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1 **Inter-annual and inter-individual variations in survival exhibit strong seasonality in a**
2 **hibernating rodent**

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12 **Keywords:** mark-recapture, *Tamias sibiricus*, seasonal survival, hibernation, male-biased
13 mortality

14 **Abstract:**

15 Most research on the demography of wild animal populations has focused on characterizing
16 the variation in the mortality of organisms as a function of intrinsic and environmental
17 characteristics. However, such variation in mortality is difficult to relate to functional life
18 history components (e.g. reproduction, dispersal, hibernation) due to the difficulty in
19 monitoring biological processes at a sufficiently fine timescale.

20 In this study, we used a 10-year individual-based data set with an infra-annual timescale to
21 investigate both intra- and inter-annual survival patterns according to intrinsic and
22 environmental covariates in an introduced population of a small hibernating rodent, the
23 Siberian chipmunk. We compared three distinct periods related to particular life history
24 events: spring reproduction, summer reproduction and hibernation. Our results revealed
25 strong interactions between intrinsic and temporal effects.

26 First, survival of male chipmunks strongly decreases during the reproduction periods, while
27 survival is high and equal between sexes during hibernation. Second, the season of birth
28 affects the survival of juveniles during their first hibernation, which does not have long-
29 lasting consequences at the adult stage. Third, at an inter-annual scale, we found that high
30 food resource availability before hibernation and low chipmunk densities specifically favour
31 subsequent winter survival. Overall, our results confirm that the well-known patterns of
32 yearly and inter-individual variation of mortality observed in animals are themselves strongly
33 variable within a given year, suggesting that they are associated with various functional
34 components of the animals' life history.

35 **Introduction**

36 The mortality risk faced by wild animals depends on their intrinsic conditions [e.g. age-related
37 experience, body condition, quality of immune system (e.g. Forslund and Part 1995;
38 Chantepie et al. 2015; Théoret-Gosselin et al. 2015)], their instantaneous energetic
39 requirements, which vary according to the life history component that they are experiencing,
40 such as reproduction or migration (e.g. Clutton-Brock 1988; Kirkwood and Rose 1991), and
41 their exposure to extrinsic sources of mortality [e.g. adverse climatic conditions, disease,
42 predation (e.g. Coulson et al. 2001)]. Thus, understanding the processes underlying mortality
43 requires characterization of the variations in the mortality of organisms as a function of their
44 characteristics (e.g. young vs. old, male vs. female), their conditions (e.g. spatial, or temporal
45 variation, e.g. habitat, resource availability) and their actions (e.g. foraging, breeding,
46 dispersing, migrating, hibernating, etc.), which requires in turn the monitoring of biological
47 processes at a sufficiently fine timescale (e.g. Grant et al. 2005; Kraus et al. 2008; Hardouin et
48 al. 2012, 2014). Recent demographic studies have shown that precise information on
49 individual statuses can be used to gain insight into the relationships between mortality and
50 some functional life history components. For example, the relationship between reproduction
51 and mortality can be approached through comparisons between the survival of breeders and
52 non-breeders using multi-state modelling (Robert et al. 2012). However, such approaches (1)
53 require data on individual statuses, which are often lacking; (2) do not allow for the study of
54 fine timing (e.g. seasonal pattern) of mortality if sampling is conducted at a larger timescale
55 (e.g. an annual time step); and (3) cannot be used if no variance exists within the population
56 with respect to the life history component of interest (e.g. if all individuals in the population
57 breed, migrate or hibernate).

58 In virtually all natural environments, the biology and ecology of organisms are affected by
59 climatic seasonality leading to seasonal variations in life history components and cyclicity in

60 iteroparous organisms that can live several years. In such species, a long-term survival
61 assessment conducted at an appropriate infra-annual timescale is a method of gaining insight
62 into the processes associated with mortality, notably by understanding (1) how intra-annual
63 patterns of mortality vary between seasons prominently associated with particular components
64 of the life history (e.g. breeding, migration, hibernation); (2) how specific seasonal variation
65 in biotic (e.g. abundance of resources, interspecific interactions) and abiotic factors (e.g.
66 changes in local meteorological conditions) affects patterns of mortality across seasons (e.g.
67 Aars and Ims 2002; Rödel et al. 2004); and (3) how these intra-annual variations contribute to
68 overall mortality and its inter-annual variation (e.g. Kraus et al. 2008; Kerbiriou et al. 2009;
69 Duriez et al. 2012; Leyrer et al. 2013; Noël et al. 2013; Radchuk et al. 2014).

70 In mammals, the energetic investment of reproduction is particularly important in females
71 during gestation and lactation (Gittleman and Thompson 1988), as well as in males in their
72 mating behaviour [including male–male competition, energy and time expenditure to locate
73 and mate with females (e.g. Lane et al. 2010)]. In relation to finite internal energy reserves
74 (Stearns 1989, 1992; Roff 1992), energy allocation to reproduction is predicted to be costly
75 and may involve fitness costs, such as a decrease in short- and long-term fecundity or survival
76 (e.g. Descamps et al. 2009; Hamel et al. 2010). Such investments and associated costs induce
77 a seasonality of breeding at the most energetically favourable periods, particularly in
78 temperate latitudes (Bronson 2009). The high-energy cost of reproduction events contrasts
79 with hibernation, which in temperate-zone mammals is generally regarded as an energy-
80 saving strategy to survive seasonal periods of energy shortage (harsh climatic condition, food
81 or water shortage), ensuing from pre-hibernal energy storage [body fat reserves and/or food
82 storage (Humphries et al. 2003)] and/or hibernal metabolic depression (Heldmaier 1989;
83 Wang 1989). Although physiological costs are involved in torpor and arousal patterns [e.g.
84 decreased immunocompetence (Prendergast et al. 2002)], the hibernation period seems to be

85 associated with high monthly survival probabilities over winter, compared with the active
86 season, and appears to have a positive effect on the lifespan of mammal hibernators
87 (Wilkinson and South 2002; Humphries et al. 2003; Turbill et al. 2011).

