

1 **Habitat use of coexisting *Microtus* vole species under competition**
2 **and predation risk**

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22 vole species under competition and predation risk

23 Abstract

24 Competing species and predators can alter the habitat use of animals but both factors are
25 rarely simultaneously controlled for. We studied in experimental enclosures how closely
26 related species, the sibling vole (*Microtus levis* Miller, 1908) and the field vole (*M. agrestis*
27 L., 1761), adjust their habitat use when facing either the competing species or simultaneously
28 competition and predation risk. The species responded differently in their proportional use of
29 two habitat types, a low cover (productive but riskier) and a high cover (safer but poorer).
30 When alone, field voles used the low cover habitat according to availability at low densities,
31 but decreased its use with increasing density. Sibling voles, however, avoided the low cover
32 habitat in single-species populations. Under interspecific competition, the habitat use patterns
33 switched between species: sibling voles used the low cover habitat according to availability,
34 with decreasing use as densities increased. Sibling voles responded to predation risk by
35 showing a stronger density-dependent decrease in the use of low cover habitat. Field voles,
36 initially using mostly high cover, did not change behaviour under risk of predation. Our
37 results highlight the importance of considering both predation risk and interspecific
38 competition when interpreting patterns of habitat selection among coexisting species.

39 Keywords: coexistence, density-dependent habitat use, field vole, *Microtus agrestis*, *Microtus*
40 *levis*, sibling vole
41

42 Introduction

43 Competition for resources is one of the ecological factors known to have a strong impact on
44 animal communities (e.g. Hairston et al. 1960; Gurevitch et al. 1992) and may refer both to
45 the exploitative use of resources (exploitation competition, Schoener 1983) and to direct
46 antagonistic actions towards other individuals to monopolize a contested resource
47 (interference competition, Case and Gilpin 1974). Both types of competition can occur within
48 (intraspecific) and between species (interspecific). On an evolutionary time scale,
49 interspecific competition often results in resource partitioning (Schoener 1974; Pacala and
50 Roughgarden 1982; Roughgarden 1976; Abrams 1980; Luiselli 2006; Wauters et al. 2002).
51 As ecological consequences of competition, animals can for example modify their spatial or
52 temporal use of food, shelter or habitat (Koplin and Hoffmann 1968; Johannesen and
53 Mauritzen 1999; Ziv and Kotler 2003). Common responses are for example habitat shifts
54 (Koplin and Hoffmann 1968; Ziv et al. 1993) and niche contractions (Eccard and Ylönen
55 2002).

56 The outcome of competitive interactions between species can depend on habitat type and
57 differences in relative competitive strength of species between habitats (Morris and Grant
58 1972), and initial relative population density of competing species (Abramsky et al. 1990).
59 Consequently, competitive interactions and the densities of competing species may have
60 profound implications for habitat selection. Density-dependent habitat selection based on
61 ideal-free distribution (Fretwell and Lucas 1970) assumes that individuals select habitats to
62 maximize their fitness so that the relative use of the higher quality habitat declines as
63 population density increases, accompanied by an increased use of the lower quality habitat. In

64 territorial animals, or interactions between species with different competitive strength,
65 density-dependent habitat selection may follow an ideal-despotic distribution (Fretwell and
66 Lucas 1970) where subordinates will be outcompeted from higher quality habitats, leading to
67 an increase in the use of lower quality habitats. Therefore, when two species prefer the same
68 high-quality habitat (at low densities), increasing total density may force the less competitive
69 species to increase its use of a low-quality habitat.

70 Predation can alter interspecific competitive interactions substantially (for reviews see Sih
71 et al. 1985; Gurevitch et al. 2000; Chase et al. 2002). In fact, predation may even override the
72 effects of interspecific competition altogether or change the outcome of competition (Persson
73 1991; Abramsky et al. 1998; Lin and Batzli 2001; Jermacz et al. 2015). As examples,
74 generalist predators may promote the coexistence of competing species through prey
75 switching, a process in which predators reduce densities of a given prey species as soon as
76 they begin to outnumber those of their competitors (Chase et al. 2002). Predators specialized
77 on a dominant competitor may initially promote coexistence by alleviating interspecific
78 competition. While the most conspicuous effect of predation is the removal of individuals,
79 predators can also have non-consumptive effects on their prey (Preisser et al. 2005). The
80 responses of prey to the presence of predators may include a decrease in feeding activity or
81 reduction in movements (Abramsky et al. 1998; Norrdahl and Korpimäki 1998; Koivisto and
82 Pusenius 2003; Salo et al. 2008; Haapakoski et al. 2015), or movement to a safer habitat
83 (Kotler et al. 1991; Creel et al. 2005). Furthermore, when facing a variety of predators, prey
84 might experience a trade-off between relative safety from one predator type and increased
85 vulnerability to another. For example, avoidance of avian predators that favour open areas for
86 hunting may predispose voles to small mustelids, like least weasels (*Mustela nivalis* L., 1766),

87 which prefer hunting in cover (Korpimäki and Norrdahl 1989; Brandt and Lambin 2007). The
88 presence of a competing species can indirectly increase predation risk by attracting more
89 predators (apparent competition, Holt 1977), or lead to predator satiation if the total density of
90 competitors is sufficiently high (Hastings and Powell 1991).

91 Interspecific competition in rodents is well studied (for reviews see Grant 1972; Eccard
92 and Ylönen 2003). However, the majority of these studies have not controlled for predation
93 (but see e.g. Hughes et al. 1994; Schofield 2003; Jermacz et al. 2015). Here we evaluate the
94 effects of interspecific competition and population density on habitat use of two coexisting
95 small mammal species, the sibling vole (*Microtus levis* Miller, 1908) and the field vole (*M.*
96 *agrestis* L., 1761), and whether predation pressure changes their habitat use under
97 competition. The sibling vole and the field vole are the two most common vole species
98 inhabiting the grasslands of western Finland (Korpimäki and Norrdahl 1991). Both species are
99 folivorous, consume similar food resources, and coexist in seemingly similar habitats
100 (Myllymäki 1977) but sibling voles seem to be better adapted to cultivated fields than field
101 voles are (Myllymäki 1977; Norrdahl and Korpimäki 1993). Both species show synchronous
102 high-amplitude cyclic population oscillations with a cycle length of three years in our study
103 area (Huitu et al. 2004; Korpimäki et al. 2005). The sibling vole is slightly smaller and agile
104 than the field vole, it occurs in patches with relatively high densities (Norrdahl and Korpimäki
105 1993) and it appears to be a superior competitor over the field vole in the absence of predation
106 (Norrdahl and Korpimäki 1993; Koivisto et al. 2007). Despite this, the field vole is usually
107 more abundant in the wild than the sibling vole (Huitu et al. 2004). The mechanism allowing
108 the coexistence of these two species is not yet fully understood, but predation appears to play
109 an important role in the process (Norrdahl and Korpimäki 1993; Koivisto et al. 2008; Hoset et

110 al. 2009). Coexistence of the two competitors could also reflect food differentiation not yet
111 identified.

112 We conducted an experiment in large outdoor predator-proof enclosures and fenced
113 control areas experiencing natural predation pressure. The grass of one third of each enclosure
114 and control area was cut and maintained short by mowing, thus creating a habitat with a high
115 risk of avian predation but constantly renewing food resources in the form of fresh grass.
116 Earlier studies have shown that the proportion of sibling voles compared to field voles was
117 smaller in hay fields with taller vegetation, but higher in intensively cultivated fields with
118 lower vegetation (Myllymäki 1977; Norrdahl and Korpimäki 1993). Despite being
119 competitively superior on a population level (Koivisto et al. 2007), sibling voles have smaller
120 body size than field voles and will thus most likely lose in one-on-one competition (Norrdahl
121 and Korpimäki 1993). Sibling voles are also more susceptible to predation than field voles
122 (Norrdahl and Korpimäki 1993; Koivisto et al. 2008), probably due to their tendency for
123 aggregation. Based on this information, and assuming that the low cover habitat has best
124 nutritional quality, we predicted that: 1) In the absence of predation and competition both
125 species will use the low cover habitat according to availability, but in a density-dependent
126 manner following ideal-free distribution, i.e., relative use of low cover habitat decreases with
127 increasing density. 2) Under competition, but in the absence of predation, sibling voles will
128 use the low cover habitat more than field voles, but 3) in the presence of predators, sibling
129 voles will respond more strongly to predation risk than field voles by shifting their habitat use
130 to high cover.

