alive in autumn ($n = 1305$) survived to spring, but
270 this was highly variable (21.4 – 94.1 %; Table 1). Juvenile over winter survival was higher with
271 increased cone availability ($\beta = 0.38 \pm 0.11$, $z = 3.45$, $P < 0.001$; Table 2) and years of lower
272 adult population density ($\beta = -0.69 \pm 0.15$, $z = -4.45$, $P < 0.001$). Juvenile females were more
273 likely to survive over winter than males ($\beta = 0.49 \pm 0.16$, $z = 3.1$, $P = 0.002$), as were juveniles
274 with higher growth rates ($\beta = 0.22 \pm 0.10$, $z = 2.13$, $P = 0.033$). Birth date had no effect on over
275 winter survival ($\beta = -0.01 \pm 0.09$, $z = -0.08$, $P = 0.936$), nor were there any differences between

276 study areas ($\beta = 0.19 \pm 0.18$, $z = 1.06$, $P = 0.289$). The random effect of litter identity explained a
277 significant amount of variation ($\sigma^2 = 0.665$; likelihood ratio test $X^2 = 7.867$, $df = 20$, $P = 0.005$),
278 but the random year effect did not contribute to the model ($\sigma^2 < 0.001$; likelihood ratio test $X^2 =$
279 0 , $df = 20$, $P = 1$) given the inclusion of litter identity.

280

281 *Territory ownership and over winter survival*

282 Sixty-one percent of juveniles alive in autumn owned a territory, and territory owners were more
283 likely (79 %) to survive over winter than those who did not own a territory (33 %; $\beta = 2.78 \pm$
284 0.23 , $z = 12.06$, $P < 0.001$). Increased lynx abundance was associated with a decrease in the over
285 winter survival of juveniles without territories ($\beta = -0.68 \pm 0.28$, $z = -2.41$, $P = 0.016$), but had no
286 effect on the over winter survival of juveniles that held territories by autumn (interaction
287 between lynx abundance and territory ownership, $\beta = 0.99 \pm 0.23$, $z = 4.22$, $P < 0.001$; Fig 1).
288 Mustelid abundance was somewhat more strongly (interaction between mustelid abundance and
289 territory ownership, $\beta = 0.31 \pm 0.18$, $z = 1.75$, $P = 0.080$) associated with lower winter survival
290 for juveniles without a territory ($\beta = -0.38 \pm 0.14$, $z = -2.70$, $P = 0.007$) than for juveniles that
291 held territories by autumn ($\beta = -0.07 \pm 0.14$, $z = -0.49$, $P = 0.624$; Fig 2). The effects of predators
292 on juvenile survival over winter were not associated with the abundance of alternate prey (lynx
293 by hare interaction, $P = 0.187$; mustelid by vole interaction, $P = 0.203$), but both the hare ($\beta =$
294 0.40 ± 0.20 , $z = 1.99$, $P = 0.046$) and vole ($\beta = -0.59 \pm 0.13$, $z = -4.57$, $P < 0.001$) abundances
295 influenced juvenile over winter survival.

296 Temperature had opposing effects on survival for juveniles with and without territories
297 by autumn (Fig 3). Juveniles without territories by autumn were less likely to survive warm
298 winters ($\beta = -0.35 \pm 0.18$, $z = -1.99$, $P = 0.047$), but this effect reversed for autumn territory
299 owners (interaction $\beta = 1.11 \pm 0.21$, $z = 5.31$, $P < 0.001$), which were more likely to survive
300 warm winters ($\beta = 0.76 \pm 0.13$, $z = 5.31$, $P < 0.001$).

301

302 **Discussion**

303

304 Juvenile red squirrels that acquired territories by autumn were far more likely to survive the
305 winter than those that had not yet acquired a territory. Average survival of juveniles that acquired
306 territories before the start of cone caching (79 %) was comparable to survival of early-life adults

307 in this population (80 %; McAdam et al., 2007). Juveniles without territories by autumn had
308 much lower survival (33 %). Although it is possible that juveniles without a territory had in fact
309 moved off our study area, we cannot test this with our available dataset. However, the effect of
310 long-distance dispersal is expected to be small as survival is equal between juveniles originating
311 from the centre of the study area and those at the edge (Kerr, Boutin, LaMontagne, McAdam, &
312 Humphries, 2007).

313 Territory ownership also affected how susceptible juveniles were to predators and
314 weather over winter. Juveniles without territories by autumn were more susceptible to predators
315 than those that had already settled. Territory ownership provides access to arboreal nests,
316 tunnels, and increased familiarity with the local habitat (Clarke et al., 1993). Juveniles without
317 territories by autumn may be travelling more through potentially high-risk environments as they
318 forage for food or search for territories over winter, thereby increasing their vulnerability to
319 predators (Garrett & Franklin, 1988; Metzgar, 1967). Higher rates of litter loss in red squirrels
320 during years of high mustelid abundance (Studd et al., 2015) suggest that mustelids may enter
321 red squirrel nests (and likely tunnels), whereas lynx cannot access these structures. This may
322 explain why the relationship between mustelid abundance and over winter survival was not as
323 strongly influenced by territory acquisition as was the relationship between lynx abundance and
324 survival.

325 Survival of juveniles without a territory was higher in colder winters, with the opposite
326 being true for juveniles holding a territory by autumn. We predicted that cold winters would lead
327 to lower over winter survival of territory owners, and we expected this to be magnified for non-
328 territory owners, not reversed. There are some situations in which colder winters lead to higher
329 survival, such as in hibernating species (bats *Chalinolobus tuberculatus*; Pryde, O'Donnell, &
330 Barker, 2005; jumping mice *Zapus hudsonicus preblei*; Schorr, Lukacs, & Florent, 2009) where
331 this leads to less frequent arousal from hibernation (Humphries, Thomas, & Speakman, 2002).
332 Red squirrels are non-hibernating, so this mechanism cannot explain why non-territory owners
333 would benefit from colder winters.

334 We can suggest two alternative but non-mutually exclusive explanations for why
335 juveniles that acquired a territory late would have higher survival over colder winters. First, in
336 colder years the incidence of nest-sharing among non-territory owners might be higher. Nest
337 sharing, typically between kin, occurs in 19 % of female territory owners in this system, and is

338 more common in colder winters (Williams et al., 2013). We speculate that juveniles without
339 territories in autumn may be more likely to share nests with fellow non-territory owners or their
340 mothers (Larsen & Boutin, 1994; Martinig, A. R., personal observation), and this may improve
341 their survival relative to juveniles with territories in autumn. Second, the higher mortality of
342 juvenile territory owners in colder winters creates vacancies, which may allow juveniles without
343 territories prior to autumn a greater opportunity to claim a territory with cached food, enhancing
344 survival (Dunham, Warner, & Lawson, 1995). This would give them relatively improved
345 survival compared to warmer years where fewer juvenile territory owners would die. Which, if
346 either, of these mechanisms accounts for the differential effect of winter temperature remains to
347 be tested.

