Canadian Journal of Zoology
Revue canadienne de zoologie

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

Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2016-0272.R2
Manuscript Type:	Article
Date Submitted by the Author:	02-Aug-2017
Complete List of Authors:	Koivisto, E.; Turun Yliopisto, Biology Hoset, Katrine; Turun Yliopisto, Biology Huitu, Otso; Turun Yliopisto, Biology; Luonnonvarakeskus Korpimäki, Erkki; Turun Yliopisto, Biology
Keyword:	RODENTS;SHREWS < Taxon, BEHAVIOUR < Discipline, COMPETITION < Discipline, PREDATION < Discipline, SYMPATRY < Discipline, Microtus agrestis, Microtus levis

SCHOLARONE™
Manuscripts

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

Koivisto, E.^{1*}, Hoset, K.S.², Huitu, O.³⁺ and Korpimäki, E.⁴.

¹ Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland,
elanko@utu.fi

² Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland,
kathos@utu.fi

³ Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland

⁺ Current address: Natural Resources Institute Finland, FI-33720 Tampere, Finland,
otso.huitu@luke.fi

⁴ Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland ,
ekorpi@utu.fi

* **Corresponding author:** Elina Koivisto, Tel: +358-41-4492300, fax: +358-2-333 6598,
email: elanko@utu.fi

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

Abstract

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

Draft

Introduction

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

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

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

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

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

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

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

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

Methods

Study system

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

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

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

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

Conduct of the experiment

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

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

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

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

Statistical analyses

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

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

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

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

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

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

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

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

Results

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

Acknowledgements

Pirjo Isotupa, Emmu Lahtinen, Teppo Puolakka and Rauno Varjonen are thanked for assisting in field work and Mari S. Lyly for providing the animal drawings. Farmers Matti Antila and Jaakko Yli-Härsilä kindly allowed maintaining fences on their property, and the Ikola family offered accommodation and other facilities. Research was conducted under institutional animal use permit no STO/1053(8.9.199), 1132/712-92, 1286/712-86 and project animals use permit no 07-10 ESLH-2007-03499/Ym-23. This work was supported by the Academy of Finland (grant numbers 8206140, 8123379 to EKor and grant number 106036 to OH) and by the Finnish Cultural Foundation and Finnish Cultural Foundation, South Ostrobothnia Regional fund (personal grants to EKoi).

References

Abrams, P.A. 1980. Resource partitioning and interspecific competition in a tropical hermit crab community. *Oecologia*, 46(3): 365–379. Available from <http://www.jstor.org/stable/4216182> [accessed 27 October 2016].

- 401 Abramsky, Z., Rosenzweig, M.L., Pinshow, B., Brown, J.S., Kotler, B., and Mitchell, W.A.
402 1990. Habitat selection: an experimental field test with two gerbil species. *Ecology*, 71(6):
403 2358–2369. Available from <http://www.jstor.org/stable/1938646> [accessed 27 October 2016].
404
- 405 Abramsky, Z., Rosenzweig, M.L., and Subach, A. 1998. Do gerbils care more about
406 competition or predation? *Oikos*, 83(1): 75–84. Available from
407 <http://www.jstor.org/stable/3546548> [accessed 27 October 2016].
408
- 409 Bates, D., Maechler, M., Bolker, B., and Walker, S. 2014. *_lme4*: Linear mixed-effects
410 models using Eigen and S4_. R package version 1.1-7. Available from [http://CRAN.R-](http://CRAN.R-project.org/package=lme4)
411 [project.org/package=lme4](http://CRAN.R-project.org/package=lme4) [accessed 27 October 2016].
412
- 413 Bengtsson, J. 1989. Interspecific competition increases local extinction rate in a
414 metapopulation system. *Nature*, 340: 713–715. doi:10.1038/340713a0.
415
- 416 Brandt, M.J., and Lambin, X. 2007. Movement patterns of a specialist predator, the weasel
417 *Mustela nivalis* exploiting asynchronous cyclic field vole populations. *Acta Theriol.* 52(1):
418 13–25. doi:10.1007/BF03194195.
419
- 420 Case, T.J., and Gilpin, M.E. 1974. Interference competition and niche theory. *Proc. Natl.*
421 *Acad. Sci. U.S.A.* 71(8): 3073–3077. Available from
422 <http://www.pnas.org/content/71/8/3073.abstract> [accessed 27 October 2016].
423

- Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D., Richards, S.A.,
Nisbet, R.M., and Case, T.J. 2002. The interaction between predation and competition: a
review and synthesis. *Ecol. Lett.* 5(2): 302–315. doi:10.1046/j.1461-0248.2002.00315.x.
- Creel, S., Winnie, J.Jr., Maxwell, B., Hamlin, K., and Creel, M. 2005. Elk alter habitat
selection as an antipredator response to wolves. *Ecology*, 86(12): 3387–3397. doi:10.1890/05-
0032.
- Dupuch, A., Morris, D.W., and Halliday, W.D. 2013. Patch use and vigilance by sympatric
lemmings in predator and competitor-driven landscapes of fear. *Behav. Ecol. Sociobiol.*
68(2): 299–308. doi:10.1007/s00265-013-1645-z.
- Dupuch, A., Morris, D.W., Ale, S.B., Wilson, D.J., and Moore, D.E. 2014. Landscapes of fear
or competition? Predation did not alter habitat choice by Arctic rodents. *Oecologia*, 174(2):
403–412. doi:10.1007/s00442-013-2792-7.
- Eccard, J.A., and Ylönen, H. 2002. Direct interference or indirect exploitation? An
experimental study of fitness costs of interspecific competition in voles. *Oikos*, 99(3): 580–
590. Available from <http://www.jstor.org/stable/3547846> [accessed 27 October 2016].
- Eccard, J.A., and Ylönen, H. 2003. Interspecific competition in small rodents: from
populations to individuals. *Evol. Ecol.* 17(4): 423–440. doi:10.1023/A:1027305410005.

Fey, K., Banks, P.B., and Korpimäki, E. 2006. Different microhabitat preferences of field and bank voles under manipulated predation risk from an alien predator. *Ann. Zool. Fenn.* 43(1): 9–16. Available from <http://www.jstor.org/stable/23735895> [accessed 27 October 2016].

Fretwell, S.D., and Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19: 16–36.

Gelman, A., and Hill, J. 2006. *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York.

Gerkema, M.P., and Verhulst, S. 1990. Warning against unseen predator: a functional aspect of synchronous feeding in the common vole, *Microtus arvalis*. *Anim. Behav.* 40(6): 1169–1178. Available from [http://dx.doi.org/10.1016/S0003-3472\(05\)80183-6](http://dx.doi.org/10.1016/S0003-3472(05)80183-6) [accessed 27 October 2016].

Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology*, 84(11): 2809–2815. doi:10.1890/02-3114.

Grant, P.R. 1972. Interspecific competition among rodents. *Annu. Rev. Ecol. Syst.* 3: 79–106. Available from <http://www.jstor.org/stable/2096843> [accessed 27 October 2016].

- 468 Gurevitch, J., Morrow, L.L., Wallace, A., and Walsh, J.S. 1992. A meta-analysis of
469 competition in field experiments. *Am. Nat.* 140(4): 539–572. Available from
470 <http://www.jstor.org/stable/2462913> [accessed 27 October 2016].
471
- 472 Gurevitch, J., Morrison, J.A., and Hedges, L.V. 2000. The interaction between competition
473 and predation: a meta-analysis of field experiments. *Am. Nat.* 155(4): 435–453.
474 doi:0.1086/303337.
475
- 476 Haapakoski, M., Sundell, J., and Ylönen, H. 2015. Conservation implications of change in
477 antipredator behavior in fragmented habitat: Boreal rodent, the bank vole, as an experimental
478 model. *Biol. Conserv.* 184: 11–17. Available from
479 <http://dx.doi.org/10.1016/j.biocon.2014.12.023> [accessed 27 October 2016].
480
- 481 Hairston, N.G., Smith, F.E., and Slobodkin, L.B. 1960. Community structure, population
482 control, and competition. *Am. Nat.* 94: 421–425.
483
- 484 Halliday, W.D., and Morris, D.W. 2013. Safety from predators or competitors? Interference
485 competition leads to apparent predation risk. *J. Mammal.* 94(6): 1380–1392. doi: Available
486 from <http://dx.doi.org/10.1644/12-MAMM-A-304.1> [accessed 27 October 2016].
487
- 488 Hansson, S. 1995. Effects of exploitative food competition on food niche dynamics – a
489 simulation analysis. *Ecol. Model.* 77(2–3): 167–187. doi:10.1016/0304-3800(93)E0075-E.
490

