

1

2 Article Type: Letters

3 Indirect effects on fitness between individuals that have never met via
4 an extended phenotype

5

6 Running title: Extended phenotypes and indirect effects

7

8 David N. Fisher^{1,2}, Jessica A. Haines^{3,4}, Stan Boutin⁴, Ben Dantzer^{5,6}, Jeffrey E. Lane⁷, David
9 W. Coltman³, and Andrew G. McAdam¹

10 1. Department for Integrative Biology, University of Guelph, Guelph, Ontario N1G 2W1,
11 Canada

12 2. Department of Psychology, Neuroscience & Behaviour, McMaster University,
13 Hamilton, Ontario L8S 4K1, Canada

14 3. Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G
15 2E9, Canada

16 4. Department of Biological Sciences, MacEwan University, Edmonton, Alberta T5J
17 4S2, Canada

18 5. Department of Psychology, University of Michigan, Ann Arbor, Michigan 48109-
19 1043, USA

20 6. Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor,
21 Michigan 48109-1043, USA

22 7. Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan S7N
23 5E2, Canada

24

25 *corresponding author: davidnfisher@hotmail.com

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/ELE.13230](https://doi.org/10.1111/ELE.13230)

This article is protected by copyright. All rights reserved

26

27 Article type: Letter

28 Words in abstract: 149

29 Words in main text: 5199

30 Number of references: 71

31 Number of figures: 3

32 Number of tables: 1

33 Number of text boxes: 0

34

35 Authorship statement

36 DNF and AGM conceived of the research question. SB initiated the long-term study and all authors
37 contributed to field logistics, data collection and the writing of the manuscript. DNF drafted the
38 manuscript and conducted the data analysis, with guidance from AGM. All authors approved of the
39 final manuscript for submission.

40

41 Data accessibility

42 The data used for these analyses will be made available on Dryad upon publication

43

44 **Key words:** extended phenotype, indirect effect, inheritance, KRSP, quantitative genetics, resource
45 hoarding, *Tamiasciurus*, territory

46 Abstract

47 Interactions between organisms are ubiquitous and have important consequences for phenotypes
48 and fitness. Individuals can even influence those they never meet, if they have extended phenotypes
49 that alter the environments others experience. North American red squirrels (*Tamiasciurus*
50 *hudsonicus*) guard food hoards, an extended phenotype that typically outlives the individual and is
51 usually subsequently acquired by non-relatives. Hoarding by previous owners can, therefore,
52 influence subsequent owners. We found that red squirrels bred earlier and had higher lifetime
53 fitness if the previous hoard owner was a male. This was driven by hoarding behaviour, as males and

54 mid-aged squirrels had the largest hoards, and these effects persisted across owners, such that if the
55 previous owner was male or died in mid-age, subsequent occupants had larger hoards. Individuals
56 can, therefore, influence each other's resource dependent traits and fitness without ever meeting,
57 such that the past can influence contemporary population dynamics through extended phenotypes.

58

59 Introduction

60

61 Organisms socially interact when they mate, fight and compete for resources. Social interactions
62 mean individuals will influence the traits and fitness of other individuals, both positively through
63 cooperation, but also negatively through competition for limited resources, while other interactions
64 may have neutral consequences (Scott 1977; Moore *et al.* 1997). It is often implicitly assumed that
65 organisms need to meet to influence each other, but this need not always be the case. If organisms
66 possess extended phenotypes (traits of the individual that exist outside their physical body; Dawkins
67 1978, 1982) then they can alter the environment that others experience. "Ecosystem engineers"
68 (Jones *et al.* 1994) such as earthworms (Thompson *et al.* 1993) and beavers (*Castor spp.*; Naiman *et al.*
69 *al.* 1986; Rosell *et al.* 2005) are well known to alter the environment for their own benefit (see also
70 the separate but related concept of: "niche construction", Odling-Smee *et al.* 2003; Scott-Phillips *et al.*
71 *al.* 2014), and so will influence any organisms that use the modified environment. By altering the
72 environment that another individual might experience, organisms can influence the plastic traits of
73 others, or perhaps even their fitness, despite never actually meeting (Laidre 2012).

74 Beyond these classic examples of "ecosystem engineers" it is not yet clear how broadly
75 applicable such effects may be. Yet, many organisms alter their environment by building dens, nests
76 or burrows, which can influence organisms that subsequently choose to use or live in these
77 structures (Bailey 2012). Furthermore, organisms may leave imprints on the environment such as
78 scent cues that can influence those that encounter them, without direct physical contact (Cisterne *et al.*
79 *al.* 2014; Dewan *et al.* 2018). Aspects of organisms' extended phenotypes are potentially extensive
80 and varied (Dawkins 1978, 1982), facilitating myriad potential consequences for others.

81 It is, therefore, necessary to test how extended phenotypes can cause individuals to
82 influence the phenotypes and fitness of those they never meet and assess the consequences for
83 ecological and evolutionary processes. To do this, we studied a population of North American red
84 squirrels (*Tamiasciurus hudsonicus*; hereafter "red squirrels") at a study site in the Yukon Territory of
85 Canada for 30 years. Red squirrels defend territories of approximately 0.34 ha (LaMontagne *et al.*
86 2013), centred on a "midden", a pile of white spruce (*Picea glauca*) cone scales, within which red
87 squirrels cache food they require to survive over winter (Smith 1968b). Stored food typically consists

88 of white spruce cones (the red squirrels' main food source in this population) harvested that autumn
89 ("new cones") as well as cones stored from previous years' crops ("old cones"). The presence of
90 these food stores is also associated with increased local mammal and bird abundance (Posthumus *et*
91 *al.* 2015). Middens vary in the number of cones of each type they contain, with larger hoards leading
92 to improved overwinter survival of the occupant (Larivée *et al.* 2010; LaMontagne *et al.* 2013),
93 earlier breeding in the spring for females and increased reproductive success for males (Haines
94 2017). Therefore, they are analogous to fat stores, which can then be mobilised to fuel survival and
95 reproduction. The difference is that red squirrels store their resources in the ground, not on their
96 bodies, and hence these stores represent an *extended* phenotype.

97 Along with being an important contributor to the current occupant's survival and fitness,
98 middens last well beyond the lifespan of a single individual. Any given midden may be defended over
99 time by a sequence of many individuals that are typically not related and do not overlap in tenure
100 (Hatt 1929; Smith 1968b, 1981), although in some cases a female squirrel will "bequeath" her
101 territory to one of her offspring, and leave to find another territory (Price & Boutin 1993; Berteaux &
102 Boutin 2000; Boutin *et al.* 2000; Lane *et al.* 2015). Spruce cones cached in a midden can be
103 consumed at least four years post-caching (Donald & Boutin 2011; S. Boutin, unpublished data), so
104 cones cached by previous owners can be used by the next squirrel that acquires the territory.
105 Therefore, the number of cones cached in a squirrel's midden is an extended phenotype, and
106 furthermore may well be influenced by both the current and the previous occupant of the territory.
107 This then creates a mechanism through which the previous owner can influence the resource-
108 dependent traits, and so possibly fitness, of the current occupant.

