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1 **Are habitat loss, predation risk and climate related to the drastic decline in a**
2 **Siberian flying squirrel population? A 15-year study**

3

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22

23 **Abstract**

24

25 To devise effective conservation actions, it is important to know which factors are associated
26 with the population parameters of a declining population. Using mark-recapture methods, we
27 estimated the annual population size, growth rate and survival probability of an ear-tagged flying
28 squirrel population over a 15-year period in a 4,500 ha study area in western Finland. The species is
29 considered vulnerable, but detailed knowledge concerning population sizes or trends is lacking. The
30 population parameters and changes therein were regressed against habitat availability, an indicator
31 of predation pressure, and mean winter temperature (an indicator of climate change), to reveal
32 potential reasons for trends in the population. The best-fit models suggested the annual growth rate
33 to be below one, and on average it was $0.93 (\pm 0.06; SE)$ across the 15-year period. The survival
34 probability was about $0.22 (\pm 0.03)$ for juveniles and $0.50 (\pm 0.03)$ for adults. The population size of
35 adult flying squirrels decreased from $65 (\pm 11)$ individuals in 1995 to $29 (\pm 6)$ individuals in 2009.
36 The number of flying squirrels was associated with the amount of available habitat, but the decline
37 in population size was more rapid than the loss of habitat area. If the current decreasing trend in
38 habitat availability continues, the population might become extinct by the year 2020. To halt the
39 population decline, it is necessary to refrain from clear-cutting mature spruce stands until new
40 suitable habitats develop from the maturation of younger forests.

41 **Keywords:** Alternative prey hypothesis · Landscape change · Mark-recapture analysis · Population
42 regulation

43

44 **Introduction**

45

46 Ecology is a science that aims to understand species distribution and abundance. This task is
47 particularly urgent for species that are declining or endangered. Caughley (1994) distinguished
48 between two paradigms in conservation biology: the small-population paradigm and the declining-
49 population paradigm. The small-population paradigm attempts to estimate the probability of
50 extinction of a stochastically fluctuating population, and does not deal with the reasons why the
51 population has become small. The declining-population paradigm aims to identify the underlying
52 causes of the decline and to prevent further declines, and is thus the correct approach in
53 conservation biology when trying to prevent a species from becoming seriously threatened
54 (Caughley 1994). Studying a declining population over a long period of time enables trends and
55 fluctuations in population parameters to be related to environmental variables, thereby gauging
56 potential causes for them, which allows more effective conservation planning.

57 The Siberian flying squirrel (*Pteromys volans*, L. 1758) is classed as vulnerable in Finland by
58 the IUCN (International Union for Conservation of Nature, 2010) classification (Rassi et al. 2010).
59 The species is included in the Habitats Directive Annex IV of the European Union (92/43/EEC) and
60 is therefore declared to be in need of strict protection. The species is considered to have declined in
61 Finland since the mid-20th century (Hokkanen et al. 1982; Selonen et al. 2010). It has allegedly
62 suffered from intensive forestry that has resulted in the reduction of optimal habitats, i.e., spruce-
63 dominated old forests mixed with deciduous and cavity trees (Hokkanen et al. 1982; Hanski et al.
64 2001a). Habitat loss is considered the main reason for the endangered status of the species (Rassi et
65 al. 2010). In addition to habitat loss, habitat fragmentation might limit the distribution of the flying
66 squirrel in forest landscapes (Reunanen et al. 2000). Increased predation pressure from raptors has
67 also been suggested to be related to the population decline (Hokkanen et al. 1982), although flying
68 squirrels are not common in the diet of avian predators (Selonen et al. 2010). As a boreal forest

69 species, the flying squirrel might also be affected by climate change. For many boreal animals,
70 winter conditions limit populations (Forsman and Mönkkönen 2003). At northern latitudes, winter
71 temperatures will probably increase more due to climate change than summer temperatures (ACIA
72 2005), and thus, northern populations might face particularly altered winter temperatures, and
73 increased winter temperatures as a consequence of climate change might improve flying squirrel
74 survival. However, the long-term effects of climate change might be negative, because climate
75 change in the southern boreal zone will probably create a suboptimal environment for Norway
76 spruce (Kellomäki et al. 2008), resulting in lower habitat availability. To date, direct demonstration
77 of population declines based on stringent population monitoring of marked individuals has been
78 lacking (but see Lampila et al. (2009) for estimates of demographic parameters in three flying
79 squirrel populations over 12 years). Therefore, there is no direct evidence for habitat alteration,
80 predation or climate change as the cause of declines in flying squirrel populations.