88 In the present study, we examine both intra- and inter- annual survival patterns in a small
89 iteroparous mammal, with an emphasis on three contrasting seasons related to particular life
90 history events: reproduction (two seasons), and hibernation. Although reproduction and
91 hibernation are hypothesized to affect the seasonal pattern of survival, surprisingly few
92 studies have attempted to assess the survival rates of free-living mammals during both the
93 active and hibernation seasons (e.g. Bieber et al. 2012; Bergeron et al. 2013). To tackle this
94 question, we analysed capture-mark-recapture data collected over 10 years, with an infra-
95 annual resolution, on the Siberian chipmunk (*Tamias sibiricus*), a small mammalian
96 hibernator introduced to an oak-hornbeam forest in France. In its introduced area, this species
97 is characterized by two reproductive seasons (in early spring and early summer) and a
98 hibernation period (from September–October to March); the beginning, the emergence and
99 the duration of these depend on individual age and sex, as well as environmental conditions in
100 which individuals hibernate in underground burrows with stored food [mainly tree seeds
101 (Chapuis et al. 2009)].

102 We first quantify the inter- and intra-annual variation in survival of the Siberian chipmunks in
103 relation to age and sex. Because the timing of births can affect survival (e.g. Feder et al.
104 2008), we examined whether spring-born and summer-born juveniles differ in their
105 probability to survive the first hibernation period, as well as in their survival rates as adults
106 (after the first winter). Second, we focus on the potential influence of environmental
107 conditions on seasonal patterns of survival, including the effects of local meteorological
108 conditions, food availability prior to hibernation, population density and winter groundwater
109 height, used as an index of potential death-related burrow flooding.

110 We predict that the mortality probability per unit of time will be lower during the hibernation
111 period than during the reproductive periods, and we test whether this seasonal pattern will be
112 influenced by age, sex and/or birth season. Because chipmunks do not rely on the same
113 resources in the different seasons, the inter-annual differences in survival are expected to vary
114 between seasons (i.e. we predict an interaction between seasons and years on survival).
115 Additionally, we hypothesize that food availability and chipmunk density before the
116 hibernation period, as well as the meteorological conditions and high groundwater height in
117 winter, are likely to influence survival during and immediately after hibernation (for resource
118 availability only).

119 **Material and methods**

120 *Study species*

121 Siberian chipmunks *Tamias sibiricus* are short-lived, ground-dwelling, solitary and sedentary
122 sciurids native to Asia that were introduced into Europe to be sold as pets from the 1960s
123 (Chapuis et al. 2009). Siberian chipmunk populations were observed a decade after their
124 introduction in several European suburban forests and urban parks, including 11 settled
125 populations recorded in France (Chapuis et al. 2009; Pisanu et al. 2013).

126 In France, chipmunks hibernate from September–October to February–March [the beginning
127 and duration of hibernation and an individual’s emergence depend on individual age and sex,
128 as well as environmental conditions (Chapuis et al. 2009)] and can reproduce twice a year.

129 They use a single burrow to hibernate and several burrows during the year. This promiscuous
130 species exhibits a scramble competition mating system with a mating season extending from
131 the hibernation emergence date until the first half of July with two peaks in births: one in the
132 spring (i.e. mainly in April with juveniles emerging from their birth burrow from May to early
133 June) and the second in the summer [i.e. mainly in July with emergence from late August to
134 September (Marmet et al. 2012)]. All juveniles were classified as either ‘spring-born’ or

135 'summer-born'. Regardless of the birth season, individuals become sexually mature in their
136 second year (after their first hibernation) without sexual size dimorphism. Consequently,
137 individuals were considered as adults the year following their birth. Before entering
138 hibernation, adults and juveniles stored food (tree fruits—*Quercus* spp., *Carpinus betulus*,
139 *Prunus avium*) within their burrows, providing energy reserves during the hibernation period,
140 characterized by repeated arousals from torpor (Chapuis et al. 2009). In the summer, the
141 chipmunk diet is wide ranging and mainly composed of insects (e.g. Coleoptera,
142 Lepidoptera), fruits (e.g. cherry, hazelnut, blackberry) and herb seeds (Chapuis et al. 2009).

143 *Study site and monitoring*

144 Population monitoring has been conducted since 2004 at the La Faisanderie site (14 ha;
145 48°39'N, 02°29'E), located in the temperate Sénart Forest (3200 ha), 22 km south-east from
146 Paris. The study area consisted of three main types of habitats: a 6-ha semi-open oak grove
147 (herbaceous layer, 90 %; shrubby layer, 5 %; arboreal layer, 60 % dominated by *Quercus*
148 *robur* and *Quercus petraea*), a 6.5-ha closed oak-hornbeam grove (herbaceous layer, 10 %;
149 shrubby layer, 30 %; arborescent layer, 90 % dominated by *Q. robur*, *Q. petraea*, and *C.*
150 *betulus*), and a mix of grassland and buildings representing an additional 1.5 ha (Marmet et al.
151 2009).

152 The population has been monitored using capture-mark-recapture methods. Throughout the
153 study site, chipmunks were live trapped in baited Sherman traps during their main activity
154 period from March to October. A grid consisting of 80 geo-localised traps was used in 2004
155 and was surrounded by 24 extra traps during the subsequent years [see description in Marmet
156 et al. (2009)]. Two monthly capture sessions were performed at 15-day intervals, each
157 consisting of 3 and 2 consecutive trapping days in 2004 and 3 and 5 consecutive days between
158 2005 and 2007. From 2008 onward, only a 5-day-long trapping session was conducted each
159 month. At first capture, individuals were ear tagged and implanted with a subcutaneous

160 transponder chip (Marmet et al. 2009). At each trapping event, the date and trap location were
161 recorded, as well as the chipmunk identity. Body mass, age (adult or juvenile, based on the
162 date of capture and body mass), birth season (spring-born or summer-born chipmunks) and
163 sex were also noted at the first capture of an individual in a trapping session. Some
164 individuals could not be aged and were assigned as undetermined for age and birth season.
165 After being handled, the chipmunks were released at their point of capture.