109 We identified how the previous occupant of the territory influences the traits (cone hoard
110 sizes, as well as the date a female gives birth in the spring; "parturition date"), and the fitness
111 (estimated as lifetime reproductive success; LRS) of the current owner. Since cones are placed in the
112 ground in the autumn when we measured hoard size, we expected no influence of the previous
113 owner on the size of new cone hoards, but we did expect the previous owner to influence the size of
114 old cone hoards. Females give birth earlier when they have access to increased food resources
115 (Réale *et al.* 2003; Kerr *et al.* 2007; as this increases the chance their pups will acquire a territory and
116 so recruit into the population; Williams *et al.* 2014; Fisher *et al.* 2017), so we expected that traits of
117 the previous occupant that were associated with larger cone hoards would be the traits that cause
118 the subsequent hoard owner to breed earlier. We made the same prediction for LRS; traits of the
119 previous owner that are associated with larger hoard sizes should confer higher fitness on the
120 current occupant of the territory.

121

122 Methods

123

124 Data collection

125 We followed individually marked squirrels as part of the Kluane Red Squirrel Project (KRSP) in the
126 Yukon Territory of Canada from 1987 through 2017. We used different subsets of this entire dataset
127 for our analyses here. In each year, we monitored marked females in two unmanipulated 40-ha.
128 study areas (“Kloo” and “Sulphur”) for signs of pregnancy and to tag their pups. We also tagged any
129 immigrants and, therefore, tracked all squirrels resident in the population for their entire lifetime
130 (see: McAdam et al. 2007 for further details on the study system). We enumerated the entire
131 population in spring and autumn censuses to determine ownership of territories. These territories
132 are exclusive and are based around large piles of discarded cone scales (middens). Middens are
133 semi-permanent, so the same midden can be owned sequentially by multiple different squirrels
134 across an extended period of time. For example, one midden remained active throughout the entire
135 study period (between 1987 and 2017) and was owned by 13 different squirrels across this 31-year
136 period. We assigned ownership of a midden based on territorial vocalizations called ‘rattles’ (Smith
137 1968a, 1978), and only included squirrels owning a midden in our analysis, i.e. those that had
138 recruited into the population. We focus here on territory ownership in the autumn, as this is when
139 spruce cones are available to be stored, and so when we measured the size of cone hoards in
140 middens. We recognised previous territory owners when the identity of the territory owner in one
141 autumn was different to that in the previous autumn. We only included the first instance of a
142 squirrel holding a given territory in the analysis, so there were not multiple records if a squirrel held
143 the same territory for several years, but we did include a squirrel multiple times if it was observed
144 holding different territories in different years (although this is not that common as red squirrels do
145 not “trade-up” their territory when vacancies are available; Larsen & Boutin 1995). Each squirrel-
146 midden combination, therefore, only had a single previous owner, and since middens left
147 undefended through the death of the owner are typically taken over by new individuals quickly
148 (Price *et al.* 1986; Siracusa *et al.* 2017a, b), the previous owner typically held the territory a single
149 year ago. If the midden was undefended for >1 year, the previous owner would be more than 1 year
150 in the past, which we accounted for by fitting an interaction between the traits of the previous
151 owner and the number of years between them and the current owner (see Data analysis).

152 From 2012 through 2017 we estimated the number of cones stored in the primary middens
153 of all squirrels defending territories. We did this in late September after most caching was
154 completed. Some squirrels owned more than one midden in the autumn, but we did not consider
155 secondary middens as they are not held by the majority of squirrels and are not used extensively for

156 resource storage when they are held. For each midden, we identified its perimeter as the location
157 where the cone bracts gave way to typical forest floor, measured the longest axis and the
158 perpendicular width at the midpoint of the long axis. Assuming an elliptical shape (following: Larivée
159 *et al.* 2010), we estimated the area as :

$$\frac{\text{length}}{2} \times \frac{\text{width}}{2} \times \pi$$

160 Within each quarter of the midden, we placed two 30 cm X 30 cm square quadrats at approximately
161 $\frac{1}{4}$ and $\frac{3}{4}$ of the distance from the centre of the midden towards the perimeter, such that each
162 quarter of the midden had two quadrats placed wholly within it, giving eight in total (method
163 adapted from Larivée *et al.* 2010). If the midden was very small, such that a quarter could not fit two
164 quadrats, then only a single quadrat was placed. We then excavated all quadrats to a depth of 10 cm
165 from the surface of the bract pile and counted the number of old and new cones found within. If an
166 excavated tunnel was found, new and old cones inside were counted to a depth of 30 cm, but not
167 out of the area of the quadrat. If cones are not buried in middens they will open, releasing their
168 seeds. This makes them useless as food to red squirrels, so we did not count opened cones even if
169 they were within our quadrats. We calculated the number of old and new cones per cm² of midden
170 surface sampled (accounting for the number of quadrats), multiplied by the area of the midden, and
171 then rounded to the nearest whole number, to give an estimate of the size of the old and new cone
172 hoard in the midden (old and new cones indexes). We were able to separately count old and new
173 cones, as new cones are purple and green, and were often sticky with sap, while old cones were dark
174 brown and never sticky.

175 For the six-year period (2012-2017), we were able to assess the effect of previous owners on
176 old and new cone hoard sizes. Across a much-extended period of data collection, we were also able
177 to estimate effects of previous owners on female parturition dates (springs of 1992-2017) and the
178 LRS of males and females (squirrels born from 1991-2009; although LRS of males was not available
179 until 2003, see below). Due to maternities identified at birth since 1987, and paternities identified
180 based on genetic analysis of ear biopsies since 2003, we have very good information on the number
181 of offspring each individual has, and their survival, and also a well-resolved pedigree (Gunn *et al.*
182 2005; Lane *et al.* 2007; McFarlane *et al.* 2011). We estimated LRS as the total number of pups an
183 individual dammed or sired that survived to 200 days. As we do not typically monitor individuals
184 over winter, this requires individuals to have survived their first winter and recruited into the
185 population as adults in the spring when we conduct a population census. We excluded individuals for
186 which we had missed one or more breeding events, individuals that died of unnatural causes such as
187 dying in a trap, individuals that were born after 2009 (as their LRS would be underestimated), as well
188 as males pre-2003 for which we were not able to assess siring success. These restrictions gave us the

189 following sample sizes: cone hoards, 323 measures, 148 unique females and 125 unique males;
190 parturition date, 525 measures across 402 unique females; and LRS, 393 measures across 274
191 unique females and 119 unique males. As mentioned above, female red squirrels may bequeath
192 their territory to an offspring, which tends to be a daughter and the fastest growing pup in the litter
193 (Berteaux and Boutin 2000; Robertson *et al.*, *in prep*). We repeated all analyses with all instances of
194 the previous occupant being the mother excluded ($n = 30, 69$ and 65 for both types of cone,
195 parturition dates and LRS respectively). Those results are qualitatively similar to the ones we present
196 here, and so we present them in the supplementary materials (Tables S1-4).