81 In many ecosystems, predators are the driving force behind small mammal population cycles
82 (Hanski et al. 2001b). The alternative prey hypothesis (Angelstam et al. 1984) suggests that
83 generalist predators, including many owl and hawk species, switch to alternative prey when the
84 number of main prey, which is voles, declines. If predation is a major limiting factor for flying
85 squirrels, it is to be expected that in poor vole density years, particularly immediately following a
86 vole population crash, flying squirrels would experience a stronger predation pressure than in a high
87 density vole year (e.g., Korpimäki et al. 1990), resulting in lower survival and a population decline.
88 If winter conditions are a limiting factor, a higher survival over time with an increase in mean
89 winter temperature would be expected.

90 In this study, we estimated the annual population size, growth rate and survival probability of
91 the flying squirrel over a 15-year time period in a 4,500 ha study area in western Finland. To
92 address the role of human-induced landscape change, predation and climate, we regressed annual
93 fluctuations in population parameters against variables reflecting habitat availability: an indicator of

94 potential predation pressure and an indicator of climate change. Usually, endangered species
95 populations are only monitored for a short period of time and very little is known about the annual
96 variation in population sizes. If considerable annual variation is evident, snap-shot studies might
97 produce biased information on species abundance.

98

99 **Material and methods**

100

101 Study species

102

103 The Siberian flying squirrel is a nocturnal arboreal mammal that inhabits boreal forests from
104 Siberia to western Finland and Baltic regions. It inhabits old spruce-dominated (*Picea abies*) forests
105 with deciduous trees for food (Hanski et al. 2001a). Even though the species can feed in and move
106 through younger forest stands (Selonen et al. 2001; Reunanen et al. 2004), it is highly dependent on
107 mature forests. The species nests in tree cavities formed by great-spotted woodpeckers
108 (*Dendrocopos major*), twig dreys of the red squirrel (*Sciurus vulgaris*), nest boxes or even
109 buildings. Female flying squirrels give birth to usually two to three offspring once or twice a year
110 (Hanski et al. 2001a). The sex ratio of juveniles is approximately 1:1. On average, juvenile males
111 disperse 1.8 km and females 2.5 km away from their natal sites (Selonen et al. 2007). The flying
112 squirrel is a territorial animal. According to Hanski et al. (2000) the mean sizes of male and female
113 home-range (measured by 95% minimum convex polygons) are 40.0 ha and 5.7 ha, respectively.
114 Both males and females show a high degree of site fidelity.

115

116 Study area and data collection

117 The data were collected during years 1995–2009 in Alavus, western Finland. The Alavus
118 population breeds in nest boxes, which makes it possible to ear-tag and monitor nearly all

119 individuals in the population. Nest boxes were placed systematically in 1994 in suitable breeding
120 habitats within an area of 4,500 ha ($5 \times 9 \text{ km}^2$; Mäkelä 1999, 2001). The coordinates of the SW-
121 corner of our rectangular study area are $62^\circ 45' \text{N}$, $23^\circ 31' \text{E}$. All forest stands within the 10,000 ha
122 study area, except for one small protected area ($<10 \text{ ha}$), are managed for timber production. As a
123 consequence, even mature forests contain very little dead-wood or very few cavity trees. The
124 number of boxes decreased almost every year because of the harvesting of suitable habitats (201
125 boxes in 1995; 124 boxes in 2009) and the density of nest boxes within suitable habitats decreased
126 from 7.5 boxes/10 ha in 1995 to 5.2 boxes/10 ha in 2009. However, nest box densities were three-
127 fold (in 1995) to six-fold (in 2005) higher than the density of flying squirrels (see results) and the
128 number of nest boxes per individual flying squirrel increased slightly during the study (3.1
129 boxes/individual in 1995; 4.3 boxes/individual in 2009). Hanski et al. (2000) showed that over a
130 year, a female flying squirrel uses five nests and a male eight nest sites on average, of which 36%
131 are twig dreys and 64% are woodpecker cavities or nest boxes. Therefore, it is unlikely that the
132 availability of nest boxes limited flying squirrel abundance.