131

132 **Methods**

133 **Study system**

134 The experiment was conducted in summer and autumn 2004 in Lapua, western Finland (63°
135 N, 23° E) at four separate study sites. The study sites were established in 1996 on old
136 farmland, are located 1.5–7 km apart and fall within an area of 12 km². The sites are mostly
137 dominated by graminoids such as canary grass (*Phalaris arundinacea* L.), and herbs, e.g.,
138 nettle (*Urtica dioica* L), creeping thistle (*Cirsium arvense* L.) and fireweed (*Epilobium*
139 *angustifolium* L.). A more detailed description of the study sites and vegetation can be found
140 in Norrdahl et al. (2002). All applicable international, national, and institutional guidelines for
141 the care and use of animals were followed. All procedures involving animals were performed
142 in accordance with the ethical standards of the institution at which the studies were conducted
143 (see Acknowledgements for further details). The animals were cared for in accordance with
144 guidelines such as the Guide to the Care and Use of Experimental Animals. This research
145 adhered to the legal requirements of Finland and all institutional guidelines.

146 Each of the four sites contained two 0.5–hectare predator-proof enclosures, which were
147 constructed using hardware cloth (mesh size 12.7 mm) extending 0.5 m below and 1.3 m
148 above ground. A metal sheet (40 cm) was fastened to the upper edge of the fence to prevent
149 climbing by voles and mammalian predators. To prevent access by avian predators, the
150 enclosures were covered with nylon net (mesh size 10 cm). In addition, three sites contained a
151 0.5–hectare control area each (hereafter control), which was surrounded by a low fence (40
152 cm in height, 60 cm below ground). Each control area had six evenly distributed access points
153 where the top of the fence was lowered to a ca. 30 cm height to facilitate the entry of small
154 mustelids (least weasels and stoats *Mustela erminea* L., 1758). In fact, a few weasels were
155 caught in vole traps in the control areas during vole trapping and signs of mustelids (e.g.

156 faeces) were detected also outside trapping periods. Thus, control fences enabled all predators
157 to enter and exit at will, while preventing the dispersal of voles. This set-up allowed us to
158 compare control populations with enclosed predator-free vole populations while avoiding
159 interpretation problems that could result from possible fence effects.

160 In each enclosure and control area, 48 traps (multiple capture Ugglan live-traps, Grahnb,
161 Sweden) were distributed evenly ca. 10 m apart. The traps were placed individually under
162 inverted plastic boxes (40×30×25 cm) that provided protection from weather. The grass of the
163 central 1/3 strip of each area was kept short (10–20 cm) by mowing approximately every two
164 weeks throughout the summer (low cover habitat), and was thus short at the initiation of the
165 experiment. In the non-mowed sections, the natural vegetation reached a height of 100–200
166 cm during the experiment (high cover habitat). Between the low and the high cover habitat
167 sections there was a 1.5 m wide zone which was treated with herbicide (RoundUp, Monsanto
168 Europe S.A., Belgium) to remove edge vegetation to measure the actual habitat selection
169 instead of occasional visits (Klemola et al. 2000). One-third (16) of the traps were distributed
170 in the low cover habitat and two-thirds (32) in the high cover habitat (Fig. 1).

171

172 **Conduct of the experiment**

173 Before the beginning of the experiment, we removed all rodents from the areas primarily by
174 live-trapping. In the enclosures also snap traps were used to remove the last few remaining
175 individuals not entering the live-traps as for the successful conduction of the experiment it
176 was essential that the enclosures were free of voles. Snap traps were placed under covers to
177 prevent birds from getting caught. Traps were checked at regular intervals and the trapped
178 voles were stored in a freezer for purposes of other studies. Voles used in the experiment were

179 originally caught from the wild in Lapua and surroundings and kept in single-species
180 populations for a month in two 0.5-ha predator-proof enclosures to reproduce. Individual
181 voles were allocated randomly to different treatments and areas for the experiment. Only
182 sexually mature individuals were used, as judged by a perforate vagina in females or scrotal
183 testes in males. In early July, we released four pairs (four females + four males) of field voles
184 or four pairs of sibling voles in the centre (short vegetation patch) of randomly selected
185 predator-proof enclosures [treatment: “no competition, no predation”, (C-P-); $n = 2$ enclosures
186 for each species, Fig. 1]. Two pairs each of both species were released in the centre of the
187 remaining enclosures [“competition, no predation”, (C+P-); $n = 4$ enclosures] and the centre
188 of fenced controls [“competition, predation”, (C+P+); $n = 3$ fenced controls]. Thus, all
189 replicates were founded with an equal density of 8 voles per enclosure (16 voles/ha). A
190 treatment “no competition, predation, (C-P+)” is unfortunately missing from a full 2x2 design
191 due to logistic reasons, i.e. limited number of available study sites.

192 Population growth of voles was monitored by live-trapping on seven occasions from the
193 end of July to the beginning of November, using standard capture-mark-recapture techniques.
194 The time between trappings was ca. 2.5 weeks, being shortest at the beginning of the
195 experiment and longer towards the end of the experiment (range 2-4 weeks). Each trapping
196 period lasted six days. Two sites were trapped first for three days and then the other two sites
197 were trapped for the next three days. Traps were baited with Rat/Mouse Breeding Diet pellets
198 (Altromin GmbH, Germany) and checked three times per day, in the morning (at 6:00), in the
199 afternoon (14:00) and in the evening (21:00). Voles were marked individually, weighed,
200 sexed, and their current reproductive status noted. In all enclosures during the whole study

201 period we caught altogether 11 bank voles (*Myodes glareolus* Schreber, 1780), one house
202 mouse (*Mus musculus* L., 1758) and 20 harvest mice (*Micromys minutus* Pallas, 1771) in
203 addition to the study species. Of these species, only bank voles are potential competitors for
204 the study species. Bank voles have a different diet than *Microtus* voles, but they can still
205 compete for space. *Microtus* voles are, however, competitively superior to bank voles
206 (Henttonen et al. 1977), so we did not expect bank vole presence in this low numbers to affect
207 the competitive outcome between the *Microtus*. However, all the other rodents than *Microtus*
208 voles were removed from the experimental enclosures when encountered to avoid any
209 potential interference in our results. They were taken out of the enclosure and released to a
210 suitable habitat in a nearby location.

211

212 **Statistical analyses**

213 Estimates of population density for voles were calculated from trapping data using the
214 jackknife estimator for model M_h in the program CAPTURE (Otis et al. 1978) with separate
215 estimates for each species in all enclosures. Results of the ensuing differences in population
216 dynamics of the voles when protected from predation, with and without the competing species
217 present are reported in Koivisto et al. (2007).

218 As an individual habitat selection index, we calculated the proportion of captures for each
219 individual vole that occurred within the low cover habitat. Due to low population densities,
220 particularly in the beginning of the experiment, we pooled enclosure-specific data from the
221 first three trapping occasions into one period. Data for trapping occasions four and five, and
222 for six and seven, were similarly combined into two separate periods, thereby reducing the
223 number of trapping periods to three. Individuals appear in the data only once per period, but

224 they may appear in more than one period across the whole dataset. Due to the unbalanced
225 study design (no treatment C-P+ due to constraints of study sites), the effects of competition
226 and predation were tested separately (C+P- vs. C-P- and C+P+ vs. C+P-, respectively). This
227 separation allowed us to observe how competition affects habitat use of field voles and sibling
228 voles, and how predation moderates the habitat use under competition. However, we cannot
229 evaluate whether predation without competition would elicit similar responses as predation
230 with competition or not. All analyses were performed using R statistical software (Version
231 3.1.2, R Core Team 2014).