197

198 Data analysis

199 We used mixed-effect models to determine the effects of the previous occupant on current cone
200 hoard estimates, parturition dates and LRS. This involved four linear models, either with the old cone
201 hoard size, new cone hoard size, parturition date or LRS as the response variable, all fitted in R using
202 the package “MCMCglmm” (Hadfield 2010).

203 For the models of both types of cone hoard and parturition dates, we included the random
204 effect of squirrel identity, since some squirrels had multiple measurements of hoard sizes and
205 parturition dates. Given we also included a term to estimate the additive genetic variance (which
206 was negligible for cone hoard size, see supplementary materials), this allowed us to also estimate
207 permanent environment effects (where individuals are consistently different from one-another, but
208 for reasons not due to additive genetic differences or other variables included in the model). In
209 every model we also fitted the identity of the previous owner as an additive genetic effect, which
210 allowed us to estimate variance in indirect genetic effects from previous midden owners. These
211 were always very close to zero and are discussed in the supplementary materials. We also used the
212 pedigree to calculate the genetic relatedness between the territory owner and the previous
213 occupant (r). We included in all models the random effect of year, to account for year-to-year
214 variations in the traits at the population level.

215 We added a different set of fixed effects to each model to control for contemporary factors
216 (traits of the current occupant and environmental influences) that might influence the traits. To the
217 models of old and new cone hoard sizes, we included the current occupant’s sex, age, study area,
218 and the linear effect of year. Within an individual's lifetime, cone hoards have been shown to
219 increase and then decrease (Haines 2017). We therefore estimated a different relationship between
220 hoard sizes and age before and after the approximate age of peak cone hoard sizes by including a
221 term for whether the squirrel was older than three years or not (approximately the age of peak cone
222 hoards), and the interaction between this term and age. Fitting two relationships like this is

223 preferable to using age² to detect initial increases followed by decreases (Simonsohn 2018; e.g. due
224 to senescence) although the results for models in which age was fitted as a quadratic term instead
225 led to similar conclusions (not shown). For parturition date, we included the occupant's age in years
226 as a categorical variable (with 7- and 8-year olds, the oldest, grouped together), to account for non-
227 linear trends (typically late parturition dates as a yearling breeder and potential senescent delays in
228 old age), the individual's study area, and a linear effect of year. For LRS we included the individual's
229 study grid, a linear effect of year, and whether the individual experienced a "mast year" (when
230 spruce trees produce a super abundance of cones; Kelly 1994; LaMontagne & Boutin 2007) or not in
231 their lifetime, as this has been shown to greatly increase LRS (Descamps *et al.* 2008; Hämäläinen *et*
232 *al.* 2017).

233 To investigate whether the previous occupant influenced the traits of the current owner, in
234 all models we included the sex and lifespan of the previous owner as fixed effects, with separate
235 relationships for lifespan of the previous owner below and above three years of age. We included
236 sex of the previous owner because males have been found to cache more and have larger hoards
237 (Donald & Boutin 2011; Archibald *et al.* 2013), which could influence the next owner of the territory.
238 We also included the interaction between these traits of the previous owner and the time in years
239 between the current and previous owners, because we predicted that previous occupants farther in
240 the past should affect the current occupant less. We also included the main effect of this lapsed
241 time, which represented the length of time the midden was unoccupied before the current
242 occupant. As unoccupied middens will have their stored cones gradually removed by other red
243 squirrels, we expected larger values of this lapsed time to be associated with smaller old cone
244 hoards, later parturition dates, and lower LRS estimates.

245 For cone hoards and LRS we used a Poisson error-structure with a log-link function, an
246 inverse Gamma prior for each random effect ($V = 1$, $\nu = 0.002$, chosen to be non-informative), and
247 500,000 iterations, with the first 10,000 discarded, and 1/40 of the remaining iterations kept, to
248 form the posterior distributions. For parturition date, we used the same specifications, except a
249 normal error structure and link function. For all models, we standardised each continuous predictor
250 by subtracting the mean and dividing by the standard deviation, which improves model convergence
251 and interpretability of regression coefficients (Schielzeth 2010). We also scaled parturition dates in
252 this way, but not cone hoard sizes or LRS, as this transformation gives negatives and non-integers,
253 unsuitable for Poisson models. Importance of terms was judged by the distance of the mode of the
254 posterior distribution from zero, and the spread of the 95% credible intervals. Successful
255 convergence was assessed with Heidelberger and Welch's convergence diagnostic (Heidelberger &

256 Welch 1983), while we performed three runs of each model to ensure different chains reached the
257 same qualitative result.

258

259 Results

260

261 Males have larger hoards and leave more cones for the next territory owner, thereby
262 influencing resource-dependent traits of the next occupant

263 The sex of the previous midden owner had important consequences for the current midden owner,
264 which acted through the extended phenotype of the size of the hoard. Males hoarded more new
265 cones, (coefficient plots for all models are given in Fig. 1). This effect on hoard size carried over to
266 the next owner of the midden. If the previous midden owner was a male, the current occupant had a
267 larger old cone hoard (Figs. 1a & 2a), an earlier parturition date (Figs. 1c & 2b, although this effect
268 marginally overlapped zero), and a higher LRS (Figs. 1d, 2c). For example, if the previous owner was
269 male rather than female, the current occupant is expected to acquire a midden with an extra 1318
270 old cones. If each cone contains an average of 2.53 kJ (Fletcher *et al.* 2010), this equates to an
271 additional 3337 kJ. Furthermore, a female that acquired her midden from a male would give birth
272 2.26 days earlier on average, and have 0.59 more offspring survive to 200 days over her lifetime than
273 a female that acquired her midden from another female. As expected, this effect of the sex of the
274 previous occupant on the size of the old cone hoard weakened with increasing number of years
275 between the current and previous owner (Fig. 1a). Surprisingly, the effect of whether the previous
276 owner was a male on LRS was enhanced with increasing time between the previous and current
277 owner (although this effect marginally overlapped zero; Fig 1d).