- 491 Hastings, A., and Powell, T. 1991. Chaos in a three-species food chain. *Ecology*, 72(3): 896-
492 903. doi: 10.2307/1940591.
- 493
- 494 Henttonen, H., Kaikusalo, A., Tast, J., and Viitala, J. 1977. Interspecific Competition
495 between Small Rodents in Subarctic and Boreal Ecosystems. *Oikos*, 29(3): 581–590.
496 doi:10.2307/3543596 .
- 497
- 498 Holt, R.D. 1977. Predation, apparent competition and the structure of prey communities.
499 *Theor. Popul. Biol.* 12(2): 197–229.
- 500
- 501 Hoset, K.S., Koivisto, E., Huitu, O., Ylönen, H., and Korpimäki, E. 2009. Multiple predators
502 induce risk reduction in coexisting vole species. *Oikos*, 118(9): 1421–1429.
503 doi:10.1111/j.1600-0706.2009.17263.x.
- 504
- 505 Hughes, J.J., Ward, D., and Perrin, M.R. 1994. Predation risk and competition affect habitat
506 selection and activity of Namib Desert gerbils. *Ecology*, 75(5): 1397–1405.
507 doi:10.2307/1937463.
- 508
- 509 Huitu, O., Norrdahl, K., and Korpimäki, E. 2004. Competition, predation and interspecific
510 synchrony in cyclic small mammals. *Ecography*, 27(2): 197–206. doi:10.1111/j.0906-
511 7590.2003.03684.x.
- 512

- 513 Jermacz, J., Dzierżyńska, A., Kakareko, T., Poznańska, M., and Kobak, J. 2015. The art of
514 choice: predation risk changes interspecific competition between freshwater amphipods.
515 Behav. Ecol. 26(2): 656–664. doi:10.1093/beheco/arv009.
- 516
- 517 Johannesen, E., and Mauritzen, M. 1999. Habitat selection of grey-sided voles and bank voles
518 in two subalpine populations in southern Norway. Ann. Zool. Fenn. 36(4): 215–222.
519 Available from <http://www.jstor.org/stable/23735729> [accessed 27 October 2016].
- 520
- 521 Klemola, T., Koivula, M., Korpimäki, E., and Norrdahl, K. 2000. Experimental tests of
522 predation and food hypotheses for population cycles of voles. Proc. R. Soc. Lond. B Biol. Sci.
523 267(1441): 351–356. doi:10.1098/rspb.2000.1008.
- 524
- 525 Koivisto, E., and Puseenius, J. 2003. Effects of temporal variation in the risk of predation by
526 least weasel (*Mustela nivalis*) on feeding behavior of field vole (*Microtus agrestis*). Evol.
527 Ecol. 17(5): 477–489. doi:10.1023/B:EVEC.0000005594.40721.17.
- 528
- 529 Koivisto, E., Huitu, O., and Korpimäki, E. 2007. Smaller *Microtus* vole species competitively
530 superior in the absence of predators. Oikos, 116(1): 156–162. doi:10.1111/j.2006.0030-
531 1299.15254.x.
- 532
- 533 Koivisto, E., Huitu, O., Sundell J., and Korpimäki, E. 2008. Species-specific limitation of
534 vole population growth by least weasel predation: facilitation of coexistence? Oikos, 117(1):
535 6–12. doi:10.1111/j.2007.0030-1299.15938.x.

536

537 Koivisto, E., Hoset, K.S., Le Tortorec, A.H., Norrdahl, K., and Korpimäki, E. 2016. Mobility
538 of a small mammalian predator changes according to the activity patterns of potential
539 intraguild predators. J. Zool. (Lond.) 298(2): 121–127. doi:10.1111/jzo.12293.

540

541 Koivunen, V., Korpimäki, E., Hakkarainen, H., and Norrdahl, K. 1996. Prey choice of
542 Tengmalm's owls (*Aegolius funereus funereus*): preference for substandard individuals? Can.
543 J. Zool. 74(5): 816–823. doi:10.1139/z96-094.

544

545 Koplin, J.R., and Hoffmann, R.S. 1968. Habitat overlap and competitive exclusion in voles
546 (*Microtus*). Am. Midl. Nat. 80(2): 494–507. doi:10.2307/2423541.

547

548 Korpimäki, E. 1992. Diet composition, prey choice and breeding success of Long-eared Owls:
549 effects of multiannual fluctuations in food abundance. Can. J. Zool. 70(2): 2373–2381.
550 doi:10.1139/z92-319.

551

552 Korpimäki, E., and Norrdahl, K. 1989. Avian predation on mustelids in Europe 1: occurrence
553 and effects on body size variation and life traits. Oikos, 55(2): 205–215.
554 doi:10.2307/3565424.

555

556 Korpimäki E., and Norrdahl, K. 1991. Do breeding nomadic avian predators dampen
557 population fluctuations of small mammals? Oikos, 62(2): 195–208. doi:10.2307/3545265.