232 Effects of competition (1068 captures of 837 individuals from 8 populations) and
233 predation (634 captures of 505 individuals from 7 populations) were analysed separately by
234 fitting generalized linear mixed models using the function glmer in package lme4 (Bates et al.
235 2014) with individual habitat selection index as a response variable, assuming a binomial
236 response distribution because the index is based on proportions. We set enclosure identity as a
237 random intercept to control for the experimental design, but did not include individual ID as
238 only a small fraction of individuals (ca 20%) were observed more than once. Treatment
239 (competition or predation), species, trapping period, the combined average density of both
240 vole species in each enclosure, and their two- and three-way interactions were evaluated as
241 explanatory variables. Combined density for both species was mean centred, i.e. the mean
242 value was subtracted from the mean, to facilitate model convergence and parameter
243 estimation, following suggestions by Gelman and Hill (2006). True densities ranged 2.7 –
244 91.50 (sibling vole populations, C-), 10.0 – 93.0 (field vole populations, C-), 3.7 – 93.0
245 (combined populations without predation, C+P-) and 6.7 – 70.5 (combined populations with

246 predation, C+P+). We used the combined vole density as models fitted with combined density
247 had lower AICc-values than models fitted with intraspecific density and allowed more
248 flexibility in modelling. Estimates and figures indicate that combined vole density
249 approximated intraspecific density, and results are essentially the same regardless of which
250 density measure we use (see Supplementary material S1 for results using centred intraspecific
251 density).

252 We checked the models for (multi-) collinearity by calculating variance inflation factors
253 (VIF) for the models. VIF values above 10 indicate collinearity issues (Graham 2003). We
254 found that in both competition and predation models that simultaneously included trapping
255 period and rodent density as explanatory factors, routinely showed VIF values above 20. The
256 high VIF values suggest high collinearity between the two factors as models run with only
257 density or period showed VIF values < 5 . Furthermore, density significantly increased with
258 successive trapping occasions (competition sub-data: $R^2_{\text{adj}} = 0.14$, $F_{1,22} = 4.845$, $P = 0.039$;
259 predation sub-data: $R^2_{\text{adj}} = 0.38$, $F_{1,19} = 13.350$, $P = 0.002$), and we have no reason to believe
260 that other factors mediated through trapping period would affect distribution between high
261 and low cover habitats differently. Therefore, we further report findings from models
262 (competition and predation) that include species, treatment and centred density with two- and
263 three-way interactions. Including trapping period in the models did not change the results
264 qualitatively, i.e. the response to density did not differ between trapping occasions.

265 Since changes in relative habitat use with increasing density may differ between age
266 groups, we also ran similar models as described above that included age (adult or juvenile)
267 and interactions with centred combined density, species and treatment. Although there were
268 significant effects of the interaction between age and treatment, the proportional use of the

269 low cover habitat did not differ markedly between age groups. We therefore describe these
270 results in Supplementary material S2.

271

272 Results

273 The two vole species responded differently to the presence of interspecific competition in
274 their use of the low cover habitat as evident from significant interactions between treatment
275 and species ($\chi^2 = 23.6$, $P < 0.001$) and density and species ($\chi^2 = 4.8$, $P = 0.029$). The
276 interaction effect between density and species was further affected by treatment (three-way
277 interaction: $\chi^2 = 11.4$, $P < 0.001$, results from the full model in Table 1). Sibling voles' use of
278 low cover habitat did not respond to vole density in single-species populations (C-P-) and was
279 consistently lower than expected based on availability (0.33, i.e. 1/3 of the enclosure area). In
280 mixed-species populations (C+P-), sibling voles used low cover habitat slightly below to
281 availability at low density and decreased use of this habitat (C+P-, Fig. 2) with increasing
282 density. Field voles used the low cover habitat according to availability at low density in
283 single-species populations, and decreased their use of low cover habitat with increasing
284 density (Fig. 2). In mixed-species populations, field voles used the low cover habitat less than
285 availability and the use did not respond to increasing density (Fig. 2).

286 The two species also differed in their responses to predation as seen from the significant
287 main effect of species ($\chi^2 = 20.8$, $P < 0.001$), two-way interaction between species and
288 density ($\chi^2 = 7.6$, $P = 0.006$), and three-way interaction between treatment, density and
289 species ($\chi^2 = 8.7$, $P = 0.003$, full results in Table 1). Field voles did not respond to the
290 predation treatment (C+P+) by changing their use of the low cover habitat (Fig. 3). Sibling

291 voles used the low cover habitat as much in presence of predation as in the absence of
292 predation, but the use of low cover habitat by sibling voles decreased more strongly with
293 density in presence of predators than in the absence of predators (C+P-, Fig. 3).

294

295 Discussion

296 We found significant differences in habitat use between the two vole species in response to
297 sympatric interspecific competitors, population density and predation risk. When the species
298 occurred alone, without the influence of competition or predation risk, field voles used the
299 low cover habitat according to habitat availability (0.33, i.e. one third of the enclosure area) at
300 low population densities while showing a density-dependent decrease in proportion of use,
301 following so ideal-free distribution and supporting our first prediction. A potential
302 mechanistic explanation for this observed pattern is that field voles favour certain plants that
303 were more abundant in the mowed area when vole densities were low. As densities grew, the
304 preferred plants may have been eliminated (see Norrdahl et al. 2002), which could have led to
305 a decrease in the relative use of low cover habitat (Hansson 1995).

306 Conversely, in absence of interspecific competition sibling voles used the short grass
307 below to its availability, even at low densities without predation risk, thus contradicting our
308 first prediction in contrast to field voles. This pattern could be due to sibling voles being more
309 susceptible to predation than field voles (Norrdahl and Korpimäki 1993; Koivisto et al. 2008;
310 Hoset et al. 2009) and innately perceiving low cover habitat as too risky. Even though there
311 was no actual predation in the predator-proof enclosures, there can be occasional avian
312 predators, including Eurasian kestrels (*Falco tinnunculus* L., 1758), short-eared owls (*Asio*

313 *flammeus* Pontoppidan, 1763) and long-eared owls (*A. otus* L., 1758) flying above the
314 enclosures, which may elicit anti-predatory behaviour (Gerkema and Verhulst 1990). Based
315 on the overall higher use of high cover habitat by voles, the main source of predation risk also
316 in the control areas with natural predation was more likely the presence of avian predators
317 than the presence of small mustelids hunting in the cover (see Haapakoski et al. 2015).

318 When exposed to interspecific competition but not to predation risk, field voles used the
319 low cover habitat less than in single-species populations, while sibling voles conversely used
320 the low cover habitat more in mixed-species populations than in single-species populations.
321 We found thus support for the prediction that sibling voles use the low cover habitat more
322 than field voles under competition. In fact, sibling voles used low cover habitat close to its
323 availability at low densities and showed density-dependent response in the relative habitat
324 use. Field voles neither used low cover habitat under competition, nor showed any density-
325 dependent response in use. This is probably due to sibling voles being better adapted to low
326 vegetation cover habitats than field voles. Alternatively, sibling voles might have responded
327 differently to increasing population densities in the presence of field voles than when alone
328 due to their better tolerance towards higher densities of conspecific than interspecific
329 competitors, as sibling voles are known to form high-density patches (Norrdahl and
330 Korpimäki 1993).