278

279 Mid-aged squirrels have larger hoards and leave more cones for the next territory
280 owner

281 We found that the lifespan of the previous midden owner influenced the current midden owner
282 through hoard size. Within the lifetime of current owners, old and new cone hoard sizes both
283 showed no initial increase before three years of age, and then declined with age for squirrels that
284 were older than three years (Fig. 3a & b). Concurrent with this late-life decline in hoard size, red
285 squirrels that lived longer than three years of age left fewer old cones to the next occupant of the
286 territory the longer they lived (Fig. 3c). We also found that parturition dates were later if the
287 previous occupant lived longer, with no change in this relationship pre- and post- three years of age
288 (Fig. 3d). Note, however, that each of these effects slightly overlapped zero, suggesting they should

289 be interpreted with caution. Parturition dates were also latest in yearlings, earliest at ages 5 and 6,
 290 and tended to be later at ages 7 and 8. LRS was unaffected by the age of the previous owner.

291 While not of direct interest to this study, contemporary effects on traits remained.
 292 Individuals had a higher LRS if they experienced a mast year in their lifetime. Old but not new cone
 293 hoards were smaller and parturition dates later on one study area (Sulphur) compared to the other
 294 (Kloo), but LRS was not different. No trait showed a consistent change across years, while LRS was
 295 lower the longer the midden had been unoccupied (although this effect marginally overlapped zero.
 296 The model intercept and estimates of the variance components are given in Table 1.

297 Repeating these analyses after removing instances in which the previous owner was the
 298 squirrel's mother, did not qualitatively change the results (see Supplementary materials, Tables S1-
 299 4). Estimates of direct genetic variance for cone hoard sizes were negligible, and so it is not
 300 surprising that we did not detect any indirect genetic effects from the previous owner for any trait
 301 (see Supplementary materials, Table S5). Including cases where the previous owner was the mother,
 302 the relatedness between the previous and current midden owner was 0.092, 0.110 and 0.085 for
 303 both types of cone, parturition dates and LRS respectively.

304
 305 Table 1. Model intercept and variance component estimates for each model. For variance
 306 components, we give the posterior distribution mode, with the 95% credible intervals in
 307 parentheses. "NA" indicates the term was not estimated in the model. Note the "Year" term in the
 308 LRS model is birth year, whilst in the other models it is the year the trait was expressed.

Trait	Model intercept	Permanent environmental	Year	Residual
Old cones	6.91	0.007	2.078	3.230
		(< 0.001 to 1.068)	(0.442 to 16.85)	(1.967 to 4.912)
New cones	1.82	0.007	43.13	6.153
		(< 0.001 to 2.365)	(9.974 to 713.7)	(3.026 to 9.155)
Parturition date	0.609	<0.001	0.714	0.199
		(<0.001 to 0.032)	(0.386 to 1.408)	(0.158 to 0.252)
LRS	-0.494	NA	0.263	0.004
			(0.074 to 0.824)	(< 0.001 to 1.265)

309
 310 Discussion

311
 312 Indirect effects have been suggested to play a "special role" in evolution (Bailey *et al.* 2018), as they
 313 cause individuals to influence each other's phenotypes and fitness (Griffing 1967; Scott 1977; Moore

314 *et al.* 1997). Here we have documented that indirect effects can occur between organisms that often
315 never meet and may not even have been alive at the same time, facilitated through an extended
316 phenotype. Extended phenotypes have received much theoretical interest since Dawkins (Dawkins
317 1978, 2004, Jones *et al.* 1994, 1997; Sterelny *et al.* 1996; Jablonka 2004; Turner 2004; Hunter 2009;
318 Bailey 2012), but extending empirical work to a range of systems has lagged behind. Individuals of
319 many species hold territories that they may modify, for instance by digging out burrows (Weber *et*
320 *al.* 2013; Metz *et al.* 2017), building nests (Perna & Theraulaz 2017) or caching resources within
321 them (Larivée *et al.* 2010). Additionally, organisms may alter the environment by constructing some
322 structure in it, such as a spider's web (Blamires *et al.* 2017a, b), or leave scent cues to be detected by
323 others (Cisterne *et al.* 2014). Therefore, there is the potential for effects mediated by these
324 extended phenotypes to be widespread throughout the natural world, yet our study is the first to
325 quantify influences on life-history traits and fitness of other individuals mediated through an
326 extended phenotype.

327

328 Sex of previous owner influences cone hoards, parturition dates and fitness

329 If the previous owner of the territory was a male, current occupants had earlier parturition dates
330 and higher LRSs, due to acquiring larger hoards of old cones. We expect this is applicable more
331 broadly, hence any trait which is related to how much an organism alters its environment might be
332 expected to predict how much it influences other organisms indirectly. Often, only one sex of a
333 species controls a territory, builds a nest, or engages in some form of environmental manipulation. It
334 is therefore only this sex which is expected to exert indirect effects through these environmental
335 changes, and anything which alters the survival and so relative prevalence of this sex, or its
336 distribution in the environment, will alter the influence of these indirect effects.

337 Finding more cones in middens previously owned by males appears to suggest that males
338 hoard more cones than females, then fail to use them, as they are still present for the next occupant.
339 Male energy expenditure during the mating season is approximately as high as female energy
340 expenditure during lactation (Lane *et al.* 2010), so it is unlikely that males simply do not need to use
341 these resources to fuel reproduction. Instead, males may hoard more as hoard size is related to the
342 number of offspring they sire in the spring, which is not true for females (Haines 2017). Over-winter
343 mortality would prevent males from consuming these additional cones during the mating season
344 (males are more likely to die over winter than females; LaMontagne *et al.* 2013; Fisher *et al.* 2017),
345 leaving the larger hoard for the next owner. We also found that males did not have larger old cone
346 stores, which might seem to contradict the general findings that they have larger cone hoards.

347 However, this can be explained by the fact that we used only the first instance of holding a territory
348 for each squirrel, so males likely have not yet had time to enlarge their hoard of old cones.