133 Individuals were captured from nest boxes and were ear-tagged in June (during the first litter
134 in the nest) and August (during the second litter) every year. The capture history of every individual
135 was recorded so that an individual was noted as 'alive' if it was observed even once during a given
136 year. New individuals were entered into the data by their tagging age, so that an individual born in
137 the same year was marked as a juvenile and an individual born in previous years, as an adult. This
138 allowed juvenile and adult population parameters to be distinguished from each other in the
139 analysis. Data for both sexes were combined because the sample size did not allow an analysis of
140 the effects of both sex and age and because age is a more important factor affecting population
141 parameters than sex (Lampila et al. 2009).

142 Forest land covered about 70% of the 4,500 ha sized study area and included habitats from
143 seedling to mature stands of all tree species. In 2009, about 7.5%, or 237 ha of the total forest area

144 was spruce-dominated mature forest and thus can be considered as a suitable breeding habitat for
145 the species. The percentage habitat cover was evaluated during the data collection and was based on
146 aerial photographs and maps. We used forestry files of the regional Forestry Centre for the township
147 of Alavus to estimate the reduction in habitat area across the years.

148 Vole population abundance was determined by snap-trapping as described in Huitu et al.
149 (2003). Trapping was carried out in both forest and field habitats at seven sites situated within a 70
150 km radius from Alavus. To obtain an index of vole population size for each site and trapping
151 occasion, we pooled numbers of the three most numerous small rodent species caught within the
152 area: the field vole *Microtus agrestis*, the sibling vole *M. levis* and the bank vole *Myodes glareolus*.
153 The number of each species in both field and forest habitats was divided by the number of trap
154 nights (number of traps set \times number of nights they remained set), and was multiplied by 100. As
155 an index for vole numbers at the flying squirrel study site, located centrally to the vole trapping
156 sites, we calculated the mean of all site-specific indices for each trapping occasion. Predators
157 exhibit very strong direct and delayed numerical responses to changes in vole numbers, typically
158 lagging behind numbers of their vole prey by 0–4 months in late summer and 9–12 months in spring
159 (Korpimäki et al. 1991, 2005; Korpimäki and Norrdahl 1991; Norrdahl and Korpimäki 1995, 2002;
160 Sundell et al. 2004). Based on this, we used the autumn vole population size in the landscape as an
161 indicator for predation pressure in the next reproductive season of the flying squirrel. Vole
162 abundance data from years 1994–2008 were used for analyses, thus, the flying squirrel population
163 size in a given year was regressed against the vole abundance in the previous autumn.

164 We included mean winter temperature into the models explaining flying squirrel population
165 dynamics. Daily data from 1995 to 2008 for mean temperature, interpolated from measuring
166 stations nearest to the town centre of Alavus (Venäläinen et al. 2005), about 15–20 km from the
167 study area, were obtained from the Finnish Meteorological Institute. Daily means were used to
168 calculate a mean winter temperature from November to February.

169

170 Statistical analyses

171

172 The modelling and parameter estimates were performed with the program MARK 5.0, which
173 provides parameter estimates for open populations of marked animals (White and Burnham 1999).
174 Before modelling, goodness-of-fit was tested using the program U-CARE 2.3 (Choquet et al. 2005),
175 which tested the assumptions of the Cormack-Jolly-Seber model (CJS; Lebreton et al. 1992) used in
176 this case. The testing was performed for the global model and separately for both marking age
177 groups. To adjust the lack of fit, we calculated the variance inflation factor, \hat{c} (Williams et al. 2002;
178 Cooch and White 2009), which estimates the amount of overdispersion of the data for a given
179 model (Lebreton et al. 1992). We then used this \hat{c} ($= 1.2$) to adjust the AIC_c into a quasi-likelihood-
180 adjusted $QAIC_c$ in MARK.