331 Under coexistence in the absence of predation, the two species behaved as previously
332 reported (Myllymäki 1977; Norrdahl and Korpimäki 1993): sibling voles used the low cover
333 habitat proportionally more than field voles. The response of field voles to interspecific
334 competition by niche contraction has previously been documented in voles (e.g. Eccard and
335 Ylönen 2002). Field voles may opt for safer, high cover habitats because of the possibility that

336 aggregations of sibling voles lure more predators to an area (apparent competition, Holt
337 1977). Alternatively, the observed pattern could also result from apparent predation, a process
338 in which subordinate animals increase their use of safe foraging patches, not as a response to
339 predation risk, but in response to the density increase of nearby dominant competitors (Morris
340 2009; Halliday and Morris 2013).

341 We found partial support for prediction three, that sibling voles respond more strongly to
342 predation than field voles. Sibling voles showed a steeper density-dependent reduction in their
343 use of low cover habitat when exposed to predation than in the absence of it. Overall, the
344 observed patterns were similar to what was observed in mixed-species populations in the
345 absence of predation. The observed reduction in the relative use of low cover habitat at high
346 density is in contrast to earlier accounts of sibling vole habitat preferences (Myllymäki 1977;
347 Norrdahl and Korpimäki 1993), but do follow the predictions of ideal-free distribution
348 between a preferred habitat and a less preferred habitat (Lucas and Fretwell 1970).

349 In this experiment, sibling voles in control areas may have either reacted to a perceived
350 risk of avian predation by shifting more to high cover or been selectively removed from the
351 population. Unfortunately, no data exist to verify which of these the most likely cause is.
352 Nonetheless, due to their tendency of forming high-density patches (Norrdahl and Korpimäki
353 1993), sibling voles have been suggested to be particularly vulnerable to patch-searching
354 avian predators (Korpimäki 1992; Koivunen et al. 1996). By contrast, field voles under
355 interspecific competition barely used the low cover habitat to begin with, so there was no
356 need for them to shift habitat in response to avian predation risk. While the use of high cover
357 might be effective against avian predators, it may predispose voles to small mustelids hunting
358 under cover (Korpimäki and Norrdahl 1989; Brandt and Lambin 2007). Data from the same

359 enclosures show that weasels almost solely used the high cover habitat, while avian predators
360 preferred low cover (Koivisto et al. 2016). Voles appear either to consider avian predators a
361 bigger threat than mammalian predators or to have more evolved anti-predator strategies
362 against the former, and commonly respond more strongly to avian predation risk (Korpimäki
363 et al. 1996; see also Fey et al. 2006).

364 Based on the differences in responses found here, the coexistence of these two sympatric
365 small mammal species cannot be explained by temporally consistent differences in habitat
366 use. Coexistence may, however, be facilitated by divergent fitness benefits in different
367 habitats with and without competition, as has been suggested for habitat use of *Microtus* voles
368 compared to *Myodes* voles (Morris and Grant 1972). The use of low cover habitat observed in
369 sibling voles in the absence of predators in single-species populations without competition
370 and in mixed-species populations with competition suggests that sibling voles use more the
371 safe habitat when there are no competitors, but are prone to use the more risky habitat when
372 competitors are present, indicating that the fitness benefits of each habitat depend on the
373 presence or absence of competitors. Alternatively, other yet not identified mechanisms, such
374 as differences in vigilance between the species (Dupuch et al. 2013), could explain the
375 coexistence of these vole species under temporal dynamics of fear. Although sibling voles use
376 the low cover habitat according to availability at the lowest population densities also under
377 predation, at medium densities most individuals already use the less risky high cover habitat.
378 Without predation, a higher proportion of sibling voles would still use the low cover habitat at
379 similar medium densities. Our results thus highlight the importance of including effects of
380 both predation risk and competition when interpreting the patterns of habitat distribution

381 observed in nature among coexisting species and not take them solely as a result of one or the
382 other (see also e.g. Morris 2009; Dupuch et al. 2014).

383

384

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657 Figure legends

658 **Fig. 1** Schematic illustration of the experimental design showing 1) the different treatments
659 with sample sizes on the top and 2) division of habitat types and relative location of trapping
660 stations in each enclosure and control area below.

661

662 **Fig. 2** The estimated (lines, mean \pm confidence interval) and observed (bars, mean \pm SE)
663 proportions of low cover habitat use by sibling voles (*Microtus levis*) and field voles (*M.*
664 *agrestis*) relative to vole densities in the absence (C-P-) and presence (C+P-) of interspecific
665 competitors (C). P- refers to the absence of predators. Centred vole density refers to the
666 pooled (and centred) density of both vole species when under coexistence (C+), and
667 conspecific centred density when the species occurs alone (C-). The horizontal dotted line
668 represents short grass usages according to availability (0.33).

669

670 **Fig. 3** The estimated (lines, mean \pm confidence interval) and observed (bars, mean \pm SE)
671 proportions of low cover habitat use by sibling voles (*Microtus levis*) and field voles (*M.*
672 *agrestis*) relative to vole densities in the absence (C+P-) and presence (C+P+) of avian and
673 mammalian predators (P). C+ refers to all populations including both sibling voles and field
674 voles. Centred vole density refers to the pooled density of both vole species. The horizontal
675 dotted line represents short grass usages according to availability (0.33).

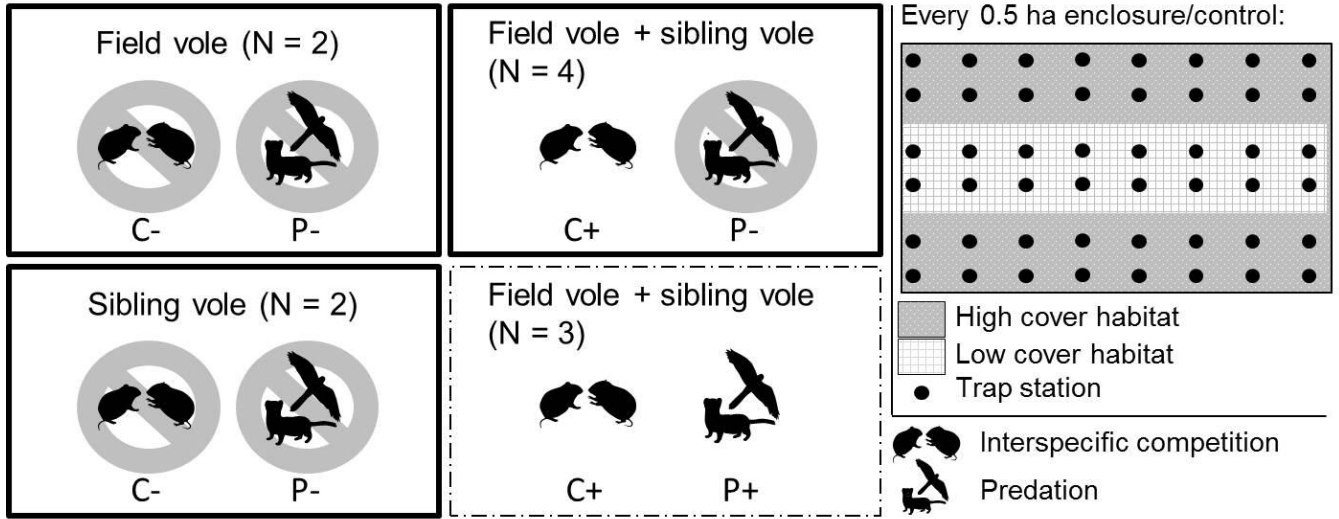
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679 Figures