349 If male red squirrels leave behind more resources, it makes it beneficial for a juvenile
350 squirrel to settle at a territory that had previously been held by a male to take advantage of the
351 extra resources. This is generally true for any case of environmental manipulation: it would be
352 advantageous for other organisms to detect and exploit any changes made by others. In the case of
353 squirrels, we do not believe there to be any choice in where a juvenile squirrel settles, because the
354 availability of territories is often very limited, with competition for them intense (Price & Boutin
355 1993; Larsen & Boutin 1994), especially in years of high density (Williams *et al.* 2014; Fisher *et al.*
356 2017). Vacant territories tend to be filled quickly (Boutin & Schweiger 1988), but we do not know
357 which traits of juveniles predict success in competing for them (Robertson *et al. in prep*). The
358 previous occupant of a territory might, therefore, be stochastic, although this may not be true in
359 other systems. Ultimately, this effect of the previous owner will still have consequences for the
360 fitness of the current occupant, and so a portion of the variance in reproductive success of a
361 population can be attributed to the caching behaviour of now-dead individuals. The effects of the
362 previous owner on fitness, therefore, have the potential to have interesting effects on the
363 distribution of fitness in a population (discussed below).

364
365 Largest hoards passed on by previous owners of intermediate age

366 We found that cone hoard sizes decreased beyond three years of age. This suggests that the ability
367 to find and/or cache cones declines in old age and is perhaps an example of a senescent decline.
368 Phenotypic senescence is increasingly commonly found in natural populations (Nussey *et al.* 2013),
369 and has been detected in this study system before (McAdam *et al.* 2007; Descamps *et al.* 2008),
370 including for cone hoard size (Haines 2017). This senescence in the stored resources an individual
371 has access to is analogous to senescence in fat reserves in organisms that store energy on their
372 bodies (“capital breeders” Jönsson 1997). This demonstrates senescence is a general phenomenon
373 that even extends beyond the commonly considered case of “performance” traits such as body mass
374 or clutch size, to include an extended phenotype, and so should be considered in other situations
375 where individuals alter their environment.

376 Additionally, the late-life decline in off-body resources has, unlike fat stores, consequences
377 for genetically unrelated individuals that did not physically interact with the focal individual:
378 subsequent owners. The size of the old cone hoard of the current owner tended to be lower if they
379 acquired a territory from a longer-lived squirrel. This demonstrates that it would be best to acquire a
380 territory from an individual that died in the prime of their life, but this is also the age when red

381 squirrels are least likely to die (Descamps *et al.* 2007). For the same reasons as described above for
382 sex, we think red squirrel juveniles have limited ability to choose the territory they first settle on,
383 and so would not be able to seek-out middens of prime-aged squirrels. Still, any factor that shortens
384 individuals' lives, and so causes individuals to die nearer the age of peak hoard size, should increase
385 the number of cones passed on to subsequent owners, the implications of which remain to be
386 explored.

387

388 Phenotypic effects not underpinned by genotypic effects

389 We estimated very low direct additive genetic variance in both old and new cone hoard sizes (see
390 Supplementary materials). Since individuals did not possess genetic variance for hoard size, it was
391 not surprising that we did not find any indirect genetic variance in their effects on the parturition
392 date or LRS of the next owner of the territory. There was, however, a modest amount of variance for
393 the indirect genetic effect on old cone hoard size, although the credible intervals were very close to
394 zero. These indirect genetic effects, might, therefore, provide a mechanism by which hoard size
395 could evolve despite the absence of direct genetic effects of hoard size. The broad confidence
396 intervals in our indirect genetic variance estimate, however, suggest caution in this interpretation.
397 Further investigation of indirect genetic effects acting through extended phenotypes is needed to
398 determine whether they provide a general route through which traits lacking direct genetic variance
399 could evolve.

400

401 Whose phenotype is it anyway?

402 The indirect effects from previous owners that we have identified have the potential to influence
403 evolutionary processes. While we estimated that indirect genetic effects acting through the previous
404 midden owner were very small (see Supplementary materials) for resource dependent traits and
405 fitness, we still estimated phenotypic effects of previous owners on these traits. This means that
406 evolutionary change will conform less well to models of evolution that only consider contemporary
407 effects, as past individuals can influence current traits and fitness. Since stored resources in this
408 system depend on the masting of spruce trees, past environments can influence contemporary
409 resource dependent traits, requiring us to possibly model these ecological "memory" effects to
410 understand trait distributions (Filotas *et al.* 2014). Maternal effect models of evolution might be
411 useful here, as such models incorporate a lag in evolutionary change (Kirkpatrick & Lande 1989),
412 something which may be occurring here. Quantifying how past environments, past individuals and
413 historical selection can influence contemporary traits, and the consequences of this for ecological

414 and evolutionary processes is an exciting next step for this line of research to take. In general, a
415 given individual's phenotype, and even its fitness, might only partly be under direct control, and
416 some aspects of its phenotype may be influenced by individuals with whom it has not directly
417 interacted through extended phenotypes.

418 419 Conclusions

420 Due to an extended phenotype, the food hoard size, the date of spring breeding, and the lifetime
421 reproductive success of a red squirrel currently occupying a territory are influenced by the previous
422 owner of the territory. This means that key traits, and even the fitness of an individual, are not
423 under its direct influence but are influenced by previous individuals, and so possibly previous
424 environments. A greater appreciation of what can be considered extended phenotypes, including
425 the phenotypes of individuals when they interact with others, and their quantitative genetic
426 underpinnings, will give us a greater appreciation of how these traits influence the ecology and
427 evolution of populations.

428 429 Figure legends

430 Figure 1. Coefficient plots displaying estimated means and 95% credible intervals (CRIs) of the
431 models for a) old cone hoards, b) new cone hoards, c) parturition dates (note negative values
432 indicate earlier dates) & d) lifetime reproductive success. As the study area "Kloo" was the default,
433 the effect of study area is how the trait mean differs on "Sulphur". "Age" refers to the effect of age
434 of the current occupant on the trait, while "Post-peak:Age" refers to the additional effect of age
435 when the individual was older than 3 years. "Post-peak mean" indicates whether traits in individuals
436 older than 3 had different means. "Previous sex" indicates the additional effect of the previous
437 owner being a male, with it being a female the default. "Previous lifespan (PL)" refers to the previous
438 occupant's lifespan, while "PL:above 3" refers to the additional effect of this lifespan if it was above
439 3 years. "PL above 3 mean" indicates whether traits in individuals where the previous territory
440 occupant lived longer than 3 years had different means. "Lapsed time" is the time period between
441 the previous and current occupant; it is interacted with each trait of the previous occupant (e.g.
442 "Previous sex:lapsed time"). For new cone hoards the x-axis has been truncated to display the
443 effects nearer zero; the CRIs for the effect of year were -13.8 to 9.3.

444

445 Figure 2 a) Old cone hoards were larger when the previous occupant was a male. Old cone hoards
446 have been ln-transformed to improve viewability. b) Parturition dates (days since start of year, with

447 1st January as 1) tended to be earlier when the previous owner was a male. c) Estimated LRS was
448 higher when the previous owner was a male. Notches in a & b indicate 95% confidence intervals of
449 the median (the thick black bar in all plots).