558

- 559 Korpimäki, E., Koivunen, V., and Hakkarainen, H. 1996. Microhabitat use and behavior of
560 voles under weasel and raptor predation risk: predator facilitation? *Behav. Ecol.* 7(1): 30–34.
561 doi:10.1093/beheco/7.1.30.
- 562
- 563 Korpimäki, E., Norrdahl, K., Huitu, O., and Klemola, T. 2005. Predator-induced synchrony in
564 population oscillations of coexisting small mammal species. *Proc. R. Soc. Lond. B Biol. Sci.*
565 272(1559): 193–202. doi:10.1098/rspb.2004.2860.
- 566
- 567 Kotler, B.P., Brown, J.S., and Hasson, O. 1991. Factors affecting gerbil foraging behavior and
568 rates of owl predation. *Ecology*, 72(6): 2249–2260. doi:10.2307/1941575.
- 569
- 570 Lin, Y.K., and Batzli, G.O. 2001. The effect of interspecific competition on habitat selection
571 by voles: an experimental approach. *Can. J. Zool.* 79(1): 110–120. doi:10.1139/z00-184.
- 572
- 573 Luiselli, L. 2006. Resource partitioning and interspecific competition in snakes: the search for
574 general geographical and guild patterns. *Oikos*, 114(2): 193–211. doi:10.1111/j.2006.0030-
575 1299.14064.x.
- 576
- 577 Morris, D.W. 2009. Apparent predation risk: tests of habitat selection theory reveal
578 unexpected effects of competition. *Evol. Ecol. Res.* 11: 209–225.
- 579
- 580 Morris, R.D., and Grant, P.R. 1972. Experimental studies of competitive interaction in a two-
581 species system. *J. Anim. Ecol.* 41(2): 275–290. doi:10.2307/3469.

582

583 Myllymäki, A. 1977. Interactions between the field vole *Microtus agrestis* and its microtine
584 competitors in Central-Scandinavian populations. *Oikos*, 29(3): 570–580.
585 doi:0.2307/3543595.

586

587 Norrdahl, K., and Korpimäki, E. 1993. Predation and interspecific competition in two
588 *Microtus* species. *Oikos*, 67(1): 149–158. doi:10.2307/3545105.

589

590 Norrdahl, K., and Korpimäki, E. 1998. Does mobility or sex of voles affect risk of predation
591 by mammalian predators? *Ecology*, 79(1): 226–232. doi:10.2307/176877.

592

593 Norrdahl, K., Klemola, T., Korpimäki, E., and Koivula, M. 2002. Strong seasonality may
594 attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. *Oikos*, 99(3):
595 419–430. doi:10.1034/j.1600-0706.2002.12025.x.

596

597 Otis, D.L., Burnham, K.P., White, G.C., and Anderson, D.R. 1978. Statistical inference from
598 capture data on closed animal populations. *Wildl. Monogr.* 62: 1–135.

599

600 Pacala, S., and Roughgarden, J. 1982. Resource partitioning and interspecific competition in
601 two two-species insular *Anolis* lizard communities. *Science*, 217(4558): 444–446.
602 doi:10.1126/science.217.4558.444.

603

- 604 Persson, L. 1991. Behavioral response to predators reverses the outcome of competition
605 between prey species. *Behav. Ecol. Sociobiol.* 28(2): 101–105. Available from
606 <http://www.jstor.org/stable/4600523> [accessed 27 October 2016].
607
- 608 Preisser, E.L., Bolnick, D.I., and Benard, M.F. 2005. Scared to death? The effects of
609 intimidation and consumption in predator-prey interactions. *Ecology*, 86(2): 501–509.
610 doi:10.1890/04-0719.
611
- 612 Pusenius, J., and Schmidt, K.A. 2002. The effects of habitat manipulation on population
613 distribution and foraging behavior in meadow voles. *Oikos*, 98(2): 251–262.
614 doi:0.1034/j.1600-0706.2002.980207.x.
615
- 616 R Core Team 2014. R: A language and environment for statistical computing. R Foundation
617 for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/>
618 [accessed 27 October 2016].
619
- 620 Roughgarden, J. 1976. Resource partitioning among competing species – A coevolutionary
621 approach. *Theor. Popul. Biol.* 9(3): 388–424. doi:10.1016/0040-5809(76)90054-X.
622
- 623 Salo, P., Nordström, M., Thomson, R.L., and Korpimäki, E. 2008. Risk induced by a native
624 top predator reduces alien mink movements. *J. Anim. Ecol.* 77(6): 1092–1098.
625 doi:10.1111/j.1365-2656.2008.01430.x.
626