181 The data included 581 individuals (294 males and 287 females; 415 juveniles and 166 adults).
182 We estimated the population size (N) and growth rate ($\lambda = N_{t+1}/N_t$) only for the adult population,
183 because the models assume homogeneous survival and capture probabilities (Williams et al. 2002;
184 Cooch and White 2009) and survival was expected (and observed; see results) to differ between
185 juveniles and adults (Lampila et al 2009). The POPAN formulation was used to estimate population
186 size and a Pradel model to estimate the growth rate (Cooch and White 2009). All possible different
187 models with either constant or time-dependent parameters (population size or growth rate, survival
188 and recapture probabilities) were tested.

189 We estimated survival and recapture rates with juveniles included in the analysis. Age was
190 assumed to affect survival, because typically, juveniles survive less well than adults (Lampila et al.
191 2009). Furthermore, juveniles tend to disperse (Selonen and Hanski 2004), causing apparently
192 lower survival rates, since dispersal often cannot be distinguished from death. Therefore, the
193 survival and recapture probability models were allowed age-dependent estimates.

194 The model selection was based on Akaike's Information Criterion (AIC_c ; Hurvich and Tsai
195 1989), which was corrected for a small sample size. The best models with a ΔAIC_c value (i.e., the
196 difference between AIC_c value of a model and the best model) less than four were selected to
197 calculate weighted means of the estimates.

198 To study whether and how much the amount of habitat, predation pressure and winter
199 temperature affect population size, a linear regression analysis was performed with SPSS Statistics
200 20.0. All three independent variables of habitat area, the abundance of voles in autumn and mean
201 winter temperature, were entered into the model. In addition, population density was regressed
202 against year, as was the annual growth rate of the population against the proportionate change in
203 habitat area, abundance of voles and winter temperature.

204

205 **Results**

206

207 Population size and growth rate

208

209 The population size of adult flying squirrels decreased from 65 ± 11.0 ($N \pm SE$) individuals in
210 1995 to 29 ± 6.0 individuals in 2009 (Fig. 1). The lowest population size of 23 ± 4.9 adult
211 individuals was estimated for 2005. Regression of the population size against year revealed a
212 significant decline over time, with a reduction of 1.6 individuals per year ($F_{1,13} = 9.15$, $P = 0.010$);
213 the predicted population size was 48.3 for 1995 and 25.9 for 2009, i.e., a 46 % decline. There were
214 two outlier years when the population size was exceptionally high (1995 and 2006; Fig. 1), but even
215 without these outliers, the decline was strong (1.3 individuals per year) and significant ($F_{1,11} = 12.5$,
216 $P = 0.005$).

217 The regression model for population size against habitat area, vole abundance and winter
218 temperatures explained 45.5% of the variation in population size. The area of suitable habitat was

219 the only variable that was significantly associated with the population size (Table 1). The regression
220 coefficient for habitat area implies that each 10 ha reduction in habitat area was associated with a
221 decline of about eight individuals from the population. The population size was related relatively
222 linearly to habitat area (Fig. 2). However, the estimated density of individuals decreased from 1.8 to
223 1.1 per 10 ha during the study, which was statistically significant ($F_{1,13} = 5.35$, $P = 0.038$). If the
224 density of individuals had remained constant, the decline in population size would have been
225 modest (Fig. 2).

226 According to the best fit model, population growth rate varied with time. The geometric mean
227 of growth rate in the best model was 0.93 ± 0.06 (geometric mean \pm SE). However, two other
228 models also gained some support (Table 2). These models suggest that the growth rate was constant
229 over time and was significantly less than one: 0.96 ± 0.01 and 0.96 ± 0.02 ($\lambda \pm$ SE). Thus, all the
230 best fit models suggest a significant population decline. Annual growth rate estimates varied
231 between 0.71 ± 0.22 and 1.60 ± 0.65 (weighted mean \pm SE; Fig. 3). In nine study years, the upper
232 confidence limits of population growth were below or equalled one, so that in more than half of the
233 years studied, the population declined or remained constant with a 95% probability. Habitat area,
234 vole abundance and winter temperatures did not have a significant effect on population growth rates
235 (Table 3).

236

237 Survival and recapture

238

239 The seven best fit models estimating survival and recapture probabilities included either age-
240 (a) or both age- and marking age- (m) dependent survival parameters (Table 4). Age-dependent
241 survival occurred in all seven models. Therefore, the models provide strong support that survival is
242 affected by flying squirrel age. The weighted mean estimate of the seven best-fit models for the

243 survival probability of juveniles was less than half that of adults (Table 5). In contrast, modelling
244 provided little support for the marking-age dependency of survival.