348 We found both lynx and mustelid abundances were negatively associated with juvenile
349 over winter survival. Previous work found that predation does not exert a strong influence on red
350 squirrel populations in the boreal forest (Boonstra, Boutin, et al., 2001). However, in this study,
351 the relative effects of annual lynx and mustelid abundance on over winter juvenile survival (-
352 0.68 and -0.32 for those without territories by autumn) were comparable in strength to the effect
353 of cone availability (0.38), which is the primary driver of red squirrel population dynamics
354 (LaMontagne et al., 2013). The relatively strong effects of predator abundances on over winter
355 survival in this study might appear contradictory to previous findings, but two distinctions can be
356 made. First, overall population size and individual probability of survival are not directly
357 comparable. While red squirrel population size may be dictated by the availability of food and
358 territories, predation could still affect *which* individuals survive (“compensatory predation”;
359 Errington, 1946). Second, this study was concerned with over winter survival of only juveniles,
360 and predator abundances had the strongest effect on the 39 % of juveniles that did not have
361 territories by autumn. The probability of survival of these juveniles is already low, so variation in
362 survival in this subset is not likely to have a large impact on the total population size.

363 We predicted that the effects of lynx and mustelid abundances on juvenile survival would
364 be mediated by the availability of their alternate prey, but we did not find any detectable two-
365 way interactions of either predator–prey pairing on red squirrel survival. One potential
366 explanation for this could be that predator populations closely track their prey. The positive
367 correlation between lynx and snowshoe hare abundances (0.73) makes the detection of an
368 interaction difficult. For example, there were few years in our dataset with high predator and low

369 prey abundances with which to evaluate these interactions. Additionally, although lynx switch
370 from snowshoe hares to red squirrels when the former are rare (O'Donoghue, Boutin, Krebs,
371 Zuleta, et al., 1998), lynx and mustelids may predate on juvenile red squirrels opportunistically if
372 juveniles, particularly those without territories by autumn, are more susceptible to predation
373 regardless of alternate prey availability.

374 We did not anticipate that the abundance of voles and hares would be associated with
375 winter survival of juvenile red squirrels. High snowshoe hare abundance was associated with
376 increased juvenile survival over winter, while years with high vole abundances had lower
377 juvenile survival. Red squirrels will opportunistically predate on snowshoe hare leverets in the
378 spring and summer (O'Donoghue, 1994), but this additional food source should not have a strong
379 effect over winter. Voles are not in strong competition with juveniles for resources, given red
380 squirrels access arboreal food sources unavailable to voles, and red-backed voles are broad
381 omnivores, feeding on vegetation, fungi, and arthropods (Boonstra, Krebs, Gilbert, & Schweiger,
382 2001). The effect of snowshoe hare abundance on juvenile winter survival could also be a
383 statistical artifact of the correlation between lynx and hare abundance. Vole and mustelid
384 abundances are weakly correlated (0.27), so it is less likely that this explanation holds for the
385 negative affect of vole abundance on red squirrel over winter survival. These species'
386 abundances may also covary with another factor that influences juvenile survival not included in
387 our analysis, but what this factor might be remains unclear.

388 In our survival model, juveniles with higher growth rates were more likely to survive to
389 spring, but birth date had no effect. Previous work in this population has observed strong
390 selection on both birth date and growth rate in annual survival of juveniles (Dantzer et al., 2013;
391 Fisher et al., 2017; McAdam & Boutin, 2003; Williams, Lane, Humphries, McAdam, & Boutin,
392 2014). In preliminary models not including territory ownership, there was a detectable effect of
393 birth date on winter survival. Once accounting for territory ownership, birth date stopped being
394 important. This implies that early-born juveniles are likely to acquire a territory sooner, but there
395 are no further benefits of birth date for survival over winter. Both earlier birth dates and higher
396 growth rates are thought to be beneficial in territory acquisition, but there was still an effect of
397 growth rate on over winter survival after accounting for territory ownership (Table 2).
398 Furthermore, larger juveniles in the autumn are more likely to survive to spring (Larivée et al.
399 2010). Among juveniles for which we have body mass measurements in autumn ($n = 757$),

400 juveniles with higher relative growth rates were larger ($\beta = 7.95 \pm 1.61$, $t = 4.93$, $P < 0.001$), but
401 earlier birth dates also influenced body mass in autumn ($\beta = -8.89 \pm 1.25$, $t = -7.11$, $P < 0.001$) so
402 this does not explain why growth rate provides further benefits over winter but birth date does
403 not. Presumably, growth rate may be associated with other life history and behavioural traits
404 (Biro & Stamps, 2008; Réale et al., 2010; Stamps, 2007) that could affect winter survival.

405

406 *Conclusions*

407 We have identified how the timing of a life history event – territory acquisition – influences
408 juvenile over winter survival, and how it mediates biotic and abiotic factors that influence
409 survival. This gives us insight into how one trait can affect the opportunity for selection on
410 others, and therefore the functional links between phenotypes and fitness. We encourage more
411 researchers to study key life stages such as the juvenile period, when survival can be highly
412 variable and so the opportunity for selection high, to better understand how traits are selected in
413 populations. As this study was primarily concerned with over winter dynamics, investigations of
414 juveniles during their search for territories and before settlement, and which traits or conditions
415 are associated with territorial acquisition, would be informative in further explaining the
416 mechanisms behind some of the patterns we observed.

417

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428

429 **Author contributions**

430 JGH and DNF conceived the ideas and conducted the analyses; JGH, DNF, and ARM led the
431 writing of the manuscript; SB, BD, JEL, and AGM managed long term data collection and
432 revised initial drafts and analyses. All authors contributed critically to the drafts and gave final
433 approval for publication.

434

435 **Data accessibility**

436 Data used to evaluate juvenile over winter survival, along with code to recreate analyses and
437 figures, are available on Dryad at
438 <https://datadryad.org/stash/dataset/doi:10.5061/dryad.q2bvq83g0>. Note the dataset is embargoed
439 for one year from the date of publication.

