

15 **Behavioural and population responses of ground-dwelling rodents to forest edges**
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29 **Running title: Small mammals and forest edges**

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31

32 **Abstract**

33 Forest edges can affect the behaviour, physiology and demography of small mammals. We tested
34 whether there was a response in abundance, distribution, personality selection or foraging behaviour
35 of ground-dwelling rodents to a forest- meadow edge in two study areas in Northern Italy over a 1-
36 year period. We used capture-mark- recapture to evaluate species distribution, abundance, survival
37 and personality, while Giving Up Density was used to test their foraging behaviour and the cost
38 associated to it. All tests were carried out on the forest edge and at 50 and 100 m from the edge
39 along three parallel transects 90 m long. We detected two species in both areas: *Apodemus*
40 *sylvaticus* and *Myodes glareolus*. We found a neutral effect of the edge on species number, survival
41 and on individual's personality (activity/exploration tendency). Bank voles occurred more along the
42 edge and both taxa took more seeds from trays along the edge. The hypothesis of edge avoidance
43 was not confirmed in any of the variables examined. Our study supports evidence that edge effects
44 can be species-specific and that populations should be studied with a multiple test approach to
45 investigate different eco-ethological responses to the edge when trying to reveal the functioning of
46 ecotonal systems.

47

48 **Key words**

49 bank vole; wood mouse; survival; seed predation; personality; GUD

50 **1 Introduction**

51 Human-alteration of forested landscapes has increased both the destruction of suitable forest habitat
52 for many species and the proportion of forest area that lies close to an edge. The forest edge
53 becomes part of a transition zone or ecotone, that usually exhibits differences in microclimate,
54 species composition and vegetation structure compared to forest interior (Murcia 1995; Saunders et
55 al. 1991; Schnurr et al. 2004). Hence, a habitat edge can be considered a spatial discontinuity that
56 affects in some way an animal species' behavioural, physiological or demographic performance
57 (Lidicker and Peterson 1999).

58 Forest edges can affect mammals in their abundance, distribution and occurrence (Kremsater and
59 Bunnell 1999; Murcia 1995; Nams 2012). The magnitude of these effects depends both on the
60 quality of the habitat on both sides of the edge and the extent of human activity at the edge of the
61 forest, as well as the species under consideration. Rodents, because of their restricted vagility, may
62 be more susceptible to the edge effect, particularly for species that are not habitat generalists
63 (Schmid-Holmes and Drickamer 2001). Small mammals' distribution in temperate forests is
64 influenced by 3 main factors: resource availability, as food, water or nest sites (Barnum et al. 1992;
65 Bisi et al. 2016; Getz 1968); predator avoidance (Morris and Davidson 2000; Orrock et al. 2004;
66 Thorson et al. 1998); competition with other species (Jones et al. 2001; Mazzamuto et al. 2017;
67 Yunger et al. 2002). These factors can be altered by the habitat edge; for example, a higher
68 mortality of small rodents through increased predation related to a higher occurrence of predators
69 along the edge, and/or a lower plant cover that protects the prey (Ferguson 2004; Morris and
70 Davidson 2000; Orrock et al. 2004). Small mammals play an important role in the regulation of
71 many processes supporting natural ecosystems. They are not just an abundant and widespread prey
72 indispensable for numerous other vertebrates (Bontzorlos et al. 2005; Lozano et al. 2006;
73 McDonald et al. 2000), but they are also primary consumers that can actively contribute to the
74 regeneration and expansion of numerous habitats through secondary seed-dispersal (Chang and
75 Zhang 2011; Schnurr et al. 2004; Vander Wall 1990; Wauters and Casale 1996). With a worldwide
76 increase in amount of edge habitat as consequence of forest fragmentation, studying how small
77 mammals respond to these changes will increase our understanding of the functioning of
78 fragmented habitats (Donoso et al. 2004; Pfeifer et al. 2017).