450

451 Figure 3a) Old cone hoards declined with age in squirrels older than three years. b) New cone hoards
452 declined with age in squirrels older than three years. c) Cone hoards were largest if the territory was
453 acquired from an individual of intermediate lifespan and declined if the previous owner lived beyond
454 three years. d) Parturition dates (days since start of year, with 1st January as 1) were later the long
455 the previous individual lived. For all plots cone hoards have been logged to improve viewability.

456

457 Acknowledgements

458 We thank Agnes MacDonald for long-term access to her trapline, and to the Champagne and Aishihik
459 First Nations for allowing us to conduct work on their traditional territory. We thank all the
460 volunteers, field assistants and graduate students whose tireless work makes the KRSP possible. We
461 also thank Andrea Wishart for providing helpful comments on a draft of this manuscript. Funding for
462 this work was provided by the Natural Sciences and Engineering Research Council, the Ontario
463 Ministry for Research and Innovation, and the National Science Foundation. We have no conflicts of
464 interest. This is KRSP paper number XX.

465

466 References

467

- 468 Archibald, D.W., Fletcher, Q.E., Boutin, S., McAdam, A.G., Speakman, J.R. & Humphries, M.M. (2013).
469 Sex-specific hoarding behavior in North American red squirrels (*Tamiasciurus hudsonicus*). *J.*
470 *Mammal.*, 94, 761–770.
- 471 Bailey, N.W. (2012). Evolutionary models of extended phenotypes. *Trends Ecol. Evol.*, 27, 561–569.
- 472 Bailey, N.W., Marie-Orleach, L., Moore, A.J. & Simmons, L. (2018). Indirect genetic effects in
473 behavioral ecology: does behavior play a special role in evolution? *Behav. Ecol.*, 29, 1–11.
- 474 Berteaux, D. & Boutin, S. (2000). Breeding dispersal in female North American red squirrels. *Ecology*,
475 81, 1311–1326.
- 476 Blamires, S.J., Hasemore, M., Martens, P.J. & Kasumovic, M.M. (2017a). Diet-induced co-variation
477 between architectural and physicochemical plasticity in an extended phenotype. *J. Exp. Biol.*,
478 220, 876–884.

479 Blamires, S.J., Martens, P.J. & Kasumovic, M.M. (2017b). Fitness consequences of plasticity in an
480 extended phenotype. *J. Exp. Biol.*, jeb.167288.

481 Boutin, S., Larsen, K.W. & Berteaux, D. (2000). Anticipatory parental care: acquiring resources for
482 offspring prior to conception. *Proc. R. Soc. B Biol. Sci.*, 267, 2081–2085.

483 Boutin, S. & Schweiger, S. (1988). Manipulation of intruder pressure in red squirrels (*Tamiasciurus*
484 *hudsonicus*): effects on territory size and acquisition. *Can. J. Zool.*, 66, 2270–2274.

485 Cisterne, A., Vanderduys, E.P., Pike, D.A. & Schwarzkopf, L. (2014). Wary invaders and clever natives:
486 sympatric house geckos show disparate responses to predator scent. *Behav. Ecol.*, 25, 604–611.

487 Dawkins, R. (1978). Replicator selection and the extended phenotype. *Z. Tierpsychol.*, 47, 61–76.

488 Dawkins, R. (1982). *The Extended Phenotype*. Oxford University Press, Oxford.

489 Dawkins, R. (2004). Extended phenotype - But not too extended. A reply to Laland, Turner and
490 Jablonka. *Biol. Philos.*, 19, 377–396.

491 Descamps, S., Boutin, S., Berteaux, D. & Gaillard, J.-M. (2008). Age-specific variation in survival,
492 reproductive success and offspring quality in red squirrels: evidence of senescence. *Oikos*, 117,
493 1406–1416.

494 Descamps, S., Boutin, S., Berteaux, D. & Gaillard, J.M. (2007). Female red squirrels fit Williams’
495 hypothesis of increasing reproductive effort with increasing age. *J. Anim. Ecol.*, 76, 1192–1201.

496 Dewan, I., Garland, T., Hiramatsu, L. & Careau, V. (2018). I smell a mouse: Indirect genetic effects on
497 voluntary wheel-running distance, duration and speed. *Behav. Genet.*, 1–11.

498 Donald, J.L. & Boutin, S. (2011). Intraspecific cache pilferage by larder-hoarding red squirrels
499 (*Tamiasciurus hudsonicus*). *J. Mammal.*, 92, 1013–1020.

500 Filotas, E., Parrott, L., Burton, P.J., Chazdon, R.L., Coates, K.D., Coll, L., *et al.* (2014). Viewing forests
501 through the lens of complex systems science. *Ecosphere*, 5, 1–23.

502 Fisher, D.N., Boutin, S., Dantzer, B., Humphries, M.M., Lane, J.E. & McAdam, A.G. (2017). Multilevel
503 and sex-specific selection on competitive traits in North American red squirrels. *Evolution (N.*
504 *Y.)*, 71, 1841–1854.

505 Fletcher, Q.E., Boutin, S., Lane, J.E., LaMontagne, J.M., McAdam, A.G., Krebs, C.J., *et al.* (2010). The
506 functional response of a hoarding seed predator to mast seeding. *Ecology*, 91, 2673–2683.

507 Griffing, B. (1967). Selection in reference to biological groups. I. Individual and group selection
508 applied to populations of unordered groups. *Aust. J. Biol. Sci.*, 20, 127–39.

509 Gunn, M.R., Dawson, D.A., Leviston, A., Hartnup, K., Davis, C.S., Strobeck, C., *et al.* (2005). Isolation
510 of 18 polymorphic microsatellite loci from the North American red squirrel, *Tamiasciurus*
511 *hudsonicus* (Sciuridae, Rodentia), and their cross-utility in other species. *Mol. Ecol. Notes*, 5,
512 650–653.

513 Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models : The
514 MCMCglmm R package. *J. Stat. Softw.*, 33, 1–22.

515 Haines, J.A. (2017). Resources and reproductive trade-offs affect fitness, life history traits, and sexual
516 selection in red squirrels. University of Alberta.

517 Hämäläinen, A., McAdam, A.G., Dantzer, B., Lane, J.E., Haines, J.A., Humphries, M.M., *et al.* (2017).
518 Fitness consequences of peak reproductive effort in a resource pulse system. *Sci. Rep.*, 7, 9335.

519 Hatt, R.T. (1929). The red squirrel: Its life history and habits, with species reference to the
520 Adirondacks of New York and the Harvard Forest. *Roosevelt Wildl. Ann.*, 2, 11–146.