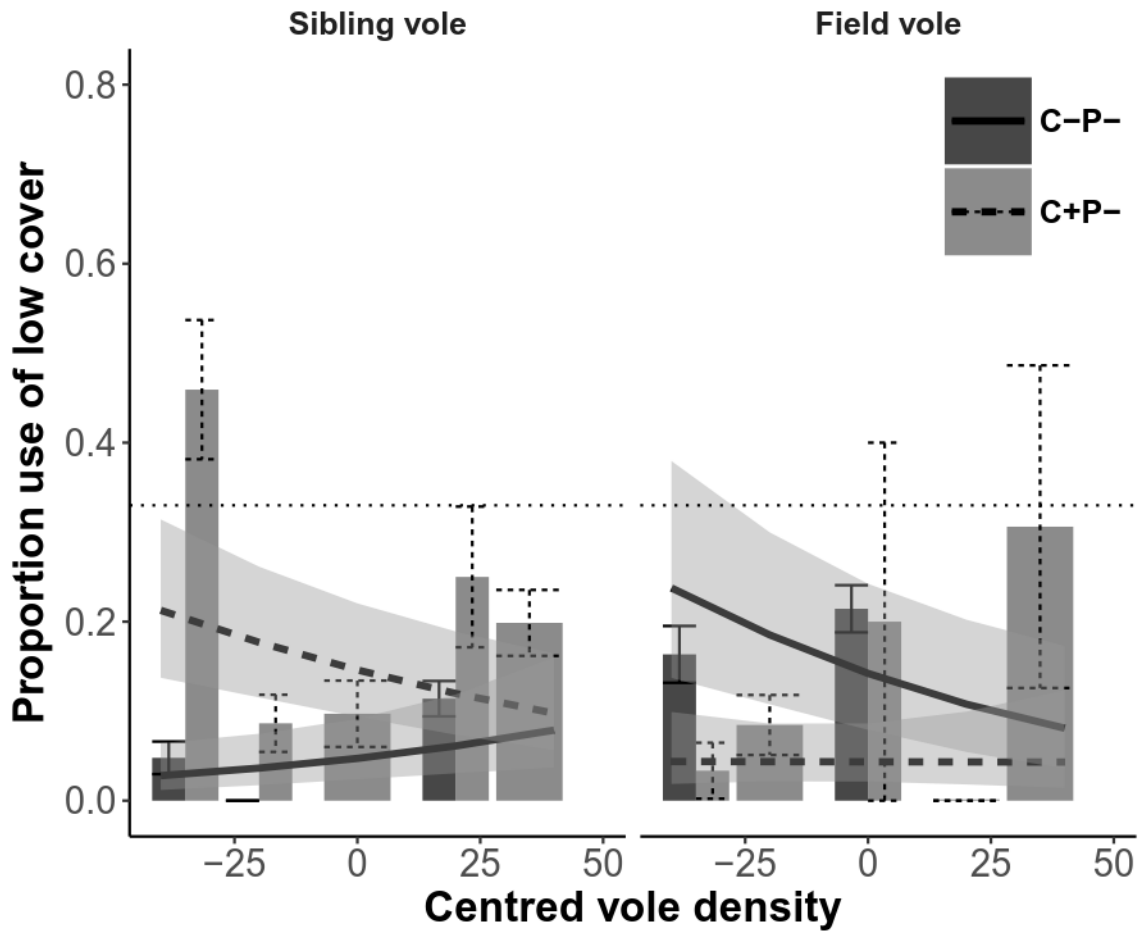
680 Fig. 1



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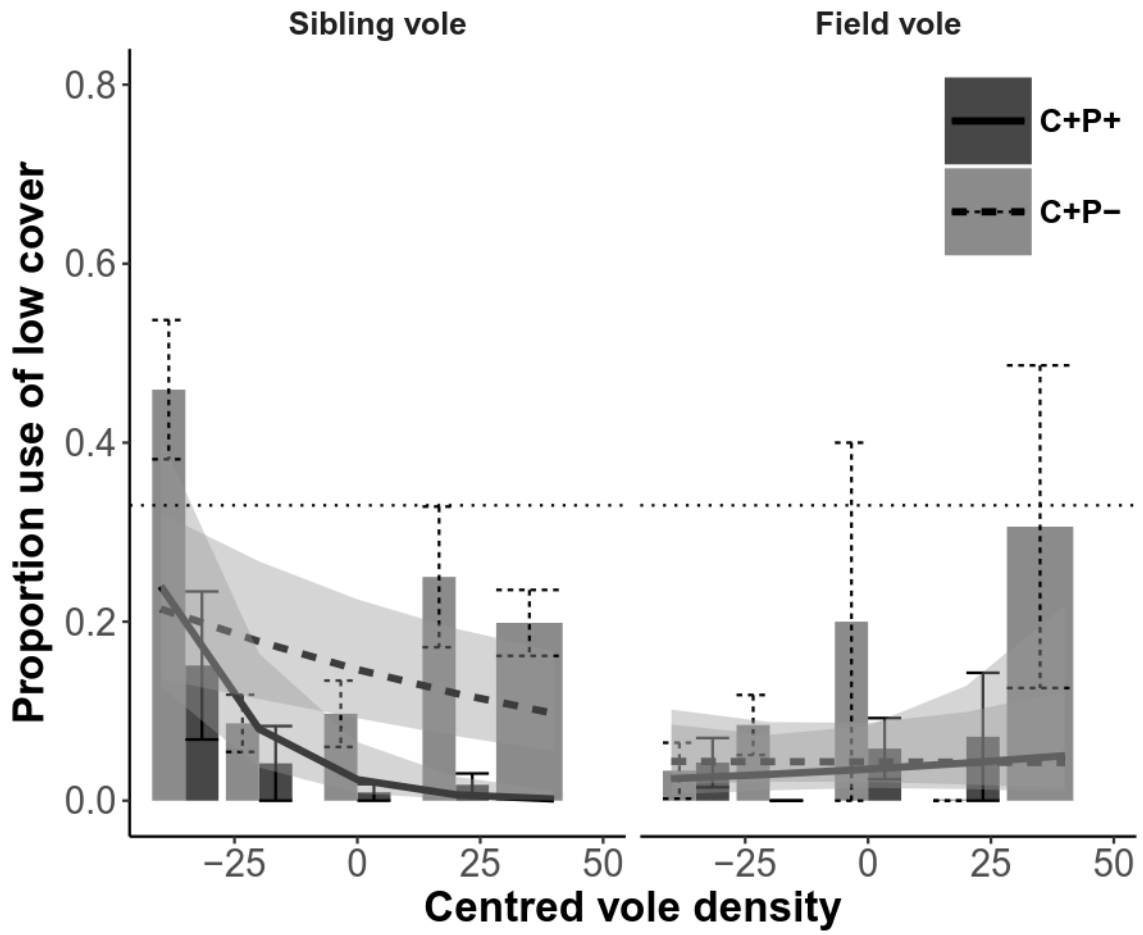
683 Fig. 2



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689 Tables

690 Table 1 Model output from generalized mixed models on the effect of competition (1068
 691 captures of 837 voles from 8 populations) and predation (634 voles from 7 populations) on the
 692 proportional use of the low cover habitat. Data provided are effect estimates and their
 693 standard errors (Estimate and Std. Error), degrees of freedom (DF), z-values and P-values.
 694 Intercept represents the species sibling vole (*Microtus levis*) in the control treatment.
 695 Treatment refers to either competition or predation, depending on the model. Species_FV
 696 refers to field voles (*M. agrestis*). All significant effects are shown in italics.
 697

	Estimate	St. Error	DF	z-value	P-value
Competition model					
<i>Intercept</i>	<i>-3.004</i>	<i>0.362</i>	<i>1</i>	<i>-8.303</i>	<i>P < 0.001</i>
<i>Treatment</i>	<i>1.238</i>	<i>0.439</i>	<i>1</i>	<i>2.819</i>	<i>P = 0.005</i>
<i>Species_FV</i>	<i>1.207</i>	<i>0.492</i>	<i>1</i>	<i>2.451</i>	<i>P = 0.014</i>
<i>Centred density</i>	<i>0.014</i>	<i>0.006</i>	<i>1</i>	<i>2.387</i>	<i>P = 0.017</i>
<i>Treatment×Species_FV</i>	<i>-2.533</i>	<i>0.589</i>	<i>1</i>	<i>-4.297</i>	<i>P < 0.001</i>
<i>Treatment×cen.den</i>	<i>-0.025</i>	<i>0.006</i>	<i>1</i>	<i>-3.895</i>	<i>P < 0.001</i>
<i>Species_FV×cen.den</i>	<i>-0.029</i>	<i>0.008</i>	<i>1</i>	<i>-3.833</i>	<i>P < 0.001</i>
<i>Treatment×Species_FV×cen.den</i>	<i>0.041</i>	<i>0.012</i>	<i>1</i>	<i>3.371</i>	<i>P < 0.001</i>