79 In this study we test the abundance, survival, distribution and foraging behaviour of ground-
80 dwelling rodents along the forest edge. Moreover, we also want to test a possible selection in
81 personality traits along the edge using indirect indices of personality. Among small mammals, an
82 individual's willingness to enter a baited trap can be considered an indication of its propensity for
83 risk-taking, because it accepts the risks associated with trapping and handling in order to obtain a

84 food reward (Réale et al. 2000). So individual trappability is often used as a measure of boldness,
85 while the number of different traps visited by an individual is used as a measure of explorative
86 behaviour (Bohn et al. 2017; Boyer et al. 2010; but see Brehm and Mortelliti 2018).
87 Previous studies reported neutral effects of habitat edges on small mammal's populations (e.g.,
88 Anderson et al. 2006), positive effects (edge attraction; e.g., Lidicker and Peterson 1999; López-
89 Barrera et al. 2005) or negative effects (edge avoidance; e.g., Delattre et al. 2009; Stevens and
90 Husband 1998). We hypothesize the case of edge avoidance, with the edge characterized by a lower
91 number of species and/or abundance, a lower survival along the edge and a lower food harvest rate.
92 Moreover, we expect relatively bolder animals living on the edge than inside the forest, since
93 individuals with risk-taking personality trait are more likely to face the increased predation risk than
94 shy individuals.

95

96 **2 Materials and methods**

97 *2.1 Study areas and design*

98 Ground-dwelling rodents were studied from June 2016 to April 2017 in two areas of Pineta
99 Regional Park (Lombardy, Italy), an area of 4828 ha characterized by acidophilic forests of
100 broadleaf and conifers, and mesophilic forests. Forests cover about 3000 ha, while agricultural land
101 is composed of stable meadows (275 ha) and crops (1325 ha). At each of the two study areas (A and
102 B) we established 3 transects 90 meters long that ran parallel along a forest- meadow edge and
103 reached 100 m into the interior of the forest. The first transect was at the edge while the second and
104 third were at 50 m and 100 m, respectively, with their sides at least 50 m and 100 m from any other
105 forest edge. Area A had the edge 200 m long with a meadow of 2 ha in front while at area B the
106 edge was 215 m long with 3 ha of meadow. The two areas were 1500 m far apart. A detailed
107 vegetation study of both areas is reported in Supplementary material (SM1).

108 *2.2 Trapping and handling*

109 In both areas, along each of the three transects, 10 single large Sherman traps (7.5×9×23 cm; HB
110 Sherman Traps Inc. Tallahassee, Florida USA) were spaced 10 m for a total of 30 traps/area.
111 Trapping was conducted in 6 trap periods at each area during June, July, September, October
112 (2016), March and April (2017). During each trap period, traps were active for three consecutive
113 nights and checked early in the morning and before sunset for a total of 6 controls per trap period
114 (trap rounds). Live traps were baited with a mixture of sunflower seeds, nutella, a piece of potato to
115 avoid dehydration, and a handful of hydrophobic cotton was added so that the captured rodents
116 could make a nest to keep warm until they were marked and released. Captured individuals were
117 identified to species level and subsequently sexed, aged, weighed and permanently marked with

118 passive integrated transponder tags (RealTrace 2016; size= 1.4 x 8.5 mm). Animals were released at
119 the place of capture. All the procedures of trapping and manipulation of animals took place in
120 compliance with the European Council Directive 92/43EEC (Italian law D.Lgs 157/92 and LR
121 3/1994) and with the Directive 2010/63/EU (Italian law D.Lgs 116/92).

122 *2.3 Foraging experiment*

123 We examined differences in the foraging behaviour of ground-dwelling rodents between the three
124 transects in each study area. We used two aluminium trays per transect (2 l capacity each; 6 trays
125 per area) filled with 2 l of sand mixed with 30 g of black oil sunflower seeds. The seed trays were
126 set out on the field 24 h every month from June 2016 to April 2017 and every month they were
127 semi-randomly placed along each transect to occupy the majority of the sites along it. The pair of
128 seed trays per transect was spaced at least 30 m apart. During the 24 h, a first control consisted of
129 sifting the sand and collecting all remaining intact seeds after 12 h followed by refilling the tray
130 with sand and mixing it again with other 30 g of sunflower seeds. The second and final control after
131 another 12 h, consisted of sifting the sand and collecting the remaining full seeds. Each time the
132 sifted seeds were air-dried and the mass was measured to determine the giving up density (GUD),
133 that indicates when the benefit obtained from foraging is balanced by the summed energetic costs,
134 the risk of predation, and the missed opportunity cost of not engaging in alternative activities
135 (Brown 1988).