166 *Environmental factors*

167 Due to the lack of data at our study site prior to 2006, we used an ordinal mean acorn
168 production index in nearby forests covering the 2004–2013 period (National Forests Office,
169 unpublished data; Online Resource 1), which was related to both the oak fructification index
170 and the averaged spring acorn biomass in our study site (acorn index categories—0, none or
171 few acorns/small crop size; 1, medium; and 2, large crop size; Online Resource 1). Due to the
172 wide range of potential dietary items in summer, resource availability could not be quantified.
173 Therefore, spring temperatures were used as a cue to identify the availability of resources in
174 the summer because temperature is a main driver of many developmental processes, including
175 plant development (Badeck et al. 2004). Additionally, we used monthly mean temperatures
176 and precipitation (Météo-France data, Melun-Villaroche station), together with groundwater
177 height measured by piezometry (Bureau de Recherches Géologiques et Minières data,
178 Montereau-sur-le-Jard station), as proxies for local meteorological data as no data were
179 available for our study site in Sénart Forest, located approximately ca. 15 km away in a
180 northwesterly direction (Online Resource 1). From capture–recapture, the monthly densities
181 of chipmunks (adults and juveniles for each sex separately) in April, June, and July were
182 estimated from spatially explicit capture–recapture models [SECR (Efford et al. 2009)]. Age
183 and sex were accounted for in SECR models because of known distinct space use behaviours
184 (Marmet et al. 2009, 2011, 2012), which may have affected both capture probabilities and

185 movement scales. We also tested for individual learned response to specific traps (Marsot et
186 al. 2013), which has been found to be a consistent behaviour for chipmunks in our population
187 (Boyer et al. 2010; Le Coeur et al. 2015b). Estimated densities for each sex were then
188 summed for each age (Online Resource 1).

189 *Survival analysis using Huggin's robust design*

190 We analysed capture history data collected from 2004 to 2013 with Huggins's closed capture
191 models within the robust design framework (Huggins 1989; Kendall et al. 1997; Hines et al.
192 2003). All models were performed in the program MARK (White and Burnham 1999), which
193 was accessed through the R (R Core Team 2014) package RMark version 2.1.6-1 (Laake and
194 Rexstad 2014). This design provided a precise estimation of survival rates by controlling for
195 unbiased capture and recapture probabilities and taking temporary migration into account
196 (Kendall et al. 1997). Five parameters were estimated, including survival (S), first capture (p),
197 recapture (c), temporary emigration (γ'') and temporary immigration ($1 - \gamma'$) probabilities.
198 Unlike Pollock's (1982) robust design, abundance parameter (N) is computed as a derived
199 parameter (i.e. outside the likelihood) from estimated capture probabilities and observed data
200 (i.e. number of captures). One advantage of these models is that chipmunk hibernation can be
201 modelled as temporary emigration (see Kendall et al. 1997; Kendall and Bjorkland 2001).

202 In relation to important life history components (hibernation, first and second reproduction),
203 April, June and August were selected as three primary sessions per year. Each of these three
204 primary sessions consisted of 3 (in 2004) or 5 (from 2005) trapping days at the beginning of
205 each month, hereafter referred to as 'secondary trapping sessions'. Then, the full sampling
206 design was composed of 30 primary sessions involving 144 secondary trapping sessions,
207 resulting in 1962 capture records (recaptures of an individual occurring the same day were not
208 included) of 526 individually marked chipmunks (individuals with known age, sex and birth
209 season only; see details in Online Resource 1) during the 10-year monitoring study (2004–

210 2013). Six groups were defined according to the sex, age (juvenile or adult; individuals of
211 undetermined age were not considered) and birth season (spring-born or summer-born
212 individuals; individuals with unknown birth season, i.e. marked as adult or undetermined age,
213 were not considered) of chipmunks. Four hundred and ten chipmunks were marked as spring-
214 born juveniles and 116 as summer-born juveniles. In addition, inter- and/or intra-annual
215 variations (i.e. year, season and full-time variabilities) were tested as additive or interaction
216 terms for the five estimated parameters. Based on this model design, we defined three
217 seasons, spring (April–June), summer (June–August) and fall-winter (August–April). Because
218 a full interaction general model would be over-parameterised, the most general model that
219 was considered included interactive effects of year, season, sex, age and birth season for S , γ'
220 and $(1 - \gamma')$, interactive effects of session, sex and birth season for c , and interactive effects of
221 sex and birth season for p (see description and notations in Table 1). To allow for the
222 comparison of estimates between seasons, we specified uneven time intervals between
223 sampling occasions (expressed in numbers of months), such that S , γ' and γ'' are expressed as
224 monthly probabilities (unless specified otherwise). Parameters values are given as the mean \pm
225 SE.

226 Model selection was based on Akaike's information criterion adjusted for small sample size
227 (AICc) (Burnham and Anderson 2002). As a general approach, we started model selection by
228 testing temporal and group effects and their interaction on capture and recapture probabilities,
229 then used the most-parsimonious models of p and c to model the emigration parameters (γ'
230 and γ'') and finally S (the complete set of models tested is available in Online Resource 2).
231 Random and Markovian temporary emigration were both tested in this analysis [i.e. for
232 random and Markovian movement, respectively, the probability of moving between
233 availability states between primary occasions i and $i + 1$ is independent/conditional on the
234 state of the individual at time $i - 1$ (Kendall et al. 1997)].

235 *Goodness-of-fit testing*

236 Prior to model selection, the capture-mark-recapture data set was tested for any violations of
237 the assumptions under the robust design (see details in Online Resource 3). Both the closure
238 assumption within primary sessions (i.e. the population is assumed closed to additions and
239 deletions within a primary session) and the detection of individual heterogeneity in capture
240 probabilities were tested with the software CloseTest (Stanley and Burnham 1999) and
241 CAPTURE (Rexstad and Burnham 1992), respectively. Because goodness-of-fit (GoF) tests
242 have not been developed for the robust design, we used two different approaches to test the fit
243 of our data. First, the GoF of the general model was tested using the approach based on cell-
244 pooling contingency tests implemented in the software RDSURVIV (Kendall and Hines
245 1999). No overdispersion was revealed ($\hat{c} = 1$). Second, we tested the fit of data to an
246 open population model using U-CARE (Choquet et al. 2009), which indicated
247 ‘underdispersion’ ($\hat{c} = 0.45$). We thus applied a conservative approach for variance
248 adjustment (i.e., $\hat{c} = 1$; Online Resource 3) (Cooch and White 2014).

249 *Temporal covariates*

250 Starting from the most parsimonious model, we tested whether the variation in environmental
251 covariates including (1) local meteorological variables (based on mean seasonal temperatures
252 and precipitation during the three time intervals related to the sampling design), (2)
253 environmental conditions (groundwater height, resource availability from oak fructification
254 index), and (3) chipmunk densities (juveniles and adults), was related to the variation in
255 survival probabilities based on an analysis of deviance (ANODEV) (Skalski et al. 1993; see
256 models tested in Online Resource 4, with a significance threshold fixed at $\alpha = 0.05$). An
257 alternative model considering a composite covariate derived from a principal component
258 analysis on the three temporal covariates (oak fructification index, mean air temperature in

259 fall-winter and population density in July) was performed and yielded similar results (Online
260 Resource 5).