521 Heidelberger, P. & Welch, P.D. (1983). Simulation run length control in the presence of an initial
522 transient. *Oper. Res.*, 31, 1109–1144.

523 Hunter, P. (2009). Extended phenotype redux. How far can the reach of genes extend in
524 manipulating the environment of an organism? *EMBO Rep.*, 10, 212–5.

525 Jablonka, E. (2004). *From Replicators to Heritably Varying Phenotypic Traits: The Extended Phenotype*
526 *Revisited. Biol. Philos.*

527 Jones, C.G., Lawton, J.H. & Shachak, M. (1994). Organisms as ecosystem engineers. In: *Ecosystem*
528 *Management*. Springer New York, New York, NY, pp. 130–147.

529 Jones, C.G., Lawton, J.H. & Shachak, M. (1997). Positive and negative effects of organisms as physical
530 ecosystem engineers. *Ecology*, 78, 1946–1957.

531 Jönsson, K.I. (1997). Capital and income breeding as alternative tactics of resource use in
532 reproduction. *Oikos*, 78, 57.

533 Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends Ecol. Evol.*, 9, 465–470.

534 Kerr, T.D., Boutin, S., LaMontagne, J.M., McAdam, A.G. & Humphries, M.M. (2007). Persistent
535 maternal effects on juvenile survival in North American red squirrels. *Biol. Lett.*, 3, 289–291.

536 Kirkpatrick, M. & Lande, R. (1989). The evolution of maternal characters. *Evolution (N. Y.)*, 43, 485–
537 503.

538 Laidre, M.E. (2012). Niche construction drives social dependence in hermit crabs. *Curr. Biol.*, 22,
539 R861–3.

540 LaMontagne, J.M. & Boutin, S. (2007). Local-scale synchrony and variability in mast seed production
541 patterns of *Picea glauca*. *J. Ecol.*, 95, 991–1000.

542 LaMontagne, J.M., Williams, C.T., Donald, J.L., Humphries, M.M., McAdam, A.G. & Boutin, S. (2013).
543 Linking intraspecific variation in territory size, cone supply, and survival of North American red
544 squirrels. *J. Mammal.*, 94, 1048–1058.

545 Lane, J.E., Boutin, S., Gunn, M.R., Slate, J. & Coltman, D.W. (2007). Genetic relatedness of mates
546 does not predict patterns of parentage in North American red squirrels. *Anim. Behav.*, 74, 611–

547 619.

548 Lane, J.E., Boutin, S., Speakman, J.R. & Humphries, M.M. (2010). Energetic costs of male
549 reproduction in a scramble competition mating system. *J. Anim. Ecol.*, 79, 27–34.

550 Lane, J.E., McAdam, A.G., Charmantier, A., Humphries, M.M., Coltman, D.W., Fletcher, Q., *et al.*
551 (2015). Post-weaning parental care increases fitness but is not heritable in North American red
552 squirrels. *J. Evol. Biol.*, 28, 1203–12.

553 Larivée, M.L., Boutin, S., Speakman, J.R., McAdam, A.G. & Humphries, M.M. (2010). Associations
554 between over-winter survival and resting metabolic rate in juvenile North American red
555 squirrels. *Funct. Ecol.*, 24, 597–607.

556 Larsen, K.W. & Boutin, S. (1994). Movements, survival, and settlement of red squirrel (*Tamiasciurus*
557 *hudsonicus*) offspring. *Ecology*, 75, 214–223.

558 Larsen, K.W. & Boutin, S. (1995). Exploring territory quality in the North American red squirrel
559 through removal experiments. *Can. J. Zool.*, 73, 1115–1122.

560 McAdam, A.G., Boutin, S., Sykes, A.K. & Humphries, M.M. (2007). Life histories of female red
561 squirrels and their contributions to population growth and lifetime fitness. *Ecoscience*, 14, 362.

562 McFarlane, S.E., Lane, J.E., Taylor, R.W., Gorrell, J.C., Coltman, D.W., Humphries, M.M., *et al.* (2011).
563 The heritability of multiple male mating in a promiscuous mammal. *Biol. Lett.*, 7, 368–371.

564 Metz, H.C., Bedford, N.L., Pan, Y.L. & Hoekstra, H.E. (2017). Evolution and genetics of precocious
565 burrowing behavior in *Peromyscus* mice. *Curr. Biol.*, 27, 3837–3845.e3.

566 Moore, A.J., Brodie, E.D.I. & Wolf, J.B. (1997). Interacting phenotypes and the evolutionary process:
567 I. Direct and indirect genetic effects of social interactions. *Evolution (N. Y.)*, 51, 1352–1362.

568 Naiman, R.J., Melillo, J.M. & Hobbie, J.E. (1986). Ecosystem alteration of boreal forest streams by
569 beaver (*Castor canadensis*). *Ecology*, 67, 1254–1269.

570 Nussey, D.H., Froy, H., Lemaitre, J.-F., Gaillard, J.-M. & Austad, S.N. (2013). Senescence in natural
571 populations of animals: widespread evidence and its implications for bio-gerontology. *Ageing*
572 *Res. Rev.*, 12, 214–25.

573 Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. (2003). *Niche Construction: The Neglected Process*
574 *in Evolution*. Princeton University Press, Princeton.

575 Perna, A. & Theraulaz, G. (2017). When social behaviour is moulded in clay: on growth and form of
576 social insect nests. *J. Exp. Biol.*, 220, 83–91.

577 Posthumus, E.E., Koprowski, J.L. & Steidl, R.J. (2015). Red squirrel middens influence abundance but
578 not diversity of other vertebrates. *PLoS One*, 10, e0123633.

579 Price, K. & Boutin, S. (1993). Territorial bequeathal by red squirrel mothers. *Behav. Ecol.*, 4, 144–155.

580 Price, K., Broughton, K., Boutin, S. & Sinclair, A.R.E. (1986). Territory size and ownership in red

581 squirrels: response to removals. *Can. J. Zool.*, 64, 1144–1147.

582 Réale, D., McAdam, A.G., Boutin, S. & Berteaux, D. (2003). Genetic and plastic responses of a
583 northern mammal to climate change. *Proc. Biol. Sci.*, 270, 591–596.

584 Rosell, F., Bozsér, O., Collen, P. & Parker, H. (2005). Ecological impact of beavers *Castor fiber* and
585 *Castor canadensis* and their ability to modify ecosystems. *Mamm. Rev.*, 35, 248–276.

586 Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients.
587 *Methods Ecol. Evol.*, 1, 103–113.