440

441 **Literature Cited**

- 442 Archibald, D. W., Fletcher, Q. E., Boutin, S., McAdam, A. G., Speakman, J. R., & Humphries,
443 M. M. (2013). Sex-specific hoarding behavior in North American red squirrels
444 (*Tamiasciurus hudsonicus*). *Journal of Mammalogy*, 94(4), 761–770. doi:10.1644/12-
445 MAMM-A-213.1
- 446 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models
447 using lme4. *Journal of Statistical Software*, 67:1–8. doi:10.18637/jss.v067.i01
- 448 Berteaux, D., & Boutin, S. (2000). Breeding dispersal in female North American red squirrels.
449 *Ecology*, 81(5), 1311–1326. doi: 10.1890/0012-9658(2000)081[1311:BDIFNA]2.0.CO;2
- 450 Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history
451 productivity? *Trends in Ecology & Evolution*, 23(7), 361–368.
452 doi:10.1016/j.tree.2008.04.003
- 453 Boonstra, R., Boutin, S., Byrom, A., Karels, T. I. M., Hubbs, A., Stuart-Smith, K., ...
454 Antpoehler, S. (2001). The role of red squirrels and arctic ground squirrels. In C. J. Krebs,
455 S. Boutin, & R. Boonstra (Eds.), *Ecosystem dynamics of the boreal forest: the Klwane*

- 456 *project* (pp. 179–215). New York: Oxford University Press.
- 457 Boonstra, R., & Krebs, C. J. (2006). Population limitation of the northern red-backed vole in the
 458 boreal forests of northern Canada. *Journal of Animal Ecology*, *75*(6), 1269–1284.
 459 doi:10.1111/j.1365-2656.2006.01149.x
- 460 Boonstra, R., Krebs, C. J., Gilbert, B., & Schweiger, S. (2001). Voles and mice. In C. J. Krebs, S.
 461 Boutin, & R. Boonstra (Eds.), *Ecosystem dynamics of the boreal forest: the Kluane project*
 462 (pp. 215–239). New York: Oxford University Press.
- 463 Boutin, S., Wauters, L. A., McAdam, A., Humphries, M., Tosi, G., & Dhondt, A. (2006).
 464 Anticipatory reproduction and population growth in seed predators. *Science*, *314*(5807),
 465 1928–1930. doi:10.1126/science.1135520
- 466 Boutin, S., Krebs, C. J., Boonstra, R., Dale, M. R. T., Hannon, S. J., Martin, K., ... Schweiger, S.
 467 (1995). Population changes of the vertebrate community during a snowshoe hare cycle in
 468 Canada's boreal forest. *Oikos*, *74*(1), 69. doi:10.2307/3545676
- 469 Carpenter, F. L. (1987). Food abundance and territoriality: To defend or not to defend?
 470 *Integrative and Comparative Biology*, *27*(2), 387–399. doi:10.1093/icb/27.2.387
- 471 Clarke, M. F., Burke, K., Lair, H., Pocklington, R., Clarke, M. F., Burke, K., ... Robert, L.
 472 (1993). Familiarity affects escape behaviour of the Eastern chipmunk, *Tamias striatus*.
 473 *Oikos*, *66*(3), 533–537. doi:10.2307/3544949
- 474 Cooper, E. B., Taylor, R. W., Kelley, A. D., Martinig, A. R., Boutin, S., Humphries, M. M., ...
 475 McAdam, A. G. (2017). Personality is correlated with natal dispersal in North American red
 476 squirrels (*Tamiasciurus hudsonicus*). *Behaviour*, *154*, 939-961. doi:10.1163/1568539X-
 477 00003450
- 478 Cowlshaw, G. (1997). Refuge use and predation risk in a desert baboon population. *Animal*
 479 *Behaviour*, *54*(2), 241–253. doi:10.1006/anbe.1996.0466
- 480 Dantzer, B., Newman, A. E. M., Boonstra, R., Palme, R., Boutin, S., Humphries, M. M., &
 481 McAdam, A. G. (2013). Density triggers maternal hormones that increase adaptive
 482 offspring growth in a wild mammal. *Science*, *340*(6137), 1215–1217.
 483 doi:10.1126/science.1235765
- 484 Descamps, S., Boutin, S., Berteaux, D., & Gaillard, J.-M. (2008). Age-specific variation in
 485 survival, reproductive success and offspring quality in red squirrels: evidence of
 486 senescence. *Oikos*, *117*(9), 1406–1416. doi:10.1111/j.0030-1299.2008.16545.x

- 487 Dunham, M. L., Warner, R. R., & Lawson, J. W. (1995). The dynamics of territory acquisition: a
 488 model of two coexisting strategies. *Theoretical Population Biology*, *47*, 347–364.
 489 doi:10.1006/tpbi.1995.1016
- 490 Errington, P. L. (1946). Predation and vertebrate populations. *The Quarterly Review of Biology*,
 491 *21*(2), 144–177. doi:10.1086/395220
- 492 Everett, R. A., & Ruiz, G. M. (1993). Coarse woody debris as a refuge from predation in aquatic
 493 communities: an experimental test. *Oecologia*, *93*(4), 475–486. doi:10.1007/BF00328954
- 494 Ferguson, G. W., & Fox, S. F. (1984). Annual variation of survival advantage of large juvenile
 495 side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. *Evolution*,
 496 *38*(2), 342–349. doi:10.1111/j.1558-5646.1984.tb00292.x
- 497 Fisher, D. N., Boutin, S., Dantzer, B., Humphries, M. M., Lane, J. E., & McAdam, A. G. (2017).
 498 Multilevel and sex-specific selection on competitive traits in North American red squirrels.
 499 *Evolution*, *71*(7), 1841–1854. doi:10.1111/evo.13270
- 500 Fisher, D. N., Haines, J. A., Boutin, S., Dantzer, B., Lane, J. E., Coltman, D. W., & McAdam, A.
 501 G. (2019). Indirect effects on fitness between individuals that have never met via an
 502 extended phenotype. *Ecology Letters*, *22*(4), 697–706. doi:10.1111/ele.13230
- 503 Fletcher, Q. E., Boutin, S., Lane, J. E., LaMontagne, J. M., McAdam, A. G., Krebs, C. J., &
 504 Humphries, M. M. (2010). The functional response of a hoarding seed predator to mast
 505 seeding. *Ecology*, *91*(9), 2673–2683. doi:10.1890/09-1816.1
- 506 Fletcher, Q. E., Landry-Cuerrier, M., Boutin, S., McAdam, A. G., Speakman, J. R., &
 507 Humphries, M. M. (2013). Reproductive timing and reliance on hoarded capital resources
 508 by lactating red squirrels. *Oecologia*, *173*(4), 1203–1215. doi:10.1007/s00442-013-2699-3
- 509 Fuller, W. A., Stebbins, L. L., & Dyke, G. R. (1969). Overwintering of small mammals near
 510 Great Slave Lake Northern Canada. *Arctic*, *22*(1), 34–55. doi:10.2307/40507757
- 511 Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toïgo, C. (2000). Temporal
 512 variation in fitness components and population dynamics of large herbivores. *Annual*
 513 *Review of Ecology and Systematics*, *31*(1), 367–393. doi:10.1146/annurev.ecolsys.31.1.367
- 514 Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large
 515 herbivores: variable recruitment with constant adult survival. *Trends in Ecology and*
 516 *Evolution*, *13*(2), 58–63. doi:10.1016/S0169-5347(97)01237-8
- 517 Galef, B. G. (1981) The ecology of weaning: parasitism and the achievement of