261 *Life expectancy*

262 Mean annual survival rates estimated for each age-class (juveniles and adults; a) were used to
263 estimate adult life expectancy depending on the sex and birth season (b) of chipmunks ($LE =$
264 $1/\ln(\phi_{(a*b+sex)}^{annual})$). Alternatively, more precise estimates of life expectancy at emergence
265 from the birth burrow were computed based on stochastic simulations, using monthly survival
266 estimates and taking into account the difference in the duration of the ‘juvenile stage’ between
267 spring-born and summer-born individuals (i.e. the time elapsed from emergence from their
268 birth burrow to the end of their first hibernation; all details presented in Online Resource 6).

269 **Results**

270 *Annual and seasonal patterns of survival*

271 The most parsimonious model [$S_{(seas*(year + sex) + b*a)} \gamma' \text{ and } \gamma''_{(seas \text{ markovian})} c_{(sess)} p_{(.)}$] revealed
272 constant capture probabilities over time ($p = 0.32 \pm 0.02$), temporal effects of season in
273 interaction with year on c , seasonal Markovian temporary migration rates (γ'' and γ'), and the
274 influence of birth season, age and their interaction with an additive effect of sex and year in
275 interaction with the seasons [i.e. $seas \times (year + sex) + b \times a$] on S (model 59; Table 2).

276 Survival probabilities fluctuated over seasons and years ($seas \times year$ interaction; Fig. 1), and
277 annual survival rates ranged from 0.17 ± 0.06 in 2012 to 0.69 ± 0.09 in 2005 (model 79) with
278 a mean of 0.28 ± 0.02 (model 93). We found no strong differences in inter-annual variation
279 among seasons, suggesting that the inter-annual pattern of survival was not shaped by a
280 specific, highly variable season between years.

281 The seasonal pattern of survival (expressed as monthly survival probability; Fig. 2a) was
282 characterized by high monthly winter survival (on average $S_{fall-winter} = 0.91 \pm 0.01$; model 94)

283 and slightly lowered survival throughout the active period ($S_{\text{spring}} = 0.88 \pm 0.03$, $S_{\text{summer}} = 0.87$
284 ± 0.04 ; model 94). The survival difference between the hibernation and breeding periods was
285 low, but considering distinct survival rates between spring and summer (on the one hand) and
286 winter (on the other) slightly improved model quality (compare, e.g. models 74 and 76 in
287 Table 2). Consequently, the probability of surviving the 8-month fall-winter season and the 4-
288 month active period was 0.47 ± 0.05 and 0.59 ± 0.06 , respectively.

289 This seasonality was strongly influenced by sex, age and birth season (Fig. 2b). At both the
290 juvenile (juv.) and adult (ad.) stages, males suffered high mortality in the summer ($S_{\text{spring-born}}$
291 $_{\text{juv.}} = 0.70 \pm 0.05$; $S_{\text{spring-born ad.}} = 0.75 \pm 0.05$ and $S_{\text{summer-born ad.}} = 0.78 \pm 0.04$; model 80),
292 whereas summer female mortality was low ($S_{\text{spring-born juv.}} = 0.93 \pm 0.05$; $S_{\text{spring-born ad.}} = 0.94 \pm$
293 0.04 and $S_{\text{summer-born ad.}} = 0.95 \pm 0.03$; model 80). Additionally, we found that juvenile
294 chipmunks had substantially lower survival probabilities than adults, regardless of their sex
295 (annual survival rate, $S_{\text{juv.}} = 0.23 \pm 0.03$ and $S_{\text{ad.}} = 0.32 \pm 0.03$; model 90). In juveniles, a
296 significant difference in the survival rates between spring-born and summer-born juveniles
297 occurred when both cohorts overlapped (fall-winter interval). We report a higher survival of
298 spring-born juveniles (0.90 ± 0.01 and 0.92 ± 0.02 for females and males, respectively) than
299 summer-born juveniles (0.81 ± 0.06 and 0.84 ± 0.05 for females and males, respectively;
300 model 80).

301 The sex-biased effect in adult survival was associated with notable sex differences in adult
302 life expectancy. The adult life expectancy was approximately 1 year for females and 9 months
303 for males. More precise estimates of life expectancy, computed at emergence from the birth
304 burrow and accounting for the birth season of individuals, revealed that the life expectancy at
305 emergence from the birth burrow ranges from 4.5 months for summer-born males to 10.5
306 months for spring-born females (details presented in Online Resource 6).

307 Recapture probabilities varied among primary sessions and ranged from 0.11 ± 0.03 in June
308 2010 to 0.80 ± 0.18 in April 2004 (model 5; see Online Resource 2, Table 2.2) with a mean of
309 0.38 ± 0.01 (model 16). During the 10-year study, the mean seasonal recapture probability
310 was lower in August ($c_{\text{August}} = 0.28 \pm 0.02$) than in April and June ($c_{\text{April}} = 0.41 \pm 0.02$ and
311 $c_{\text{June}} = 0.41 \pm 0.01$; model 12 Online Resource 2).

312 The average seasonal estimate of Markovian temporary emigration rate for animals present
313 during the previous period (γ'') was the lowest in spring and peaked during summer ($\gamma''_{\text{spring}} =$
314 0.12 ± 0.06 , $\gamma''_{\text{summer}} = 0.51 \pm 0.04$ and $\gamma''_{\text{fall-winter}} = 0.36 \pm 0.07$; model 59) whereas the
315 temporary emigration rates for animals absent in the previous primary session (γ') were higher
316 and similar between seasons ($\gamma'_{\text{spring}} = 0.49 \pm 0.10$, $\gamma'_{\text{summer}} = 0.63 \pm 0.12$ and $\gamma'_{\text{fall-winter}} = 0.55 \pm$
317 0.07 ; Model 59).