Predation model

<i>Intercept</i>	-1.762	0.268	1	-6.579	$P < 0.001$
<i>Treatment</i>	-1.964	0.602	1	-3.265	$P = 0.001$
<i>Species_FV</i>	-1.333	0.324	1	-4.113	$P < 0.001$
<i>Centred density</i>	-0.012	0.003	1	-3.484	$P < 0.001$
<i>Treatment</i> × <i>Species_FV</i>	1.749	0.672	1	2.602	$P = 0.009$
<i>Treatment</i> × <i>cen.den</i>	-0.053	0.012	1	-4.383	$P < 0.001$
<i>Species_FV</i> × <i>cen.den</i>	0.011	0.009	1	1.204	$P = 0.229$
<i>Treatment</i> × <i>Species_FV</i> × <i>cen.den</i>	0.062	0.021	1	2.948	$P = 0.003$

698

Supplementary material

Koivisto, E., Hoset, K.S., Huitu, O., and Korpimäki, E. Habitat use of coexisting *Microtus* vole species under competition and predation risk.

Supplementary material S1: Use of low cover habitat in response to intraspecific and combined vole density

Competition

The responses in use of low cover habitat to increased density was similar whether we fitted models with the combined density of both species (which equals intraspecific density in single-species populations), or only with intraspecific density (see results in Table S1 and Figure S1). Models including combined vole density had lower AICc-values than models fitted with intraspecific density ($\Delta\text{AICc} = 0.909$).

Table S1 Model output from generalized mixed models on the effect of competition (1068 observations of 837 voles from 8 populations) on the proportional use of the low cover habitat with centred intraspecific density as explanatory factor. Data provided are effect estimates and their standard errors (Estimate and St. Error), degrees of freedom (DF), z-values and P-values. Intercept represents the species sibling vole (*Microtus levis*) in the control treatment. Treatment refers to competition and Species_FV refers to field voles (*M. agrestis*). All significant effects are shown in italics.

	Estimate	St. Error	DF	z-value	P-value
Competition model					
<i>Intercept</i>	<i>-3.004</i>	<i>0.362</i>	<i>1</i>	<i>-8.301</i>	<i>P < 0.001</i>
<i>Treatment</i>	<i>1.238</i>	<i>0.439</i>	<i>1</i>	<i>2.818</i>	<i>P = 0.005</i>
<i>Species_FV</i>	<i>1.207</i>	<i>0.492</i>	<i>1</i>	<i>2.451</i>	<i>P = 0.014</i>
<i>Centred intraspecific density</i>	<i>0.014</i>	<i>0.006</i>	<i>1</i>	<i>2.387</i>	<i>P = 0.017</i>
<i>Treatment×Species_FV</i>	<i>-2.533</i>	<i>0.590</i>	<i>1</i>	<i>-4.296</i>	<i>P < 0.001</i>
<i>Treatment×cen.intra.den</i>	<i>-0.025</i>	<i>0.006</i>	<i>1</i>	<i>-3.895</i>	<i>P < 0.001</i>
<i>Species_FV×cen.intra.den</i>	<i>-0.029</i>	<i>0.008</i>	<i>1</i>	<i>-3.833</i>	<i>P < 0.001</i>
<i>Treatment×Species_FV×cen.intra.den</i>	<i>0.041</i>	<i>0.012</i>	<i>1</i>	<i>3.371</i>	<i>P < 0.001</i>

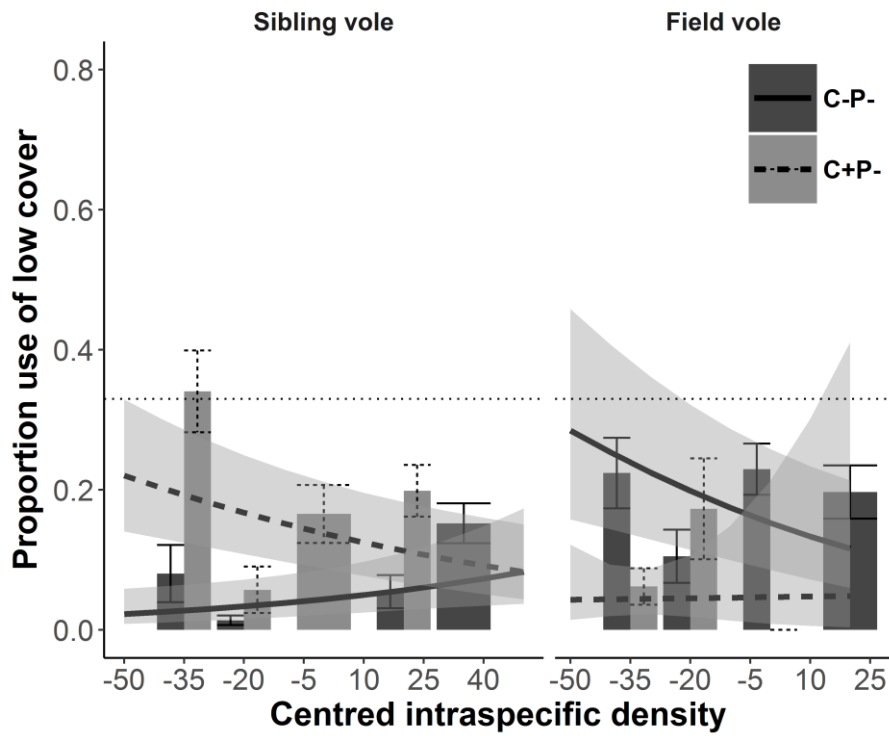


Fig. S1 The estimated (lines, mean \pm confidence interval) and observed (bars, mean \pm SE) proportions of low cover habitat use by sibling voles (*Microtus levis*) and field voles (*M. agrestis*) relative to intraspecific densities in the absence (C-P-) and presence (C+P-) of interspecific competitors (C). P- refers to the absence of predators. The horizontal dotted line represents short grass usages according to availability (0.33).

Predation

As with the models on competition, models for predation with combined density showed lower AICc-values than models with intraspecific density ($\Delta\text{AICc} = 7.652$). Models with intraspecific density as explanatory factor were also simpler and included only a significant two-way interaction between treatment and density. Results on responses in use of low cover habitat including intraspecific density are summarised in Table S2 and Figure S2.

Table S2 Model output from generalized mixed models on the effect of predation (634 voles from 7 populations) on the proportional use of the low cover habitat with centred intraspecific density as explanatory factor. Data provided are effect estimates and their standard errors (Estimate and St. Error), degrees of freedom (DF), *z*-values and *P*-values. Intercept represents the species sibling vole (*Microtus levis*) in the control treatment. Treatment refers to predation and Species_FV refers to field voles (*M. agrestis*). All significant effects are shown in italics.