245 Two out of seven best fit models included a constant recapture estimate (Table 4). These
246 models provide a summed weight for constant recapture of 0.49, which was much larger than
247 expected by chance alone (0.13). We therefore conclude that the recapture rate did not vary among
248 years and was not dependent on age or marking age. The weighted mean estimate suggested that
249 about 60% of the individuals were recaptured at each trapping occasion (Table 5).

250

251 **Discussion**

252

253 The adult flying squirrel population approximately halved in 15 years. Of the measured
254 variables, only habitat area was related to population size, indicating that population decline was
255 related to habitat loss. Our results indicate that the reduction of 5.7 ha in habitat area (the mean size
256 of the female flying squirrel home-range; Hanski et al. 2000), was associated with the loss of four to
257 five flying squirrel individuals or, assuming that half of the adult individuals were females, with the
258 loss of 2.4 females per loss of a home range. Furthermore, we observed a strong decrease in density,
259 from 1.8 to 1.1 individuals per 10 ha over the 15-year period. Thus, the decline in flying squirrel
260 numbers was faster than predicted by the loss of habitat area (compare the observed population
261 trend with the predicted trend had the density remained constant in Fig. 2). Because habitat
262 fragmentation tends to reduce population sizes more than expected based on habitat loss alone
263 (Bender et al. 1998), our results imply but do not confirm, that fragmentation effects are involved in
264 the population decline.

265 We found no support for the role of flying squirrels as an alternative prey for vole-eating
266 predators. Population size was not a function of vole population size, nor was the flying squirrel
267 population growth rate associated with the changes in vole population density. This might be

268 because of a very strong decline in the flying squirrel population with habitat area, masking any
269 effects from other factors such as variation in predation pressure or in ambient conditions. Selonen
270 et al. (2010) found that flying squirrels were consumed more frequently during years with a high
271 vole number than during years with a low number, which also does not support the alternative prey
272 hypothesis.

273 The estimates of annual growth rate varied between 0.71 and 1.60, with rather wide
274 confidence intervals. Nevertheless, the geometric mean of the growth rate (0.93) of the best model
275 and the growth rate estimates of the two next best models (0.96), indicate a significant overall
276 decrease in population size. Lampila et al. (2009) studied three local flying squirrel populations in
277 western Finland during 1992–2004, and found that in two of the populations, the mean growth rate
278 was 0.96, and in one population it declined from more than one to less than 0.80. Thus, both our
279 study and that of Lampila et al. (2009) suggest that local populations are decreasing. The growth
280 rate of 0.93 across 10 years translates into a 52% reduction in population size, which corresponds to
281 an endangered status according to IUCN criteria (IUCN 2001); correspondingly, a growth rate
282 estimate of 0.96 for the two next-best models suggest a 34% decline over 10 years (classed as
283 vulnerable). Thus, the present categorisation of the flying squirrel as vulnerable in Finland (Rassi et
284 al. 2010), despite a rather large national population size is not too pessimistic. There is also
285 evidence (Sulkava et al. 2008) that the national population is in fact smaller than that estimated by
286 Hanski (2006).

287 We found adult survival (0.48–0.50) to be about twice as high as juvenile survival (0.22).
288 This was expected because juveniles probably suffer from higher mortality and because juveniles
289 also disperse while searching for a home range (Selonen and Hanski 2004) and might thus
290 disappear from the study area and not be recaptured, lowering the apparent survival estimate.
291 Lampila et al. (2009) found corresponding survival estimates in the three flying squirrel populations
292 in Western Finland.

293 Even though the population size decreased over the 15-year study period, the models indicate
294 a constant survival over time. This suggests that survival has been at a low level from the beginning
295 of the study, resulting in growth rates below one and a decreasing population size. It is evident that
296 the recruitment of new individuals into the population via reproduction or immigration is not large
297 enough to compensate for mortality, and thus the population has declined.

298 The smaller the population is, the stronger are the effects of demographic and environmental
299 stochasticity (Lande 1998). The population change we observed between consecutive years was
300 large in some cases and, for example, between 1995–1996 and 2005–2007 population size changed
301 at least by 30 percent. Our results suggest that short-term snapshots might provide seriously biased
302 estimates of population size, even for populations that do not decline. It is evident that several years
303 of data are needed to provide unbiased estimates of mean population size. Reliably detecting
304 population trends requires an even longer time-series.