- 518 independence by altricial mammals. In: Gubernick, D. J. & Klopfer, P. H. (eds) *Parental*
 519 *care in mammals* (pp. 211-241). Boston, MA: Springer. doi:10.1007/978-1-4613-3150-
 520 6_6
- 521 Garrett, M. G., & Franklin, W. L. (1988). Behavioral ecology of dispersal in the black-tailed
 522 prairie dog. *Journal of Mammalogy*, 69(2), 236–250. doi:10.2307/1381375
- 523 Goheen, J. R., & Swihart, R. K. (2005). Resource selection and predation of North American red
 524 squirrels in deciduous forest fragments. *Journal of Mammalogy*, 86(1), 22–28.
 525 doi:10.1644/1545-1542(2005)086<0022:rsapon>2.0.co;2
- 526 Greenwood, P. J., & Harvey, P. H. (1982). The natal and breeding dispersal of birds. *Annual*
 527 *Review of Ecology and Systematics*, 13, 1–21. doi:10.1146/annurev.es.13.110182.000245
- 528 Haines, J. A., Coltman, D. W., Dantzer, B., Gorrell, J. C., Humphries, M. M., Lane, J. E., ...
 529 Boutin, S. (2018). Sexually selected infanticide by male red squirrels in advance of a mast
 530 year. *Ecology*, 99(5): 1242-1244. doi:10.1002/ecy.2158
- 531 Humphries, M. M., & Boutin, S. (2000). The determinants of optimal litter size in free-ranging
 532 red squirrels. *Ecology*, 81(10), 2867–2877. doi:10.1890/0012-
 533 9658(2000)081[2867:TDOOLS]2.0.CO;2
- 534 Humphries, M. M., Thomas, D. W., & Speakman, J. R. (2002). Climate-mediated energetic
 535 constraints on the distribution of hibernating mammals. *Nature*, 418(6895), 313–316.
 536 doi:10.1038/nature00828
- 537 Jackson, D. M., Trayhurn, P., & Speakman, J. R. (2001). Associations between energetics and
 538 over-winter survival in the short-tailed field vole *Microtus agrestis*. *Journal of Animal*
 539 *Ecology*, 70(4), 633–640. doi:10.1046/j.1365-2656.2001.00518.x
- 540 Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*,
 541 9(12), 465–470. doi:10.1016/0169-5347(94)90310-7
- 542 Kerr, T. D., Boutin, S., LaMontagne, J. M., McAdam, A. G., & Humphries, M. M. (2007).
 543 Persistent maternal effects on juvenile survival in North American red squirrels. *Biology*
 544 *Letters*, 3(3), 289–291. doi:10.1098/rsbl.2006.0615
- 545 Kerr, T. D., & Descamps, S. (2011). Why do North American red squirrel, *Tamiasciurus*
 546 *hudsonicus*, mothers relocate their young? A predation-based hypothesis. *Canadian Field-*
 547 *Naturalist*, 122(1): 65-66. doi:10.22621/cfn.v122i1.546
- 548 Krebs, C. J. (2001). General introduction. In C. J. Krebs, S. Boutin, & R. Boonstra (Eds.),

- 549 *Ecosystem dynamics of the boreal forest: the Kluane project* (pp. 3–8). New York: Oxford
 550 University Press. doi:10.1016/S0006-3495(64)86921-6
- 551 Krebs, C. J., Boonstra, R., Kenney, A. J., & Gilbert, B. S. (2018). Hares and small rodent cycles:
 552 a 45-year perspective on predator-prey dynamics in the Yukon boreal forest. *Australian*
 553 *Zoologist*, 39(4), 724–732. doi:10.7882/AZ.2018.012
- 554 Lair, H. (1990). The calls of the red squirrel — a contextual analysis of function. *Behaviour*,
 555 115(3), 254–282. doi:10.1163/156853990X00608
- 556 LaMontagne, J. M., & Boutin, S. (2007). Local-scale synchrony and variability in mast seed
 557 production patterns of *Picea glauca*. *Journal of Ecology*, 95(5), 991–1000.
 558 doi:10.1111/j.1365-2745.2007.01266.x
- 559 LaMontagne, J. M., Peters, S., & Boutin, S. (2005). A visual index for estimating cone
 560 production for individual white spruce trees. *Canadian Journal of Forest Research*, 35(12),
 561 3020–3026. doi:10.1139/x05-210
- 562 LaMontagne, J. M., Williams, C. T., Donald, J. L., Humphries, M. M., McAdam, A. G., &
 563 Boutin, S. (2013). Linking intraspecific variation in territory size, cone supply, and survival
 564 of North American red squirrels. *Journal of Mammalogy*, 94(5), 1048–1058.
 565 doi:10.1644/12-MAMM-A-245.1
- 566 Lane, J. E., McAdam, A. G., Charmantier, A., Humphries, M. M., Coltman, D. W., Fletcher, Q.,
 567 ... Boutin, S. (2015). Post-weaning parental care increases fitness but is not heritable in
 568 North American red squirrels. *Journal of Evolutionary Biology*, 28(6), 1203–12.
 569 doi:10.1111/jeb.12633
- 570 Larivée, M. L., Boutin, S., Speakman, J. R., McAdam, A. G., & Humphries, M. M. (2010).
 571 Associations between over-winter survival and resting metabolic rate in juvenile North
 572 American red squirrels. *Functional Ecology*, 24(3), 597–607. doi:10.1111/j.1365-
 573 2435.2009.01680.x
- 574 Larsen, K. W., & Boutin, S. (1994). Movements, survival, and settlement of red squirrel
 575 (*Tamiasciurus hudsonicus*) offspring. *Ecology*, 75(1), 214–223. doi:10.2307/1939395
- 576 McAdam, A. G., & Boutin, S. (2003). Variation in viability selection among cohorts of juvenile
 577 red squirrels (*Tamiasciurus hudsonicus*). *Evolution*, 57(7), 1689–1697. doi:10.1111/j.0014-
 578 3820.2003.tb00374.x
- 579 McAdam, A. G., Boutin, S., Sykes, A. K., & Humphries, M. M. (2007). Life histories of female