318 *Temporal covariates*

319 Temporal covariates, including the fructification index and the mean fall-winter temperatures,
320 were significantly correlated (linearly) with the fall-winter survival probabilities of
321 chipmunks [$R^2 = 54\%$, P -value = 0.02, model 103; $R^2 = 47\%$, P -value = 0.04, model 108;
322 Fig. 3; Online Resource 4]. A threshold was reached at the fructification index 1 (i.e. medium
323 quantity of acorns), from which survival was significantly higher than for index 0 (i.e. none or
324 few acorns). Additionally, we found that adult densities in April, June and July were slightly
325 negatively correlated with spring, summer and fall-winter survival, respectively ($R^2 = 13\%$,
326 P -value = 0.05, model 118; Fig. 4). These results suggest that higher resource availability
327 before hibernation, a warm winter and low chipmunk density favoured the probability to
328 survive the fall-winter. Spring temperatures, which are used to identify the availability of
329 resources in summer, are marginally related to summer survival ($R^2 = 41\%$, P -value = 0.06,
330 model 112). No other correlation was found (see ANODEV results and figures in Online
331 Resource 4).

332 **Discussion**

333 In iteroparous organisms that can live several years, the mortality risk is generally strongly
334 influenced by the sex and age of individuals, as well as by year-to-year environmental
335 variations including fluctuations in resources, meteorological conditions, competition,
336 predation and their interacting effects (e.g. Loison et al. 1999; Coulson et al. 2001). However,
337 such variation in mortality is difficult to relate to functional life history components due to the
338 difficulty in monitoring biological processes at a sufficiently fine timescale. Relying on
339 individual-based data collected at an infra-annual timescale in Siberian chipmunks, our study
340 uncovered strong relationships between overwinter survival and several environmental
341 factors, including resource availability, meteorological conditions and chipmunk density.
342 More generally, we provided original insights about survival variation during the reproduction
343 and hibernation periods and highlighted that strong sex-specific mortality occurs only at a
344 specific period of the year.

345 In the population of Siberian chipmunks, the seasonal pattern of survival is characterized by
346 high monthly winter survival (hibernation season, on average $S_{\text{fall-winter}} = 0.91 \pm 0.01$) and
347 slightly lower but comparable survival throughout the active period (breeding seasons, S_{spring}
348 $= 0.88 \pm 0.03$ and $S_{\text{summer}} = 0.87 \pm 0.04$, Model 94; Fig. 2a). Equally high winter survival of
349 adult chipmunks is observed, regardless of their sex and birth season. Although high monthly
350 winter survival has been observed previously in other hibernating mammals (Turbill et al.
351 2011), the seasonal pattern of chipmunk survival differs from those reported by previous
352 studies on small European hibernating mammals of similar size and with a comparable
353 duration of hibernation, such as the common dormouse, *Muscardinus avellanarius* (Bieber et
354 al. 2012) and the edible dormouse, *Glis glis* (Lebl et al. 2011). In such species, the survival
355 pattern was characterized by an increase in survival probabilities throughout the year, with the
356 lowest survival in the early active season, an increase in late summer and the highest survival

357 in winter. Moreover, in these species, as well as in the garden dormouse, *Eliomys quercinus*
358 (Schaub and Vaterlaus-Schlegel 2001), the probability of surviving the hibernation period
359 (monthly timescale) at the adult stage is close to unity, whereas in our population, the winter
360 survival probability, related to the fall and hibernation periods, is much lower, an average of
361 0.92 for adults. These differences can be attributed to distinct life histories in glirids compared
362 with Siberian chipmunks, related to the activity time (nocturnal in glirids), as well as the
363 energy storage strategy during hibernation (fat in glirids versus food hoarding in chipmunks).
364 Among closely related species, such as eastern, shadow and long-eared chipmunks, high
365 overwinter survival rates comparable to those of our population have been reported
366 [respectively, *Tamias striatus* (Bergeron et al. 2013), *Tamias senex* and *Tamias*
367 *quadrifasciatus* (Wilson et al. 2008)]. The seasonal pattern of survival (summer and winter
368 estimates) in the eastern chipmunk was also found to be similar to the pattern found in our
369 study (Bergeron et al. 2013).

370 Most importantly, we found that the seasonality of survival strongly differed between sexes.
371 Although male-biased mortality at a yearly time resolution was detected (in adults: $S_{\text{males}} =$
372 0.25 ± 0.03 , $S_{\text{females}} = 0.35 \pm 0.03$; Model 84), our results show that this sex difference only
373 occurs in summer. In adult females, we underline a similar survival pattern among seasons, as
374 found in the other small mammal hibernators previously cited (although with slightly lower
375 survival in the winter than in the late active period; in adult chipmunks: $S_{\text{spring}} = 0.86 \pm 0.03$,
376 $S_{\text{summer}} = 0.95 \pm 0.04$ and $S_{\text{fall-winter}} = 0.92 \pm 0.01$; Model 81). In contrast, males clearly suffer
377 from higher mortality in summer than in other seasons (in adults, $S_{\text{spring}} = 0.86 \pm 0.04$, S_{summer}
378 $= 0.77 \pm 0.04$ and $S_{\text{fall-winter}} = 0.93 \pm 0.01$; Model 81). This survival pattern was associated
379 with substantial differences in the adult life expectancies of males and females.

380 Higher mortality rates and shorter lifespans in males than in females are commonly observed
381 among mammal species (Neuhaus and Pelletier 2001; Clutton-Brock and Isvaran 2007; Kraus

382 et al. 2008). Various but interrelated hypotheses have been proposed to explain juvenile and
383 adult male-biased mortality: 1) Lower immunocompetence of males, which increases their
384 susceptibility to infectious disease and parasitism (Moore and Wilson 2002); 2) The costs of
385 sexual size dimorphism in the larger sex, usually males in polygynous or promiscuous
386 mammals (Promislow 1992; Moore and Wilson 2002); 3) The higher propensity of males to
387 engage in potentially risky behaviours, such as dispersal, sexual competition and roaming
388 (Greenwood 1980; Andersson 1994; Kraus et al. 2008); 4) The potential effects of deleterious
389 recessive alleles in the heterogametic sex (XY) (e.g. Libert et al. 2010) and 5) In polygynous
390 species with sexual size dimorphism, a high mortality of male juveniles in relation to a
391 biased mother's investment or adjustment of the sex of their offspring (Clutton-Brock et al.
392 1985; West and Sheldon 2002), which can also influence later adult mortality patterns
393 (Lindström 1999; Garratt et al. 2015).