305 Based on this and previous studies (Mäkelä 1999, 2001), the future of the flying squirrel
306 population in the Alavus study area does not appear hopeful. If the current decreasing trend in
307 habitat availability continues, the population might become extinct by 2020. The problem of habitat
308 loss is particularly severe because many of the cut spruce stands have been replanted with pine.
309 Pine forests, even if old, are clearly suboptimal for the flying squirrel (Hanski 1998). Furthermore,
310 in a simulation study, Kellomäki et al. (2008) predicted that climate change might substantially
311 change the dynamics of managed boreal forests in northern Europe, and that in southern boreal
312 forests, climate change will create a suboptimal environment for spruce, and that the dominance of
313 Scots pine and birch will increase. This is likely to extirpate flying squirrel from its current strong
314 holds in southern and western Finland if management does not maintain and favour spruce-
315 dominated forests.

316 Because only a small fraction of the land area in southern Finland is protected (Finnish
317 Statistical Year Book Forestry 2011), the persistence of species in general critically hinges on the

318 management of commercial forests. Our study area is very typical of southern Finland, therefore,
319 we believe that our results of a sharply declining flying squirrel population can be generalised to the
320 whole of southern Finland. Because clear-cutting even with green tree retention is detrimental to
321 flying squirrel persistence (Santangeli et al. 2013), to halt the population decline it is necessary to
322 refrain from clear-cutting mature spruce stands until new suitable habitats are developed by the
323 maturation of younger forests. Alternative management regimes such as uneven-age management
324 (Kuuluvainen et al. 2012), refraining from silvicultural thinning or applying extended forest
325 rotations might provide an economically sustainable way to support flying squirrel persistence in
326 commercial forest landscapes (M. Mönkkönen et al., unpublished data).

327

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329

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335

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- 434

435 Table 1. ANOVA for the regression model of population size against the area of suitable habitat,
 436 vole abundance and winter temperature.

	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Regression	99.141	3	33.047	3.062	0.073
Residual	118.704	11	10.791		
	<i>B</i>	<i>SE</i>	<i>t</i>	<i>P</i>	
Habitat area	0.838	0.289	2.898	0.014	
Abundance of voles	0.260	0.251	1.036	0.323	
Winter temperature	0.633	1.232	0.130	0.618	
Intercept	-175.044	71.082	-2.463	0.032	

437

438

439 Table 2. The best-fit models ($\Delta AIC_c < 4$) for survival (φ), recapture (p) and growth rate (λ)
 440 (subscript a represents age-dependence, t for time-dependence and c for constant parameters) and
 441 their ΔAIC_c , AIC_c weights and numbers of parameters.

Model	ΔAIC_c	AIC_c weight	Number of parameters
$\varphi_c p_c \lambda_t$	0.00	0.58	16
$\varphi_c p_c \lambda_c$	1.84	0.23	3
$\varphi_c p_t \lambda_c$	2.31	0.18	17

442

443

444 Table 3. ANOVA for the regression model of population growth rate against the area of suitable
 445 habitat, vole abundance and winter temperature.

	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Regression	0.091	3	0.030	0.510	0.684
Residual	0.594	10	0.059		
	<i>B</i>	<i>SE</i>	<i>t</i>	<i>P</i>	
Change in habitat area	10.913	52.028	0.210	0.838	
Change in abundance of voles	-0.059	0.050	-1.182	0.265	
Winter temperature	-0.002	0.035	-0.044	0.966	
Intercept	-9.746	51.665	-0.189	0.854	

446

447

448 Table 4. The best-fit models that estimate survival (φ) and recapture (p) (subscript a denotes age-
 449 dependence, m marking age-dependence and c constant parameters for age and marking-age
 450 groups) and their $\Delta QAIC_c$, $QAIC_c$ weights and numbers of parameters.