- 580 red squirrels and their contributions to population growth and lifetime fitness. *Ecoscience*,
581 14(3), 362. doi:10.2980/1195-6860(2007)14[362:LHOFRS]2.0.CO;2
- 582 Merritt, J. F. (1986). Winter survival adaptations of the short-tailed shrew (*Blarina brevicauda*)
583 in an Appalachian montane forest. *Journal of Mammalogy*, 67(3), 450–464.
584 doi:10.2307/1381276
- 585 Metzgar, L. H. (1967). An experimental comparison of screech owl predation on resident and
586 transient white-footed mice (*Peromyscus leucopus*). *Journal of Mammalogy*, 48(3), 387–
587 391. doi:10.2307/1377771
- 588 Millar, J. S., & McAdam, A. G. (2001). Life on the edge: the demography of short-season
589 populations of deer mice. *Oikos*, 93, 69–76. doi:10.1034/j.1600-0706.2001.930107.c
- 590 Morrison, S. F., & Hik, D. S. (2007). Demographic analysis of a declining pika *Ochotona*
591 *collaris* population: linking survival to broad-scale climate patterns via spring snowmelt
592 patterns. *Journal of Animal Ecology*, 76, 899–907. doi:10.1111/j.1365-2656.2007.01276.x
- 593 Morrison, S. F., Pelchat, G., Donahue, A., & Hik, D. S. (2009). Influence of food hoarding
594 behavior on the over-winter survival of pikas in strongly seasonal environments. *Oecologia*,
595 159(1), 107–116. doi:10.1007/s00442-008-1197-5
- 596 Morrissey, M. B., & Ruxton, G. D. (2018). Multiple regression is not multiple regressions: the
597 meaning of multiple regression and the non-problem of collinearity. *Philosophy, Theory,*
598 *and Practice in Biology*, 10(3). doi:10.3998/ptpbio.16039257.0010.003
- 599 O'Connor, C. M., Norris, D. R., Crossin, G. T., & Cooke, S. J. (2014). Biological carryover
600 effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere*,
601 5(3), 28. doi:10.1890/ES13-00388.1
- 602 O'Donoghue, M., Boutin, S., Hofer, E. J., & Boonstra, R. (2001). Other mammalian predators. In
603 C. J. Krebs, S. Boutin, & R. Boonstra (Eds.), *Ecosystem dynamics of the boreal forest: the*
604 *Kluane project* (pp. 325–336). New York: Oxford University Press.
- 605 O'Donoghue, M. (1994). Early survival of juvenile snowshoe hares. *Ecology*, 75(6), 1582–1592.
606 doi:10.2307/1939619
- 607 O'Donoghue, M., Boutin, S., Krebs, C. J., Murray, D. L., & Hofer, E. J. (1998). Behavioural
608 responses of coyotes and lynx to the snowshoe hare cycle. *Oikos*, 82, 169–183.
609 doi:10.2307/3546927
- 610 O'Donoghue, M., Boutin, S., Krebs, C. J., Zuleta, G., Dennis, L., Donoghue, M. O., ... Hofer, E.

- 611 J. (1998). Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*,
 612 79(4), 1193–1208. doi:10.1890/0012-9658(1998)079[1193:FROCAL]2.0.CO;2
- 613 Oli, M. K., & Dobson, F. S. (2003). The relative importance of life-history variables to
 614 population growth rate in mammals: Cole’s prediction revisited. *The American Naturalist*,
 615 161(3), 422–440. doi:10.1086/367591
- 616 Pryde, M. A., O’Donnell, C. F. J., & Barker, R. J. (2005). Factors influencing survival and long-
 617 term population viability of New Zealand long-tailed bats (*Chalinolobus tuberculatus*):
 618 implications for conservation. *Biological Conservation*, 126(2), 175–185.
 619 doi:10.1016/J.BIOCON.2005.05.006
- 620 Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010).
 621 Personality and the emergence of the pace-of-life syndrome concept at the population level.
 622 *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*,
 623 365(1560), 4051–4063. doi:10.1098/rstb.2010.0208
- 624 Rödel, H. G., Bora, A., Kaetzke, P., Khaschei, M., Hutzelmeyer, H., & von Holst, D. (2004).
 625 Over-winter survival in subadult European rabbits: weather effects, density dependence, and
 626 the impact of individual characteristics. *Oecologia*, 140(4), 566–576. doi:10.1007/s00442-
 627 004-1616-1
- 628 Rödel, Heiko G., Zapka, M., Talke, S., Kornatz, T., Bruchner, B., & Hedler, C. (2015). Survival
 629 costs of fast exploration during juvenile life in a small mammal. *Behavioral Ecology and*
 630 *Sociobiology*, 69(2), 205–217. doi:10.1007/s00265-014-1833-5
- 631 Rodríguez, S., van Noordwijk, A. J., Álvarez, E., & Barba, E. (2016). A recipe for postfledging
 632 survival in great tits *Parus major*: be large and be early (but not too much). *Ecology and*
 633 *Evolution*, 6(13), 4458–4467. doi:10.1002/ece3.2192
- 634 Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients.
 635 *Methods in Ecology and Evolution*, 1(2), 103–113. doi:10.1111/j.2041-210X.2010.00012.x
- 636 Schorr, R. A., Lukacs, P. M., & Florant, G. L. (2009). Body mass and winter severity as
 637 predictors of overwinter survival in Preble’s meadow jumping mouse. *Journal of*
 638 *Mammalogy*, 90(1), 17–24. doi:10.1644/07-MAMM-A-392.1
- 639 Searcy, S. P., & Sponaugle, S. (2001). Selective mortality during the larval – juvenile transition
 640 in two coral reef fishes. *Ecology*, 82(9), 2452–2470. doi:10.1890/0012-
 641 9658(2001)082[2452:SMDTLJ]2.0.CO;2