394 In Siberian chipmunks, the difference in the observed pattern between male and female
395 survival may be primarily due to their specific mating system and associated behaviour. They
396 are monomorphic and exhibit a scramble-competition mating system with promiscuity
397 (Obolenskaya et al. 2009; Marmet et al. 2012), occurring from late February–March until the
398 first half of July. As a consequence, the hypotheses related to sexual size dimorphism effects
399 on juvenile and adult survival can be rejected. According to the scramble-competition mating
400 system, male–male competition is associated with high mate-searching efforts rather than
401 physical or aggressive behaviour (Lane et al. 2010). In our study population, male chipmunks
402 were found to increase their space use to increase their chances of meeting and fertilizing
403 females (Marmet et al. 2012). This activity (associated with both breeding and roaming
404 behaviours) can induce high energetic costs for males which may exceed the corresponding
405 cost of female gestation and lactation (e.g. Lane et al. 2010) and can increase their risk of
406 predation and parasitism exposure during the breeding season (e.g. Krasnov et al. 2005; Boyer

407 et al. 2010; Le Coeur et al. 2015a). The absence of sex difference in overwinter survival
408 suggests a prominent role of risk-based processes over energy-based explanations. The two
409 remaining and non-mutually exclusive hypotheses of costly sexual risky behaviour and
410 immunocompetence handicap may then explain the low survival of males, as reported at the
411 end of the mating season.

412 Among juveniles (i.e. non-reproductive individuals), lower male survival in summer was also
413 reported. Because no sexual size dimorphism was found and the sex ratio is balanced among
414 juveniles for both cohorts (from the capture–recapture data; Online Resource 1), we exclude
415 the hypothesis of a biased parental investment. Marmet et al. (2011) previously showed in the
416 study population that natal dispersal distances are farther in males than in females.
417 Consequently, sex differences in estimates of apparent survival of juveniles may arise due to
418 both a higher survival cost of dispersal in males and higher rates of permanent emigration
419 from the study site.

420 When the two birth season cohorts overlap in the fall-winter interval (August–April), sex
421 differences are no longer detected among juveniles, but a strong birth season cohort effect was
422 observed, in which summer-born juveniles showed lower survival probabilities than spring-
423 born juveniles. In environments with marked seasonal differences, the timing of births can
424 have important fitness consequences (e.g. Kraus et al. 2005; Feder et al. 2008; Bieber et al.
425 2012). The observed phenomenon can be attributed to the short time available to summer-
426 born juveniles for growth, to find a new suitable burrow and to store enough food before
427 hibernation to survive the winter. At the adult stage, the birth season cohort differences
428 disappear (Fig. 2b).

429 Finally, we found that the seasonality of survival varied substantially among years (Fig. 1).
430 We observed in particular that (1) inter-annual variations in survival are not strongly

431 correlated among seasons (i.e. Year and Season effects are non-additive), and (2) overall
432 annual survival variations are not shaped by a particular, highly variable season (i.e. there is
433 similar inter-annual variance among seasons).

434 Our results suggest that high resource availability before hibernation, as well as good winter
435 meteorological conditions and lower chipmunk densities (slight effect), may favour the winter
436 survival of chipmunks (Figs. 3, 4; see also the analysis based on composite covariate in
437 Online Resource 5). In the chipmunk, a food-storing hibernator, the availability of energy-rich
438 seeds, including oak and hornbeam fruits and wild cherry seeds, before hibernation could be a
439 key factor influencing their foraging behaviour in late summer/fall, their hibernation survival
440 and potentially their reproduction in the next spring (e.g. Humphries et al. 2003). Associated
441 with resource availability, a high density of conspecifics can increase intraspecific
442 competition processes on foraging and storing food, as well as competition for hibernation
443 nests (Kawamichi 1996). Nevertheless, this relationship may be shaped by marginal years
444 such as 2008, which was characterized by an acorn crop failure in the fall, and the highest
445 chipmunk density and the coldest winter of the time series (i.e. nine winter periods; Figs. 3, 4)
446 were observed. Moreover, the correlation between the fructification index and the winter
447 temperature can be confusing when determining which variable is the influential one (see
448 Online Resource 4, Fig. 4.2). In their native area, Siberian chipmunks live in a wide range of
449 environmental conditions, including harsher winter conditions than the local temperate
450 conditions encountered in the study population (Chapuis et al. 2009), which makes the winter
451 temperature effect the least likely hypothesis. Further investigations of longer time series are
452 necessary to confirm these results and disentangle the effects of the various covariates.

453 *Conclusion*

454 Studying the seasonality of survival pattern in the Siberian chipmunk, a small hibernating
455 mammal, allowed us to highlight strong intra-annual variation of survival among ages and

456 sexes in relation with two main life history events, the reproduction and the hibernation. Our
457 results illustrate that accounting for intra-annual time scale in survival pattern can help
458 improve our understanding of the relationship between a key fitness component, i.e., survival,
459 seasonal life history events and environmental variations. The hypotheses developed to
460 explain costly reproductive behaviour on male survival should be further investigated by
461 performing complementary analyses on simultaneous reproduction and mortality patterns in
462 the Siberian chipmunk population. From high winter survival, our results seem to support the
463 fact that hibernation can favour slower life histories of hibernators by increasing their
464 survival, compared with non-hibernating small rodents of similar size (Turbill et al. 2011).

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673 **Table 1.** Description and notation of temporal and group effects used in Huggin's robust design
674 models. Parameters, for which a detailed effect was tested, are listed and correspond to survival (S),
675 capture (p), recapture (c), temporary emigration (γ'') and temporary immigration ($1-\gamma'$) probabilities.

Type	Notation	Description	Parameters
Temporal	t	Full-time dependance	S, γ', γ''
	sess	Session effect	p, c
	year	Year effect	$S, p, c, \gamma', \gamma''$
	seas	Season effect	$S, p, c, \gamma', \gamma''$
	2 Seas	Only two seasons: active season VS. the fall-winter	S
Group	sex	Sex effect	$S, p, c, \gamma', \gamma''$
	b	Birth season effect (spring-born and summer-born individuals)	$S, p, c, \gamma', \gamma''$
	a	Age effect - juveniles and adults (> year of birth)	S, γ', γ''
	juvbs	Effect of birth season on juveniles only	S
	.	No effect. Constant parameter	$S, p, c, \gamma', \gamma''$
Temporary migration	Markovian	Markovian temporary emigration	γ', γ''
	Random	Random temporary emigration	γ', γ''

676 **Table 2.** Summary of model selection results for survival (S) in Siberian chipmunks
677 introduced to Forest of Sénart, during the 10-year study (2004-2013). According to the model
678 selection on p , c , γ' and γ'' (see detailed model selection in Online Resource 2), each model
679 presented in the result table was defined by [γ' and γ'' (seas markovian) $C_{(sess)}$ $p_{(.)}$]. Model selection
680 is based on second-order Akaike's Information Criterion (AICc). Number of parameters (np),
681 AICc values and AICc differences between the best model and the current candidate model
682 (Δ_i) and the Akaike weight (w_i) were reported. Best models occur in bold ($\Delta_i < 2$). The fully
683 parameterized model, the 11 best models and the models that are referred to in the text were
684 detailed in this table (see complete model selection in Online Resource 2).