	Estimate	St. Error	DF	<i>z</i> -value	<i>P</i> -value
Predation model					
<i>Intercept</i>	<i>-1.734</i>	<i>0.300</i>	<i>1</i>	<i>-5.787</i>	<i>P < 0.001</i>
<i>Treatment</i>	<i>-1.776</i>	<i>0.582</i>	<i>1</i>	<i>-3.053</i>	<i>P = 0.002</i>
<i>Species_FV</i>	<i>-1.514</i>	<i>0.254</i>	<i>1</i>	<i>-5.950</i>	<i>P < 0.001</i>
<i>Centred intraspecific density</i>	<i>-0.011</i>	<i>0.003</i>	<i>1</i>	<i>-3.449</i>	<i>P < 0.001</i>
<i>Treatment</i> × <i>cen.intra.den</i>	<i>-0.053</i>	<i>0.012</i>	<i>1</i>	<i>-4.383</i>	<i>P < 0.001</i>

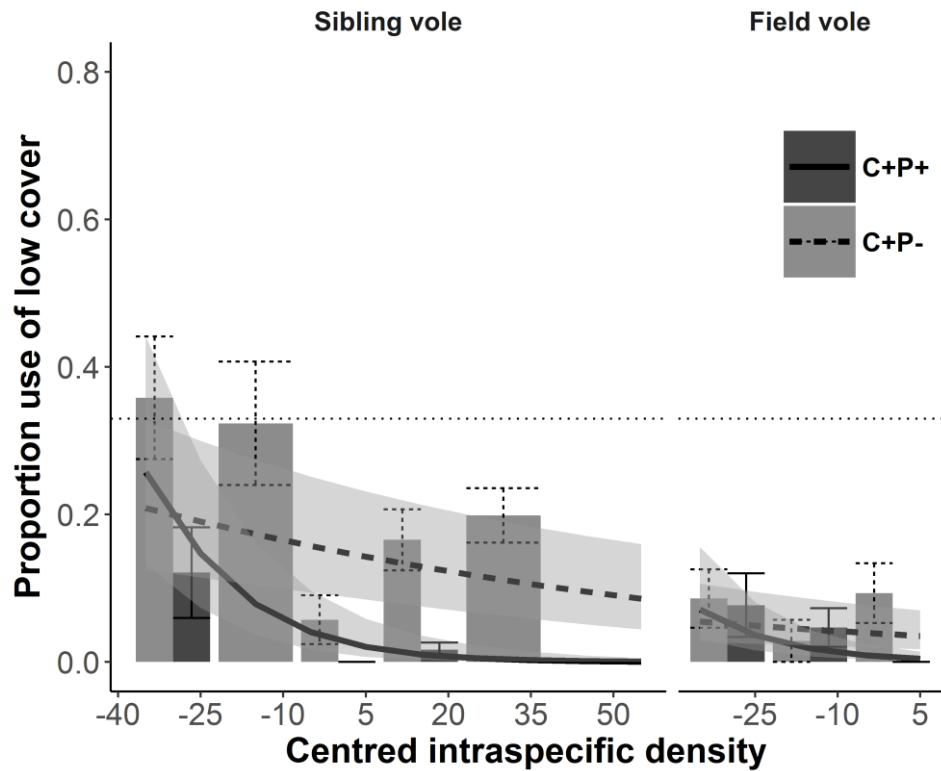


Fig. S2 The estimated (lines, mean \pm confidence interval) and observed (bars, mean \pm SE) proportions of low cover habitat use by sibling voles (*Microtus levis*) and field voles (*M. agrestis*) relative to centred intraspecific density in the absence (C+P-) and presence (C+P+) of avian and mammalian predators (P). C+ refers to all populations including both sibling voles and field voles. The horizontal dotted line represents short grass usages according to availability (0.33).

Supplementary material S2: The effect of age on habitat use

Results of competition effects on habitat use including age effects are summarised in Table S3, Figure S3 for field voles and Figure S4 for sibling voles. Results on predation effects on habitat use including age effects are summarised in Table S4, Figure S5 for field voles and Figure S6 for sibling voles.

Table S3 Model output from generalized mixed models on the effect of competition on the proportional use of the low cover habitat including age and interactions with treatment, species and density as explanatory factors. Data provided are effect estimates and their standard errors (Estimate and St. Error), degrees of freedom (DF), z-values and P-values. Intercept represents the species sibling vole (*Microtus levis*) in the control treatment. Treatment refers to competition, Species_FV refers to field voles (*M. agrestis*), and Age_juv refers to juveniles. All significant effects are shown in italics.

	Estimate	Std. Error	DF	z-value	P-value
Competition model					
<i>Intercept</i>	-2.972	0.390	1	-7.615	<i>P < 0.001</i>
Treatment	0.888	0.484	1	1.834	P = 0.067
<i>Species_FV</i>	<i>1.202</i>	<i>0.521</i>	1	<i>2.307</i>	<i>P = 0.021</i>
<i>Centred combined density</i>	<i>0.014</i>	<i>0.006</i>	1	<i>2.389</i>	<i>P = 0.017</i>
Age_juv	-0.078	0.159	1	-0.489	P = 0.625
<i>Treatment×Species_FV</i>	<i>-2.485</i>	<i>0.616</i>	1	<i>-4.033</i>	<i>P < 0.001</i>
<i>Treatment×cen.den</i>	<i>-0.030</i>	<i>0.007</i>	1	<i>-4.449</i>	<i>P < 0.001</i>
<i>Species_FV×cen.den</i>	<i>-0.029</i>	<i>0.008</i>	1	<i>-3.814</i>	<i>P < 0.001</i>
<i>Treatment×Age_juv</i>	<i>0.684</i>	<i>0.262</i>	1	<i>2.616</i>	<i>P = 0.009</i>
<i>Treatment×Species_FV×cen.den</i>	<i>0.043</i>	<i>0.012</i>	1	<i>3.494</i>	<i>P < 0.001</i>

Table S4 Model output from generalized mixed models on the effect of competition on the proportional use of the low cover habitat including age and interactions with treatment, species and density as explanatory factors. Data provided are effect estimates and their standard errors (Estimate and Std. Error), degrees of freedom (DF), z-values and P-values. Intercept represents the species sibling vole (*Microtus levis*) in the control treatment. Treatment refers to competition, Species_FV refers to field voles (*M. agrestis*), and Age_juv refers to juveniles. All significant effects are shown in italics.

	Estimate	Std. Error	DF	z-value	P-value
Predation model					
<i>Intercept</i>	-2.239	0.306	1	-7.311	<i>P < 0.001</i>
<i>Treatment</i>	<i>-1.855</i>	<i>0.604</i>	1	<i>-3.073</i>	<i>P = 0.002</i>
<i>Species_FV</i>	<i>-1.219</i>	<i>0.331</i>	1	<i>-3.679</i>	<i>P < 0.001</i>
Age_juv	0.612	0.218	1	2.807	P = 0.005
<i>Centred intraspecific density</i>	<i>-0.028</i>	<i>0.006</i>	1	<i>-5.019</i>	<i>P < 0.001</i>
<i>Treatment×Species_FV</i>	<i>1.723</i>	<i>0.674</i>	1	<i>2.554</i>	<i>P = 0.011</i>
<i>Treatment×cen.den</i>	<i>-0.045</i>	<i>0.012</i>	1	<i>-3.728</i>	<i>P < 0.001</i>
Species_FV×cen.den	0.018	0.009	1	1.858	P = 0.063
<i>Age_juv×cen.den</i>	<i>0.022</i>	<i>0.007</i>	1	<i>3.306</i>	<i>P < 0.001</i>
<i>Treatment×Species_FV×cen.den</i>	<i>0.057</i>	<i>0.021</i>	1	<i>2.674</i>	<i>P = 0.007</i>