- 642 Silvertown, J. W. (1980). The evolutionary ecology of mast seeding in trees. *Biological Journal*
643 *of the Linnean Society*, 14(2), 235–250. doi:10.1111/j.1095-8312.1980.tb00107.x
- 644 Smith, C. C. (1968). The adaptive nature of social organization in the genus of tree squirrels
645 *Tamiasciurus*. *Ecological Monographs*, 38(1), 31–64. doi:10.2307/1948536
- 646 Stamps, J. A. (2007). Growth-mortality tradeoffs and “personality traits” in animals. *Ecology*
647 *Letters*, 10(5), 355–363. doi:10.1111/j.1461-0248.2007.01034.x
- 648 Steele, M. A. (1998). *Tamiasciurus hudsonicus*. *Mammalian Species*, 586(586), 1–9.
649 doi:10.1890/0012-9623(2004)85
- 650 Stuart-Smith, A. K., & Boutin, S. (1995). Predation on red squirrels during a snowshoe hare
651 decline. *Canadian Journal of Zoology*, 73(4), 713–722. doi:10.1139/z95-083
- 652 Studd, E. K., Boutin, S., McAdam, A. G., Krebs, C. J., & Humphries, M. M. (2015). Predators,
653 energetics and fitness drive neonatal reproductive failure in red squirrels. *Journal of Animal*
654 *Ecology*, 84(1), 249–259. doi:10.1111/1365-2656.12279
- 655 van der Jeugd, H., & Larsson, K. (1998). Pre-breeding survival of barnacle geese *Branta*
656 *leucopsis* in relation to fledgling characteristics. *Journal of Animal Ecology*, 67, 953–966.
657 doi:10.1046/j.1365-2656.1998.6760953.x
- 658 Whitham, T. G. (1986). Costs and benefits of territoriality: behavioral and reproductive release
659 by competing aphids. *Ecology*, 67(1), 139–147. doi:10.2307/1938512
- 660 Williams, C. T., Gorrell, J. C., Lane, J. E., McAdam, A. G., Humphries, M. M., & Boutin, S.
661 (2013). Communal nesting in an ‘asocial’ mammal: social thermoregulation among
662 spatially dispersed kin. *Behavioral Ecology and Sociobiology*, 67(5), 757–763.
663 doi:10.1007/s00265-013-1499-4
- 664 Williams, C. T., Lane, J. E., Humphries, M. M., McAdam, A. G., & Boutin, S. (2014).
665 Reproductive phenology of a food-hoarding mast-seed consumer: Resource- and density-
666 dependent benefits of early breeding in red squirrels. *Oecologia*, 174(3), 777–788.
667 doi:10.1007/s00442-013-2826-1
- 668 Wunder, B. A., Dobkin, D. S., & Gettinger, R. D. (1977). Shifts of thermogenesis in the prairie
669 vole. *Oecologia*, 29, 11–26. doi:10.1007/BF00345359

671 **Tables**

672

Overwinter survival of juvenile red squirrels

673 Table 1. Probability of over winter survival for juvenile red squirrels alive in August 1989 –
 674 2015 ($n = 1305$), with adult density for each year (individuals/ha), number of juveniles alive in
 675 autumn (cohort size), and proportion of juveniles with territories in autumn (autumn territory
 676 owners).

Year	Adult population density (individuals/ha)	Autumn cohort size	Autumn territory owners (%)	Juvenile survival (%)
1989	1.25	6	100	66.7
1990	1.30	13	76.9	61.5
1991	1.18	28	82.1	85.7
1992	1.31	46	32.6	30.4
1993	1.23	121	59.5	71.1
1994	2.20	28	89.3	21.4
1995	1.60	75	84.0	82.7
1996	1.88	15	80.0	60.0
1997	1.86	51	88.2	94.1
1998	2.14	78	74.4	82.1
1999	3.93	25	64.0	36.0
2000	2.56	24	62.5	58.3
2001	1.84	56	60.7	51.8
2002	1.63	49	67.4	51.0
2003	1.22	34	88.2	70.6
2004	1.02	44	61.4	61.4
2005	1.05	98	38.8	66.3

Overwinter survival of juvenile red squirrels

2006	2.02	47	74.5	46.8
2007	1.40	72	54.1	55.6
2008	1.40	30	86.7	43.3
2009	0.94	44	59.1	50.0
2010	0.73	100	35.0	66.0
2011	1.75	32	87.5	81.3
2012	1.86	50	46.0	46.0
2013	1.73	54	63.0	63.0
2014	1.57	150	71.3	71.3
2015	3.15	18	44.4	44.4
Average ± SE	1.69 ± 0.13	51 ± 6.6	65.4 ± 4.1	60.0 ± 3.4

677

678

679 Table 2. Mixed effects binomial model of juveniles red squirrel over winter survival ($n = 1305$),
 680 testing whether territory ownership by autumn mediates effects of predators and temperature on
 681 over winter survival, including random effects of litter ID and year (conditional $R^2 = 0.44$).
 682 Estimates of predator and temperature effects indicate effects for the reference category of
 683 juveniles without territories in autumn.

Term	Estimate ± SE	z	P	VIF
Std. density	-0.69 ± 0.15	-4.45	< 0.001	1.96
Std. cones	0.38 ± 0.11	3.45	< 0.001	1.76
Std. growth rate	0.22 ± 0.10	2.13	0.033	1.02

Overwinter survival of juvenile red squirrels

Std. birth date	-0.01 ± 0.09	-0.08	0.936	1.16
Grid (SU)	0.19 ± 0.18	1.06	0.289	1.17
Sex (male)	-0.49 ± 0.16	-3.1	0.002	1.03
Autumn owner (yes)	2.78 ± 0.23	12.06	< 0.001	1.70
Std. lynx (non-owners)	-0.68 ± 0.28	-2.41	0.016	4.22
Std. hares	0.40 ± 0.20	1.99	0.046	3.71
Std. mustelid (non-owners)	-0.38 ± 0.14	-2.7	0.007	2.71
Std. voles	-0.59 ± 0.13	-4.57	< 0.001	2.30
Std. temperature (non-owners)	-0.35 ± 0.18	-1.99	0.047	2.16
Std. lynx : Std. hares	0.12 ± 0.09	1.32	0.187	1.64
Std. mustelid : Std. voles	0.14 ± 0.11	1.27	0.203	2.26
Autumn owner (yes) : Std. lynx	0.99 ± 0.23	4.22	< 0.001	2.26
Autumn owner (yes) : Std. mustelid	0.31 ± 0.18	1.75	0.080	2.03
Autumn owner (yes) : Std. temperature	1.11 ± 0.21	5.31	< 0.001	1.62
Random effects	Variance			
Litter ID	0.665			
Year	0.000			