N°	Models	np	AICc	Δ_i	w_i	Deviance
59	seas * (year + sex) + b * a	73	8022.49	0	0.50	6449.57
60	seas * (year + sex) + juvbs	72	8022.54	0.05	0.48	6451.78
61	seas * (year + sex) + a	71	8028.41	5.92	0.03	6459.80
62	seas * (year + a * (b + sex))	82	8034.00	11.51	0.00	6441.56
63	t + sex + juvbs	69	8042.43	19.94	0.00	6478.13
64	t + sex + b * a	70	8042.90	20.41	0.00	6476.44
65	2 Seas * (year + sex) + b * a	61	8043.20	20.71	0.00	6496.02
66	t + a * (sex + b)	71	8044.82	22.33	0.00	6476.21
67	t + b * a	69	8047.53	25.04	0.00	6483.22
68	t + sex * b * a	73	8048.72	26.23	0.00	6475.80
69	t * sex + b * a	98	8048.77	26.28	0.00	6421.15
71	t	66	8063.55	41.06	0.00	6505.68
74	2 Seas + (year + sex) + b * a	52	8085.57	63.08	0.00	6557.48
76	year + sex + b * a	51	8089.38	66.89	0.00	6563.40
79	year	47	8101.08	78.59	0.00	6583.53
80	seas*sex + b*a	46	8104.18	81.69	0.00	6588.72
81	seas * sex + a	44	8104.69	82.20	0.00	6593.43
84	sex + a	40	8115.52	93.03	0.00	6612.62

90	a	39	8120.15	97.66	0.00	6619.33
93	.	38	8122.04	99.55	0.00	6623.30
94	seas	40	8124.89	102.40	0.00	6621.98
95	t * sex * b * a	269	8386.01	363.52	0.00	6340.96

685

* interaction terms; + additive terms

686 **Figure legends**

687 **Figure 1** Yearly survival probability \pm SE (a) in relation with monthly survival rates estimated
688 at each season \pm SE (b) in the population of Siberian chipmunks introduced to the suburban
689 Forest of Sénart and monitored from 2004 to 2013. The mean annual survival was indicated in
690 grey (dashed line, panel a). The yearly and monthly survival rates were estimated from
691 Models 79 and 71, respectively. Some monthly survival probabilities were poorly estimated
692 (blank) and the annual survival rate in 2013 is not well-estimated (i.e., large SE).

693 **Figure 2** Monthly survival probabilities \pm SE of Siberian chipmunks for (a) each season
694 (spring, summer, fall-winter), (b) according to age, sex and birth season. Spr.-born and sum.-
695 born refer to spring-born and summer-born individuals, respectively. The survival rates were
696 estimated from Models 94 and 80 for (a) and (b), respectively.

697 **Figure 3** Correlation between estimated fall-winter survival probabilities and (a) the oak
698 fructification index and (b) the mean fall-winter temperatures. Open circles represent the
699 estimates from a time dependent model (standard errors SE are indicated by vertical bars).
700 The continuous line is the regression line from the survival model constrained by the temporal
701 covariate (SE is indicated by the grey shade; Models 103 and 108, respectively, Online
702 Resource 4).

703 **Figure 4** Correlation between seasonal survival probabilities (spring, summer and fall-winter)
704 and the adult density of chipmunks in April, June and July respectively. Open circles
705 represent the monthly estimates from a time dependent model (standard errors SE are
706 indicated by vertical bars). The continuous line is the regression line from the survival model
707 constrained by the adult density (SE is indicated by the grey shade; Model 118, Online
708 Resource 4).