588 Scott-Phillips, T.C., Laland, K.N., Shuker, D.M., Dickins, T.E. & West, S.A. (2014). The niche
589 construction perspective: a critical appraisal. *Evolution*, 68, 1231–43.

590 Scott, J.P. (1977). Social genetics. *Behav. Genet.*, 7, 327–346.

591 Simonsohn, U. (2018). Two-Lines: A valid alternative to the invalid testing of U-shaped relationships
592 with quadratic regressions. *SSRN Electron. J.*

593 Siracusa, E., Boutin, S., Humphries, M.M., Gorrell, J.C., Coltman, D.W., Dantzer, B., *et al.* (2017a).
594 Familiarity with neighbours affects intrusion risk in territorial red squirrels. *Anim. Behav.*, 133,
595 11–20.

596 Siracusa, E., Morandini, M., Boutin, S., Humphries, M.M., Dantzer, B., Lane, J.E., *et al.* (2017b). Red
597 squirrel territorial vocalizations deter intrusions by conspecific rivals. *Behaviour*, 154, 1259–
598 1273.

599 Smith, C.C. (1968a). The adaptive nature of social organization in the genus of three squirrels
600 *Tamiasciurus*. *Ecol. Monogr.*, 38, 31–64.

601 Smith, C.C. (1978). Structure and function of the vocalizations of tree squirrels (*Tamiasciurus*). *J.*
602 *Mammal.*, 59, 793–808.

603 Smith, C.C. (1981). The indivisible niche of *Tamiasciurus*: An example of nonpartitioning of resources.
604 *Ecol. Monogr.*, 51, 343–363.

605 Smith, M.C. (1968b). Red squirrel responses to spruce cone failure in Interior Alaska. *J. Wildl.*
606 *Manage.*, 32, 305–317.

607 Sterelny, K., Smith, K.C. & Dickison, M. (1996). The extended replicator. *Biol. Philos.*, 11, 377–403.

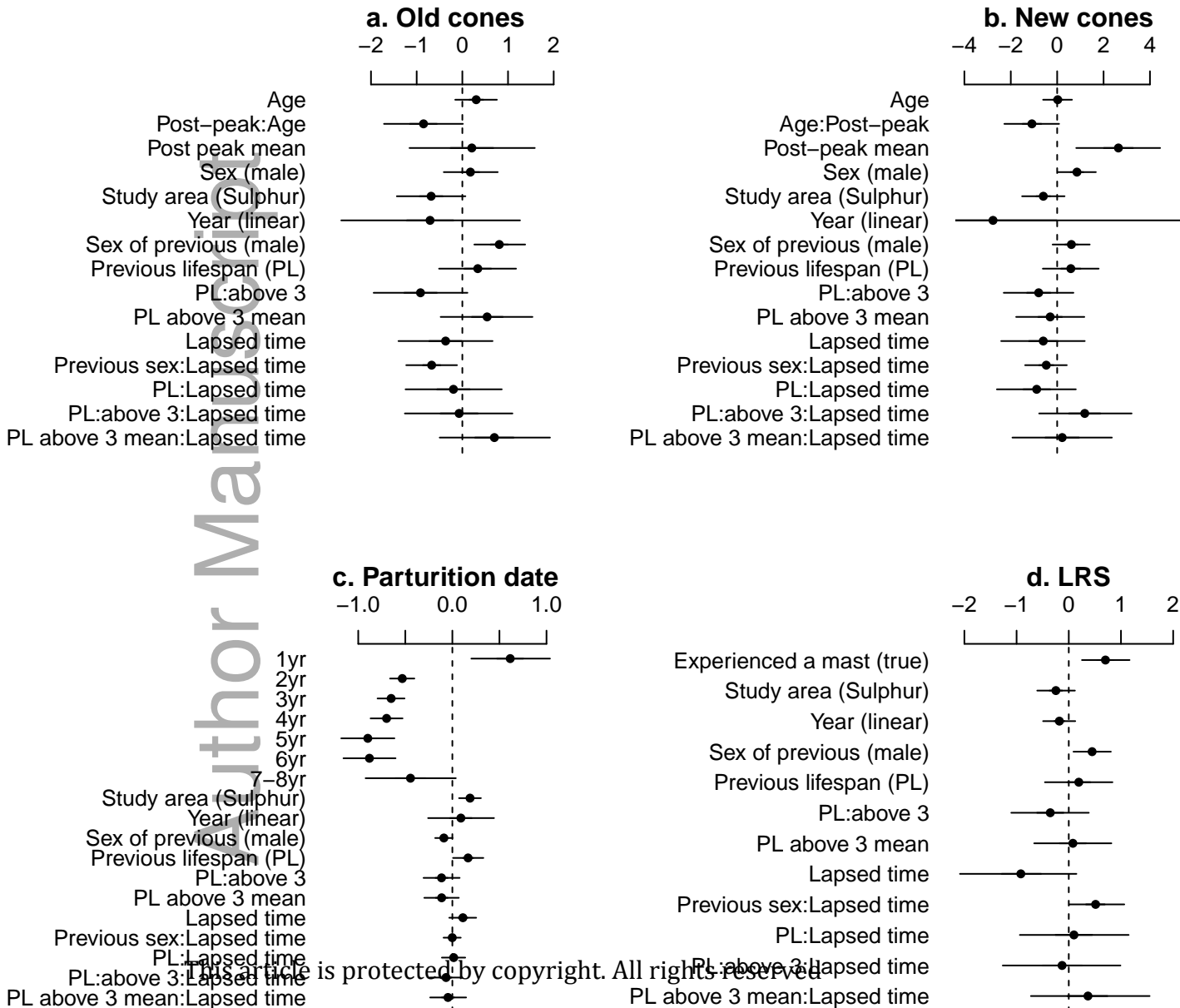
608 Thompson, L., Thomas, C.D., Radley, J.M.A., Williamson, S. & Lawton, J.H. (1993). The effect of
609 earthworms and snails in a simple plant community. *Oecologia*, 95, 171–178.

610 Turner, J.S. (2004). Extended phenotypes and extended organisms. *Biol. Philos.*, 19, 327–352.

611 Weber, J.N., Peterson, B.K. & Hoekstra, H.E. (2013). Discrete genetic modules are responsible for
612 complex burrow evolution in *Peromyscus* mice. *Nature*, 493, 402–405.

613 Williams, C.T., Lane, J.E., Humphries, M.M., McAdam, A.G. & Boutin, S. (2014). Reproductive
614 phenology of a food-hoarding mast-seed consumer: Resource- and density-dependent benefits

Author Manuscript



Author Manuscript

Sex of previous occupant

Sex of previous occupant

Sex of previous occupant