136 The experiment was carried out when the areas were not involved in trapping activities.

137 *2.4 Data analysis*

138 Our data were analysed to test for an effect of the forest edge on population parameters, personality
139 and foraging behaviour. The transect where data were collected was used as a factor to represent the
140 distance from the edge (transect 1= on the edge; transect 2= 50 m; transect 3= 100 m). Moreover,
141 our data were collected in two different areas that account for pseudoreplicates, hence the factor
142 “area” was always included in our models as a random factor to take into account possible
143 differences between study areas. Since the edge effect can be species specific (Lidicker 1999), all
144 analyses were carried out separately for each species.

145 *2.4.1 Population parameters*

146 Because of a low capture-recapture rates of the species in this study, population size (N) was
147 estimated using the minimum number of animals known to be alive (MNA, Krebs 1999) from
148 trapping data of each trap period. A Poisson regression was used to test for differences in N: we
149 considered the transect (hence distance from the edge) as explanatory variable in a Generalised
150 Linear Mixed Model (GLMM, R package lme4 v 1.1-12) with season (March- May= spring; June-
151 August= summer; September- November= autumn) added as a factor to control for seasonal

152 fluctuations in rodent numbers. Study area was added as random factor to account for
153 pseudoreplications and trap period nested in season as a second random factor to account for
154 repetitions in time. Differences in least square means (DLSM) with the Tukey p-value adjustment
155 for multiple tests were used to identify significance in pairwise comparisons.

156 The catch per unit effort (cpue) of each species per area over the entire study period (number of
157 individuals trapped/number of occasions) was calculated, and the number of trapping events for
158 each species per area over the entire study period was compared using a χ^2 test.

159 Local survival for each species was estimated using Kaplan-Meier survival curves (Kaplan and
160 Meier 1958). Proportional Hazard Regression (Cox 1972) was used to test for differences in
161 survival between transects and sexes with data stratified per area.

162 2.5.2 Indirect indices of personality

163 To assess individual consistency for trappability we estimated the repeatability (Bell et al. 2009),
164 also called Intra-class Correlation Coefficient (ICC), of the number of capture events (n_capt) of
165 each individual at each trap period with Linear Mixed Models (LMM, lme4 package; Bates et al.
166 2014). “n_capt” was the dependent variable, “ID” the random intercept term, to estimate the %
167 variance explained by repeated measures on the same individual, and sex and trap period were
168 included as fixed effects. Repeatability was estimated using the R package rptR v 0.9.2 (CI= 95%,
169 number of parametric bootstraps for interval estimation= 5000, number of permutations used when
170 calculating asymptotic p-values= 1000) (Bohn et al. 2017; Stoffel et al. 2017). Following Martin et
171 al. (2011), we included individuals with one measurement in our repeatability analysis to increase
172 power. Next we explored whether animals living on the edge were more bold than forest interior
173 animals (transect effect). We used Generalised Linear Mixed Models (GLMMs, Bolker et al. 2009)
174 with n_capt as dependent variable, transect and sex as fixed effects, using the ID and area as
175 random effects.

176 The same process was followed for the estimate of the repeatability of trap diversity using the
177 number of different traps were an individual was captured at each trap period as dependent variable
178 and for the following GLMM. Statistical analyses were carried out separately for each species using
179 the R package lme4 ver. 1.1-12 for fitting and analysing mixed models (Bates et al. 2014).

180 2.5.3 Foraging experiment

181 A GLMM (R package lme4 ver. 1.1-12) was used to test for differences in GUD between transects.
182 Factor “season” was added as a factor to account for potential effects of seasonal fluctuations on the
183 GUD, while “area” as a random factor to account for pseudoreplicates. Differences in least square
184 means (DLSM) with the Tukey p-value adjustment for multiple tests were used to identify
185 significance in pairwise comparisons.