- 627 Schoener, T.W. 1974. Competition and the form of habitat shift. *Theor. Popul. Biol.* 6: 265–
628 307. doi:10.1016/0040-5809(74)90013-6.
- 629
- 630 Schoener, T.W. 1983. Field experiments on interspecific competition. *Am. Nat.* 122(2): 240–
631 285. Available from <http://www.jstor.org/stable/2461233> [accessed 27 October 2016].
- 632
- 633 Schofield, P.F. 2003. Habitat selection of two gobies (*Microgobius gulosus*, *Gobiosoma*
634 *robustum*): influence of structural complexity, competitive interactions, and presence of a
635 predator. *J. Exp. Mar. Biol. Ecol.* 288(1): 125–137. Available from
636 [http://dx.doi.org/10.1016/S0022-0981\(03\)00004-2](http://dx.doi.org/10.1016/S0022-0981(03)00004-2) [accessed 27 October 2016].
- 637
- 638 Sih, A., Crowley, P., McPeck, M., Petranka, J., and Strohmeier, K. 1985. Predation,
639 competition, and prey communities: a review of field experiments. *Annu. Rev. Ecol. Syst.* 16:
640 269–311.
- 641
- 642 van Beest, F.M., McLoughlin, P.D., Vander Wal, E., and Brook, R.K. 2014.
643 Density-dependent habitat selection and partitioning between two sympatric ungulates.
644 *Oecologia*, 175(4): 1155–1165. doi:10.1007/s00442-014-2978-7.
- 645
- 646 Wauters, L.A., Gurnell, J., Martinoli, A., and Tosi, G. 2002. Interspecific competition
647 between native Eurasian red squirrels and alien grey squirrels: does resource partitioning
648 occur? *Behav. Ecol. Sociobiol.* 52(4): 332–341. doi:10.1007/s00265-002-0516-9.

649

650 Ziv, Y., and Kotler, B.P. 2003. Giving-up densities on foraging gerbils: the effect of
651 interspecific competition on patch use. *Evol. Ecol.* 17(4): 333–347.
652 doi:10.1023/A:1027385100393.

653

654 Ziv, Y., Abramsky, Z., Kotler, B.P., and Subach, A. 1993. Interference competition and
655 temporal and habitat partition in two gerbil species. *Oikos*, 66(2): 237–246.
656 doi:10.2307/3544810.

Draft

Figure legends

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

Fig. 2 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 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-). The horizontal dotted line represents short grass usages according to availability (0.33).

Fig. 3 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 vole densities 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. Centred vole density refers to the pooled density of both vole species. The horizontal dotted line represents short grass usages according to availability (0.33).

Field vole (N = 2)

C-

P-

Field vole + sibling vole
(N = 4)

C+

P-

Sibling vole (N = 2)

C-

P-

Field vole + sibling vole
(N = 3)

C+

P+

Every 0.5 ha enclosure/control:

Interspecific competition

Predation

High cover habitat

Low cover habitat

● Trap station

<https://mc.manuscriptcentral.com/cjz>

Fig. 2 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 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-). The horizontal dotted line represents short grass usages according to availability (0.33).

127x105mm (300 x 300 DPI)

Fig. 3 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 vole densities 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. Centred vole density refers to the pooled density of both vole species. The horizontal dotted line represents short grass usages according to availability (0.33).

127x105mm (300 x 300 DPI)

Tables

Table 1 Model output from generalized mixed models on the effect of competition (1068 captures of 837 voles from 8 populations) and predation (634 voles from 7 populations) on the proportional use of the low cover habitat. 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 either competition or predation, depending on the model. 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
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</i> × <i>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</i> × <i>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</i> × <i>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</i> × <i>Species_FV</i> × <i>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>	<i>-1.762</i>	<i>0.268</i>	<i>1</i>	<i>-6.579</i>	<i>P < 0.001</i>
<i>Treatment</i>	<i>-1.964</i>	<i>0.602</i>	<i>1</i>	<i>-3.265</i>	<i>P = 0.001</i>
<i>Species_FV</i>	<i>-1.333</i>	<i>0.324</i>	<i>1</i>	<i>-4.113</i>	<i>P < 0.001</i>
<i>Centred density</i>	<i>-0.012</i>	<i>0.003</i>	<i>1</i>	<i>-3.484</i>	<i>P < 0.001</i>

<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	$P = 0.003$

Draft