684 **Figure legends**

685

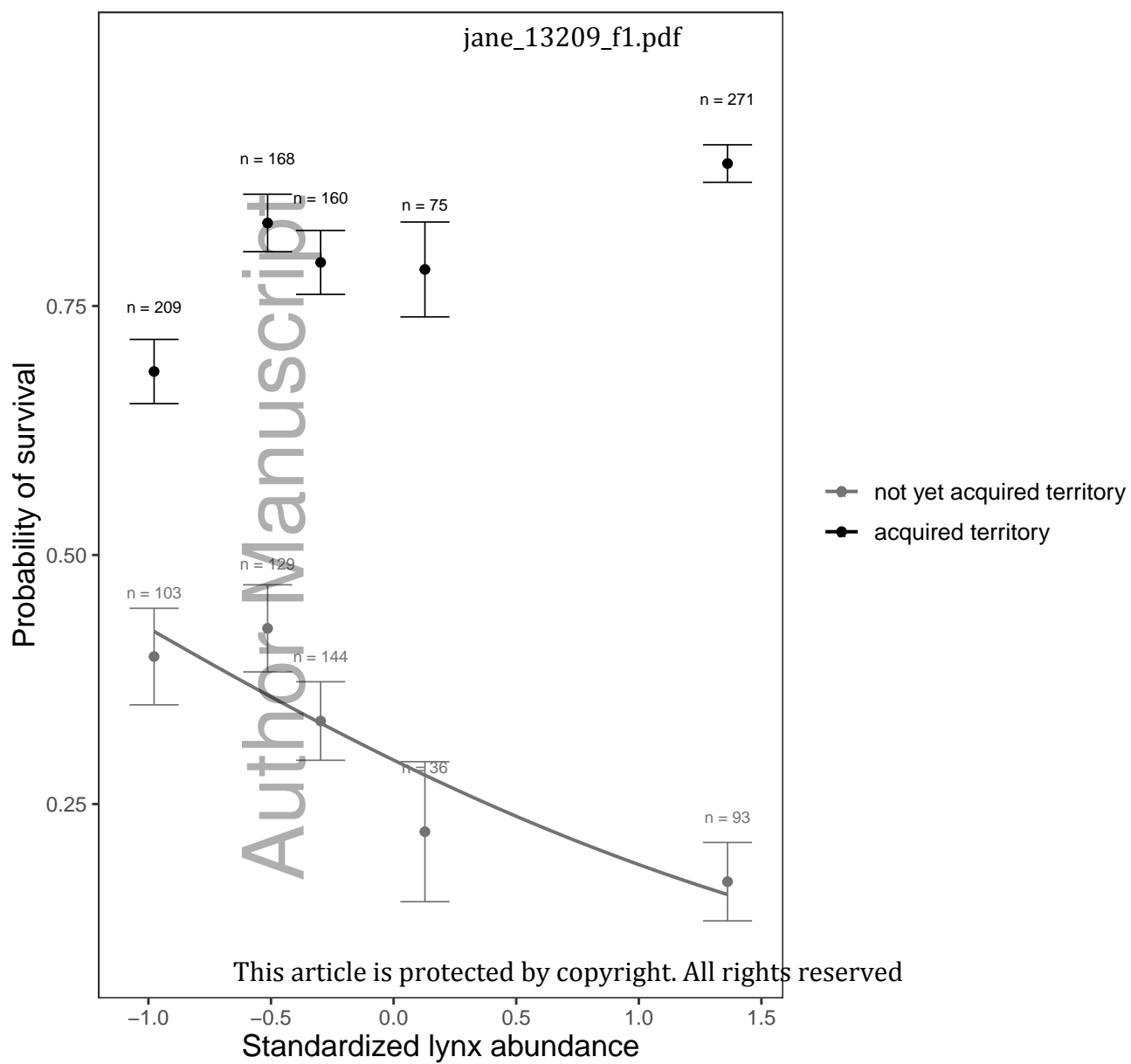
686 Figure 1. Over winter survival of juvenile North American red squirrels *Tamiasciurus*
 687 *hudsonicus* ($n = 1305$) that had or had not acquired a territory by autumn. Juveniles without
 688 territories had lower survival when lynx *Lynx canadensis* were abundant (not yet acquired
 689 territory: $\beta = -0.68 \pm 0.28$, $z = -2.41$, $P = 0.016$), whereas the survival of juveniles with territories

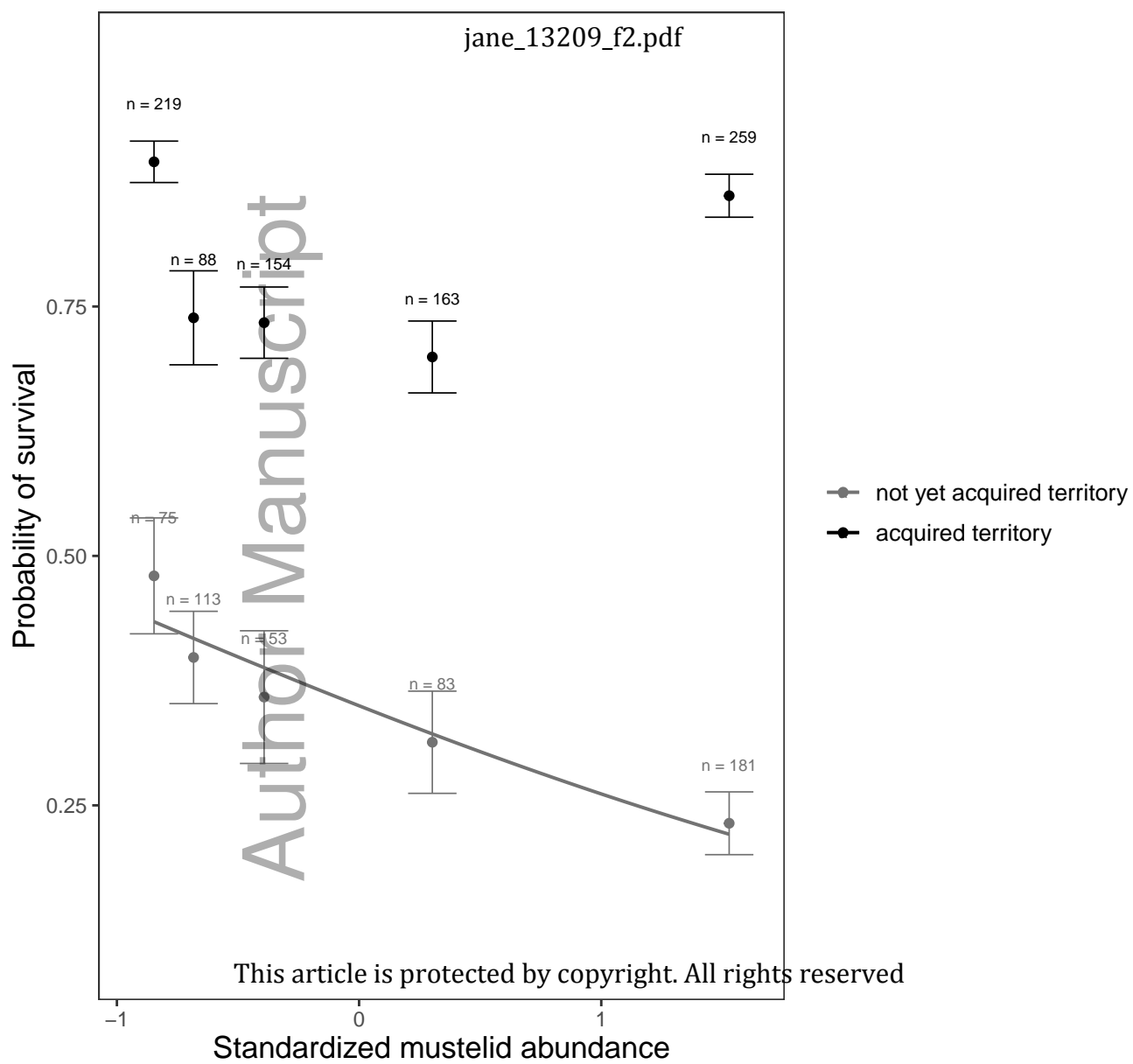
690 was unaffected by lynx abundance (acquired territory: $\beta = 0.31 \pm 0.21$, $z = 1.49$, $P = 0.14$;
691 interaction $\beta = 0.99 \pm 0.23$, $z = 4.22$, $P < 0.001$). Points represent mean survival \pm SE for each
692 quintile of standardized lynx abundance estimates. These points are shown only for illustrative
693 purposes; lynx abundance was analyzed as a continuous variable in all analyses.