186 3 Results

187 3.1 Population parameters

188 A total of 36 trap rounds (6 per trap period) of 30 different traps were carried out from June 2016 to
189 April 2017 in each of the 2 areas. *Myodes glareolus* and *Apodemus sylvaticus* were the only two
190 granivorous rodents trapped in all transects. Only four other non target individuals were trapped
191 (*Crocidura leucodon*, *Sorex* sp.). In area A 47 different bank voles were captured (22 males, 25
192 females, total captures 148, cpue 4.11) against 107 in area B (42 males, 65 females, total captures
193 327, cpue 9.08). Forty five different wood mice were trapped in area A (26 males, 19 females, total
194 captures 86, cpue 2.39) and 34 in area B (21 males, 13 females, total captures 74, cpue 2.06). The
195 catch per unit effort in both areas was significantly higher for bank vole than for wood mouse (χ^2
196 test = 25.3, df = 1, p < 0.001).

197 There was no difference in the abundance of wood mice between the edge and the forest interior (all
198 p > 0.05) or between seasons (all p > 0.05) (Fig.1; SM2,3). In contrast, bank vole numbers were
199 affected both by the distance from the edge and by season. In the interior of the forest vole numbers
200 were lower than at the edge (transect 2-transect 1: -0.31 ± 0.15 , z = -2.08 p = 0.04; transect 3-
201 transect 1: -0.55 ± 0.16 , z = -3.40 p = 0.0007) and there were fewer voles in spring than in summer
202 and autumn (spring-summer: -0.53 ± 0.19 , z = -2.75 p = 0.02; spring-autumn: -0.60 ± 0.19 , z = -
203 3.17 p = 0.004) (Fig.1). Overall, 9 voles and 6 mice in their trapping history were caught in 2
204 adjacent transects (different trapping periods), but since in our analyses the sample unit was the
205 trapping period, this didn't affect our results.

206 Kaplan- Meier survival rate for bank voles was 0.31 after 1 month (95% CI 0.25-0.40) and 0.04
207 (95% CI 0.02-0.09) after 7 months, while for the wood mouse it was 0.14 (95% CI 0.08-0.25) after
208 1 month and 0.007 (95% CI 0.0006-0.09) after 7 months. Local survival for both species did not
209 differ between sexes or transects (bank vole: Likelihood ratio test = 1.2, df = 3, p = 0.75; wood
210 mouse: Likelihood ratio test = 4.74, df = 3, p = 0.19).

211 3.2 Indirect indices of personality

212 On average (\pm SD), wood mice were captured 1.62 ± 0.85 times/ trap period and trapped in $1.40 \pm$
213 0.59 different traps. Bank voles were captured on average 2.11 ± 1.42 times/ trap period and trapped
214 in 1.50 ± 0.75 different traps. Trappability and trap diversity indices were not significantly
215 consistent within individuals of *A. sylvaticus* (both p > 0.05) but were repeatable for *M. glareolus*
216 (trappability R = 30%, 95% CI = 12-52 %, LRT = 12.3, df = 1; p = 0.0002; trap diversity R = 30%,
217 95% CI = 12-51 %, LRT = 15.1, df = 1; p < 0.0001). Hence, personality could only be analysed for
218 bank voles.

219 Trappability and trap diversity of bank voles did not differ with distance from the edge or with sex,
220 hence bold animals and/or animals with a strong tendency to explore were homogeneously
221 distributed without a preference for edge or interior habitats (Table 1).

222

223 *3.3 Foraging experiment*

224 Using camera traps set in video-mode in front of the trays allowed us to verify that only bank voles
225 and wood mice pilfered seeds from the trays. The Giving Up Density was lower on the edge than
226 the interior of the forest (transect 1-transect 2: -3.77 ± 0.10 , $df = 232$, $t = -3.42$ $p = 0.0007$; transect
227 1-transect 3: -3.33 ± 0.10 , $df = 232$, $t = -3.02$ $p = 0.003$) and on average it was lower in summer
228 than in all other seasons (DLSM all $p < 0.0001$) (Table 2) (SM4).