Model	$\Delta QAIC_c$	$QAIC_c$ weight	Number of parameters
$\varphi_a p_c$	0.00	0.33	3
$\varphi_a p_m$	1.28	0.18	4
$\varphi_{m, a} p_c$	1.56	0.15	4
$\varphi_a p_a$	1.83	0.13	4
$\varphi_{m, a} p_m$	3.01	0.07	5
$\varphi_{m, a} p_a$	3.15	0.07	5
$\varphi_a p_{m, a}$	3.31	0.06	5

451

452

453 Table 5. Weighted mean estimates of survival (ϕ) and recapture (p) and their standard errors and
 454 95% confidence intervals. 'Marking age' is the age of an individual when it was encountered for the
 455 first time and 'Age' is simply the age of an individual.

Parameter	Marking age	Age	Estimate	SE	95% CI	
survival	Juv	Juv	0.22	0.03	0.16	0.29
		Ad	0.48	0.04	0.40	0.57
	Ad	Ad	0.50	0.03	0.43	0.56
recapture	Juv	Juv	0.58	0.07	0.44	0.71
		Ad	0.59	0.07	0.45	0.72
	Ad	Ad	0.62	0.06	0.50	0.72

456

457

458 **Figure legends**

459

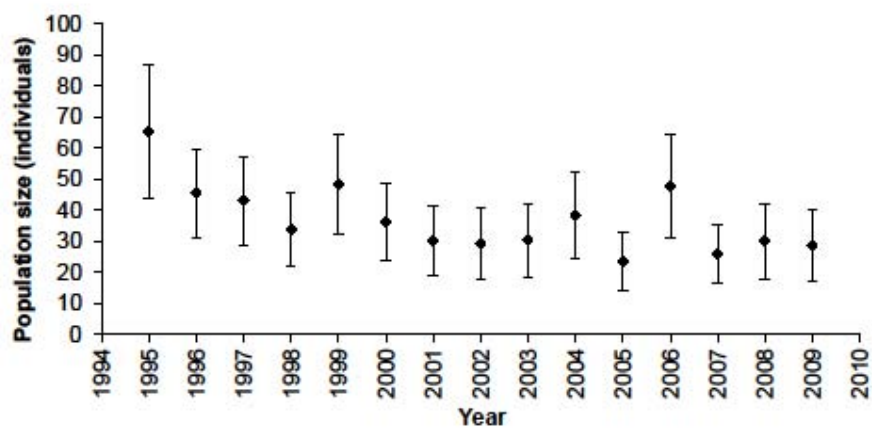
460 Figure 1. Annual population size estimates for the Alavus population with 95% confidence
461 intervals.

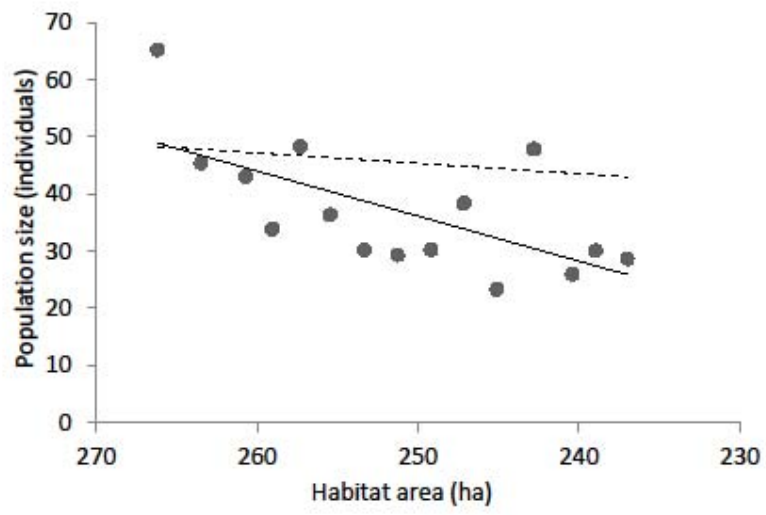
462

463 Figure 2. The relationship between population size and habitat area. The first dot on the left
464 represents the year 1995 and the last one represents the year 2009, i.e., habitat area on the x -axis is
465 represented in descending order. The trend line with a slope of 0.84 is shown. The dashed line
466 shows the population trend had the density of individuals remained at the 1995 level (1.8
467 individuals/10 ha).

468

469 Figure 3. The weighted mean estimates of the growth rates and their 95% confidence intervals of
470 the three best-fit models (Table 2) over time.





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