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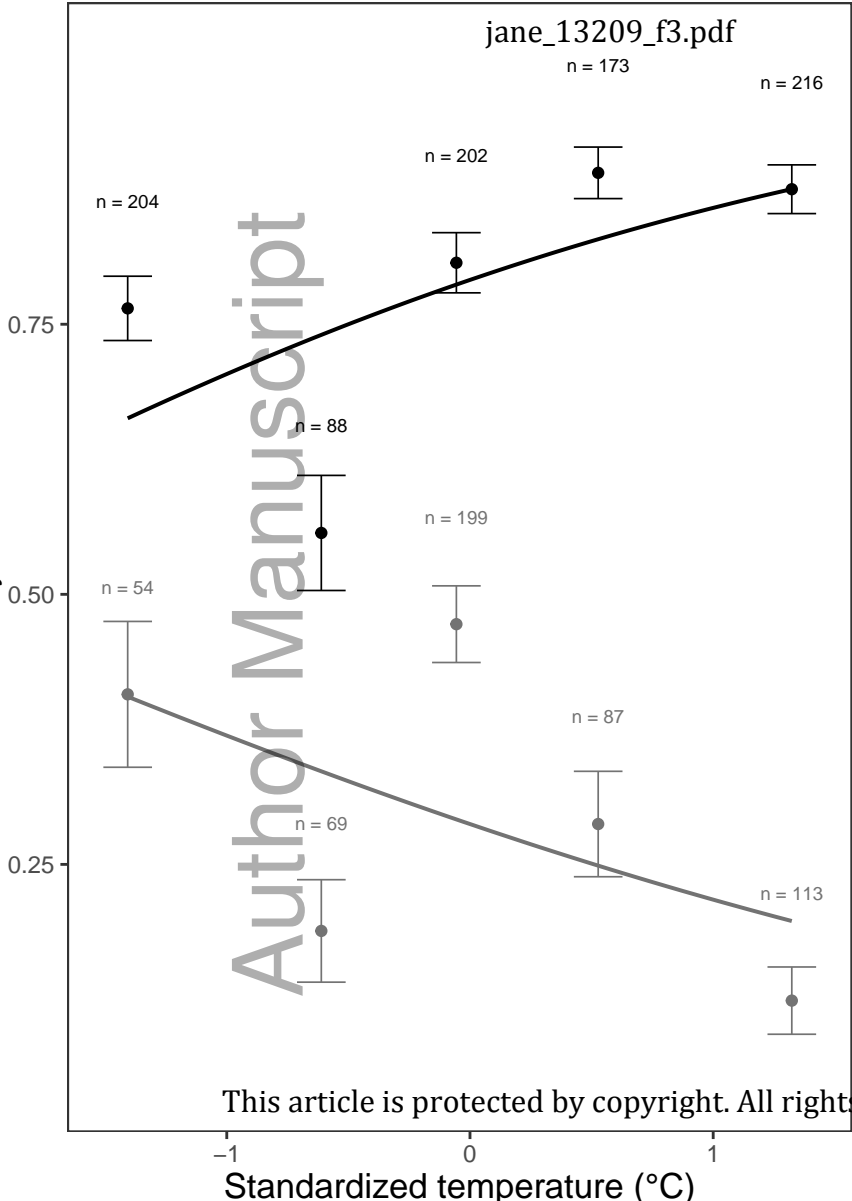
695 Figure 2. Over winter survival of juvenile North American red squirrels *Tamiasciurus*
696 *hudsonicus* ($n = 1305$) that had or had not acquired a territory by autumn was lower when
697 mustelids (short-tailed weasel *Mustela erminea*, least weasel *M. nivalis*, and marten *Martes*
698 *americana*) were abundant. Juveniles without territories by autumn were somewhat more
699 affected by mustelid abundance (not yet acquired territory: $\beta = -0.38 \pm 0.14$, $z = -2.70$, $P =$
700 0.007) than territory owners (acquired territory: $\beta = -0.07 \pm 0.14$, $z = -0.49$, $P = 0.624$;
701 interaction $\beta = 0.31 \pm 0.18$, $z = 1.75$, $P = 0.080$). Points represent mean survival \pm SE for each
702 quintile of standardized mustelid abundance estimates. These points are shown only for
703 illustrative purposes; mustelid abundance was analyzed as a continuous variable in all analyses.

704 Figure 3. Over winter survival of juvenile North American red squirrels *Tamiasciurus*
705 *hudsonicus* ($n = 1305$) that had or had not acquired a territory by autumn. Autumn territory
706 owners survived better in warmer years (acquired territory: $\beta = 0.76 \pm 0.13$, $z = 5.87$, $P < 0.001$),
707 whereas warmer winters decreased survival of juveniles without territories at this time (not yet
708 acquired territory: $\beta = -0.35 \pm 0.18$, $z = -1.99$, $P = 0.047$; interaction $\beta = 1.11 \pm 0.21$, $z = 5.31$, P
709 < 0.001). Points represent mean survival \pm SE for each quintile of standardized winter
710 temperatures. These points are shown only for illustrative purposes; winter temperature was
711 analyzed as a continuous variable in all analyses.





Probability of survival



● not yet acquired territory
● acquired territory