229

230 4 Discussion

231 We explored effects of forest - meadow edges on ground-dwelling rodents' populations in Northern
232 Italy. All our tests were conducted at different distances from the edge to detect possible responses
233 to the edge. We detected a neutral effect of the edge on the number of species present, survival and
234 on individual's personality, a species-specific edge-effect on abundance, and a positive effect (edge
235 attraction) on foraging behaviour. The hypothesis of edge avoidance was not confirmed in any of
236 the variables examined. The limitations of this study in terms of time period and sample size, in
237 particular for small mammals that are affected at a small scale by different environmental and
238 ecological factors, prevent us from making broader generalizations from our results, but we think
239 that this study is a good example of a multiple approach to a wide ecological topic as "edge effect".
240 We did not find any difference in species number between the edge and the interior of the forest.
241 We trapped in both areas the bank vole *M. glareolus* and the wood mouse *A. sylvaticus*. The wood
242 mouse lives both in open (grasslands and fields) and forested areas and has generalist food habits
243 (Gasperini et al. 2018; Sozio and Mortelliti 2016; Sunyer et al. 2016). The distribution we recorded
244 is in agreement with the generalist behaviour and the predominantly nocturnal activity of wood
245 mice (Eldridge 1968; Sunyer et al. 2016). In contrast, bank voles can be found in a variety of
246 habitats but they are mainly associated to forest habitats with a good ground cover and shrub
247 structure, that increase protection from bird and mammal predators (Gasperini et al. 2016;
248 Macdonald 2001; Mazurkiewicz 1994). Even though in our areas shrub cover was higher along the
249 edge, bank voles used both the edge and the forest interior. However, voles were more abundant at
250 the edge than at the forest interior. Since vole survival was not affected by the distance from the
251 edge, the lower number of individuals in the interior of the forest may be related to the preference
252 for high cover habitat. Studies on other species of small mammals reported contrasting results about
253 the effect of forest edges on population abundance, with less (Delattre et al. 2009; Stevens and
254 Husband 1998) or the same number of individuals (Anderson et al. 2003; Tallmon and Mills 2004)
255 along the edge than inside the forest, sometimes finding different results for the same species (e.g.
256 *Peromyscus leucopus*; Anderson et al. 2006; Wolf and Batzli 2002). Mills (1995) suggested that
257 differences between the edge and the forest interior may be related more to the different forest
258 productivity than the habitat structure itself. In our study areas, further investigations on forest
259 productivity should be carried out to confirm if the distribution of bank voles is related more to the
260 habitat structure (understorey cover) or to food availability (Manson and Stiles 1998; Wolf and
261 Batzli 2004).
262 Forest edges are often associated to higher mortality of small rodents because of increased predation
263 risk related to a higher occurrence of predators along the edge, and/or a lower plant cover that

264 protects the prey (Ferguson 2004; Morris and Davidson 2000; Orrock et al. 2004). In this study we
265 did not find a difference in survival between the edge and the interior of the forest, nor did we find
266 differences between sexes. The predators of ground-dwelling rodents in Pineta Regional Park are
267 many species of birds of prey and owls (e.g., kestrel, common buzzard, tawny owl, long-eared owl),
268 some snakes (e.g., green whip snake, Aesculapian snake) and carnivores as badger, red fox
269 and beech marten. Our result suggests that predation pressure in the area is uniform and that the
270 edge does not increase the mortality of voles and mice. Previous studies showed that rodents'
271 activity and occurrence is related to indirect (microhabitat) and not direct (olfactory and visual) cues
272 of predation risk (Orrock et al. 2004; Sivy et al. 2011; Thorson et al. 1998). Thus the presence of
273 small mammals is more related to factors such as ground cover, refuges, visibility to reduce the risk
274 of predation than to the actual presence/activity of predators. This may also be the reason why we
275 did not find any selective use of edges by ground-dwelling rodents with certain personality traits: in
276 our study areas bold voles and/or animals with a strong tendency to explore were homogeneously
277 distributed without a preference for edge or interior habitats. Unfortunately, the two indirect
278 personality indices used were not reliable for the wood mouse, probably because of a low capture-
279 recapture rate of the species resulting in lack of repeatability of these indices (see Brehm and
280 Mortelliti 2018). In the future further analyses using direct measures of personality (e.g. open field
281 test) and the correlation between personality traits and trappability would clarify the issue (Brehm
282 and Mortelliti 2018; Carter et al. 2013).