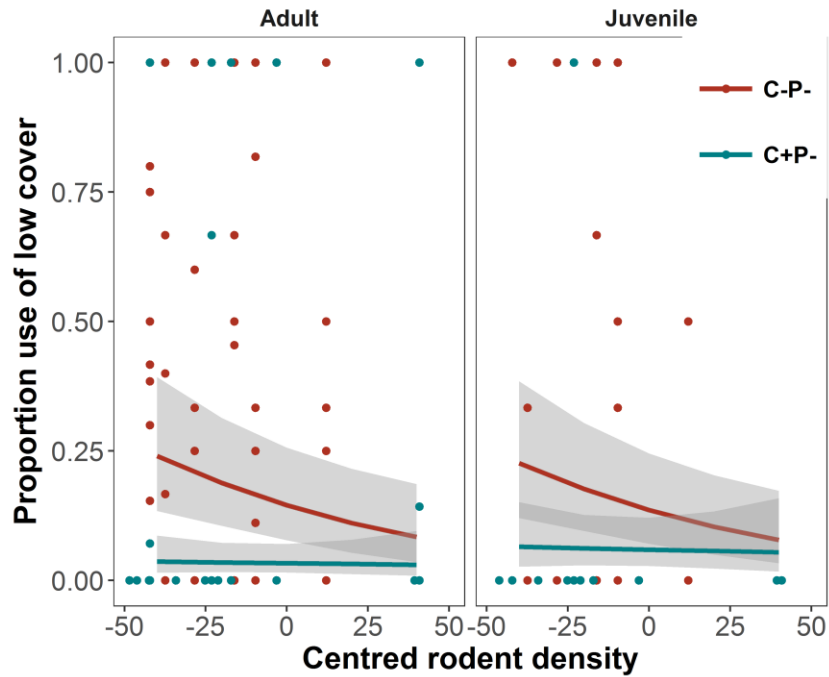


Fig. S3 Proportion use of low cover habitat for adult and juvenile field voles (*Microtus agrestis*) relative to vole densities in the absence (C-P-) and presence (C+P-) of interspecific competitors (C). P- refers to the absence of predators. Centred vole density refers to the pooled (and centred) density of both vole species when under coexistence (C+), and conspecific centred density when the species occurs alone (C-).

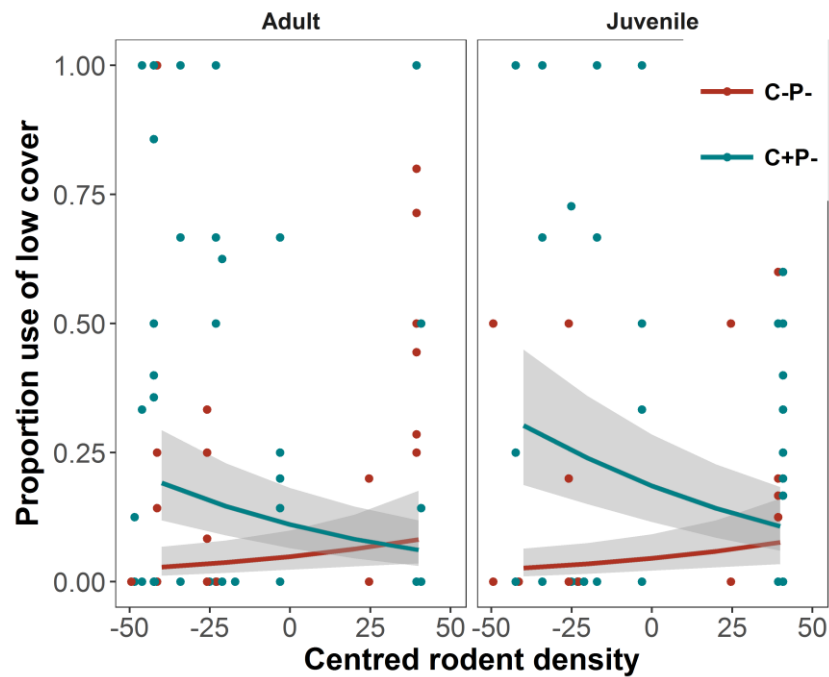


Fig. S4 Proportion use of low cover habitat for adult and juvenile sibling voles (*Microtus levis*) relative to vole densities in the absence (C-P-) and presence (C+P-) of interspecific competitors (C). P- refers to the absence of predators. Centred vole density refers to the pooled (and centred) density of both vole species when under coexistence (C+), and conspecific centred density when the species occurs alone (C-).

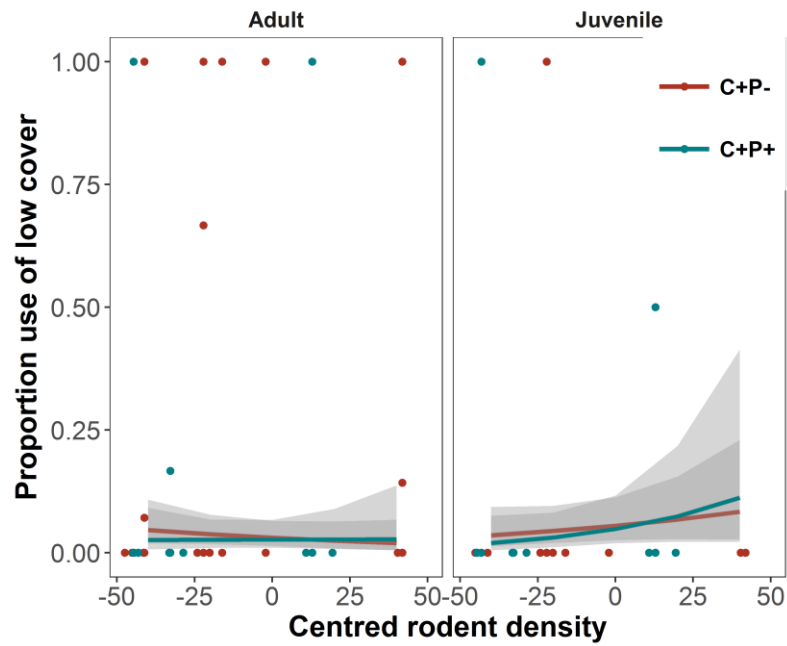


Fig. S5 Proportion use of low cover habitat for adult and juvenile field voles (*Microtus agrestis*) relative to centred vole density in the absence (C+P-) and presence (C+P+) of avian and mammalian predators (P). C+ refers to all populations including both sibling voles (*M. levis*) and field voles.

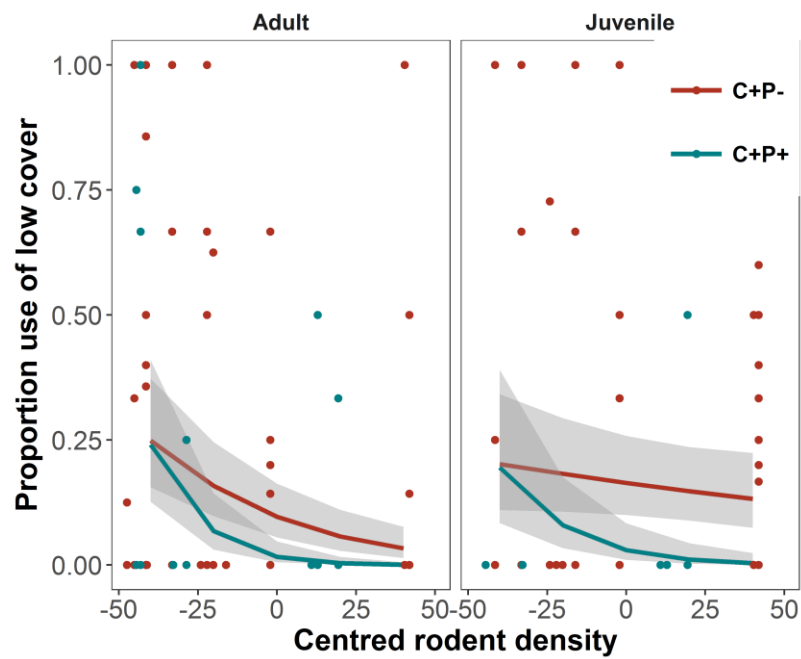


Fig. S6 Proportion use of low cover habitat for adult and juvenile sibling voles (*Microtus levis*) relative to centred vole density in the absence (C+P-) and presence (C+P+) of avian and mammalian predators (P). C+ refers to all populations including both sibling voles and field voles (*M. agrestis*).