Figure 1

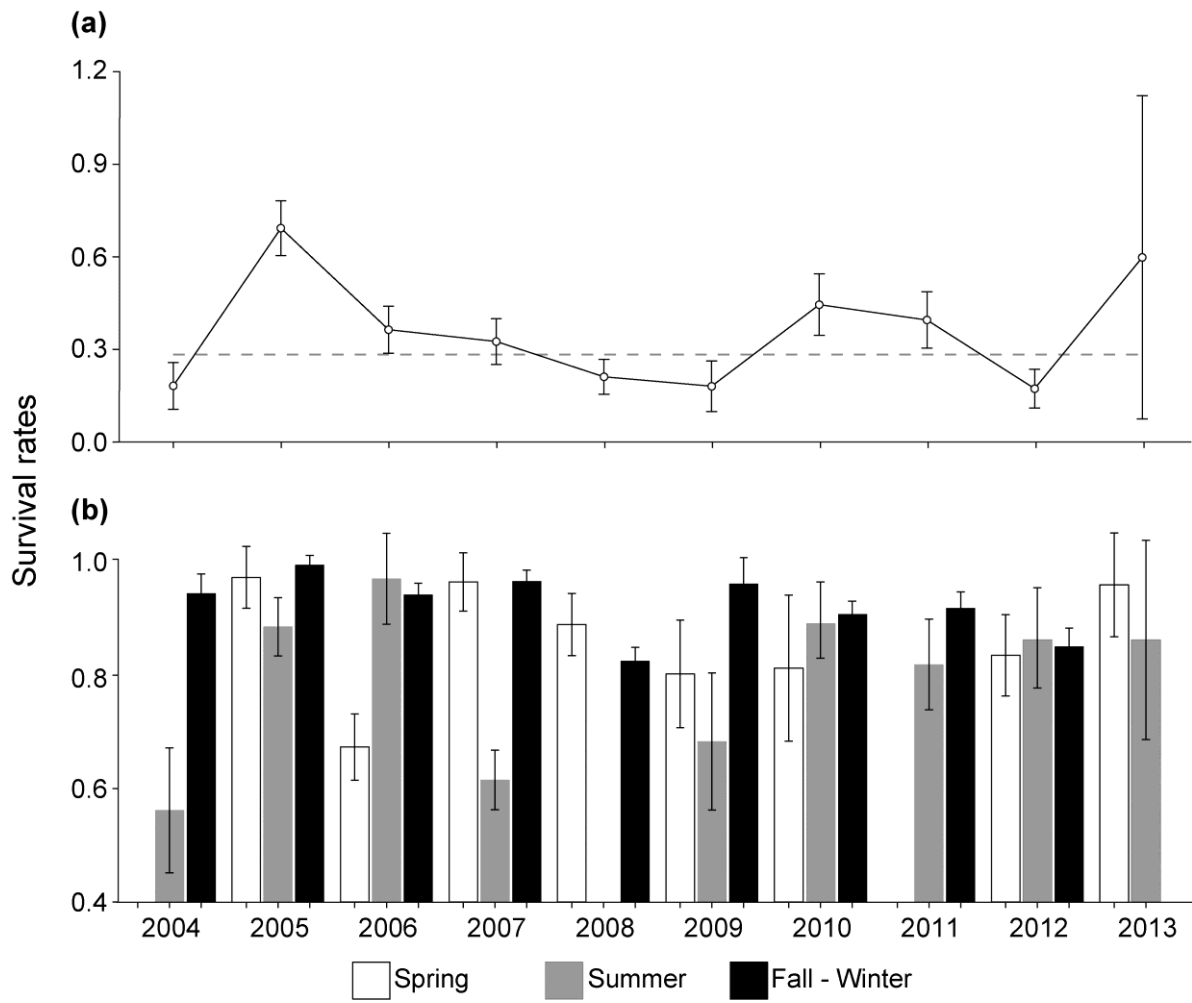


Figure 2

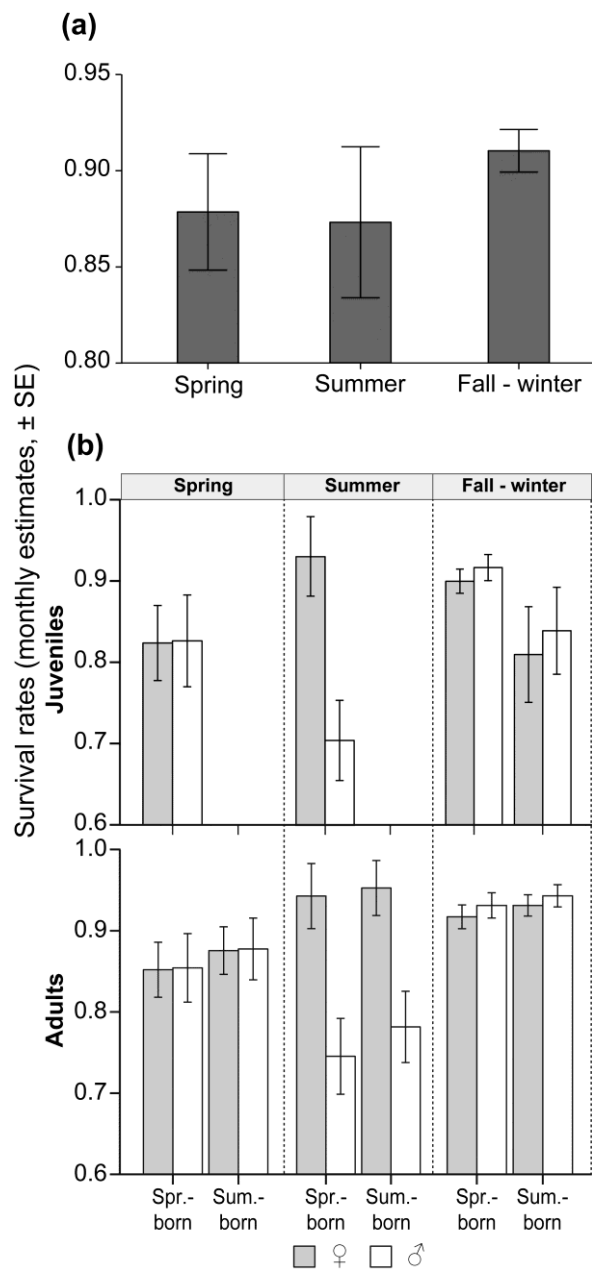


Figure 3

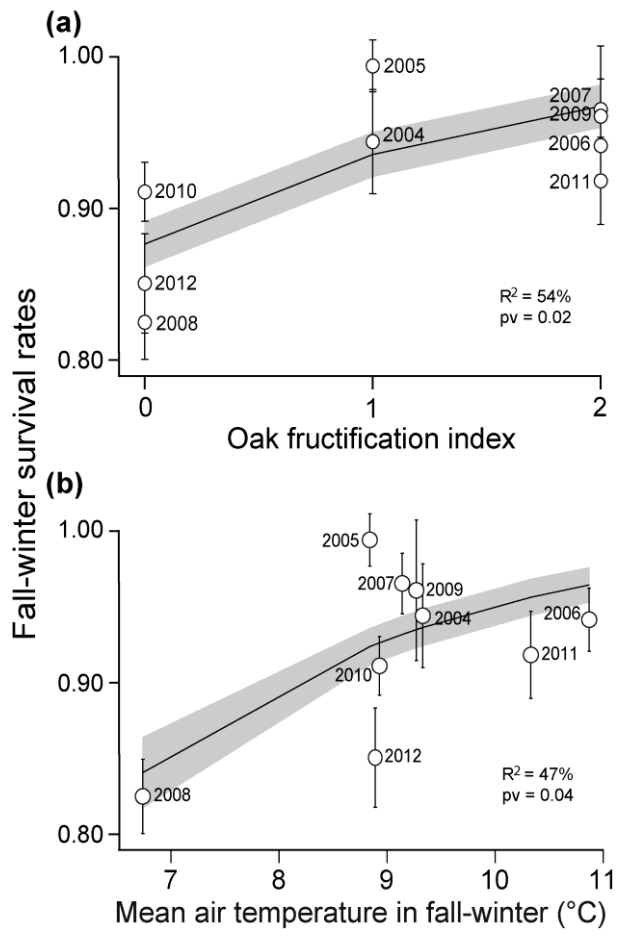


Figure 4