283 Processes such as plant-plant interactions, plant-animal interactions and forest regeneration can be
284 altered in their dynamics by the habitat bordering the forest and the forest edge itself (e.g. Donoso
285 et al. 2004). We tested the effect of the edge on the foraging behaviour of mice and voles in our
286 areas. Wood mice and bank voles are known to be seed consumers (Gasperini et al. 2018) but they
287 also cache food to enhance survival in periods of low food availability (like the winter time) and to
288 improve reproductive success during the breeding period (Hansson and Henttonen 1985; Mappes
289 1998; Sunyer 2015; Vander Wall 1990). Based on theory of Giving Up Denstiy (GUD), a high
290 GUD suggests a low benefit from foraging in a given patch compared to the summed costs of
291 energy consumption, predation risk and missed opportunities of not engaging in alternative
292 activities (Brown 1988; Olsson and Molokwu 2007; but see Price and Correll 2001). Our results
293 showed a lower GUD, thus a greater seed predation, from trays along the edge than inside the
294 forest, indicating high benefits of feeding along the edge. Some studies reported similar results
295 (Kollmann and Buschor 2003; López-Barrera et al. 2005) while others reported higher foraging
296 activity inside the forest (Moenting and Morris 2006; Morris and Davidson 2000; Vaaland Burkey
297 1993). We argue that lower GUD along the edge in our study was associated to differences in

298 microhabitat (ecotonal effect, see Lidicker 1999). Our vegetation study showed that ground cover
299 along the edge was higher than inside the forest, suggesting a higher benefit of foraging at the edge
300 because of lower predation risk linked to better cover (Birney et al. 1976; Bowers et al. 1993;
301 Brown et al. 1992; Thorson et al. 1998). López-Barrera et al. (2005) suggested that the edge can act
302 as a barrier and animals may spend more time travelling along the edge and incidentally could
303 encounter food resources, but since our measure of trap diversity (number of different traps in
304 which an individual was caught) was the same at the edge and in the forest, we exclude this
305 hypothesis.

306 We found seasonal differences in the abundance of bank voles and in GUD. There were fewer bank
307 voles in spring than in summer and autumn. This trend may be related to a reduction of the
308 population size during the winter (when no trapping occurred) because of a high mortality due to
309 low temperatures and lack of food resources (Crawley 1970; Olsson et al. 2002; van Apeldoorn et
310 al. 1992). Moreover, the GUD was lower in summer than in all other seasons; hence voles and mice
311 spent more time feeding on the trays in summer. During this season the understorey of the forest
312 and ground cover is generally denser probably reducing the predation risk perceived by ground-
313 dwelling rodents. Temporal variation in the availability of food resources in the forest can also play
314 a role in seasonal changes of the GUD (Brown et al. 1992; Olsson et al. 2002). If this was the case
315 in our study, we would expect a stronger attraction of artificial food, and thus a lower GUD, mainly
316 during the winter-early spring, which was not recorded.

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5 Conclusions

In our study we predicted a negative (edge avoidance) responses of ground-dwelling rodents to ecotonal habitat. The analyses found positive or neutral responses to the edge (even within the same species) depending on the parameter measured (e.g., number of species and distribution, foraging behaviour). Many studies have tried before to extract general conclusions on the presence or not of an edge effect on animal populations. Our study, despite its limitations in terms of sampling effort, suggests that responses to edge effects should always be considered species specific (in some cases even sex and age specific; see Lidicker 1999) and that patterns should be investigated with a multiple test approach to explore different eco-ethological responses to the edge.

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539

540 **Table 1** Comparison of indirect indices of personality of *Myodes glareolus* at different distances
 541 from the forest edge (transect) and between sexes (M: males, F: females; see methods for details).

	Contrast	Estimate ± SE	z	p
Trappability	transect 1 - 2	0.17 ± 0.11	1.51	0.13
	transect 1 - 3	0.22 ± 0.12	1.82	0.07
	M - F	0.05 ± 0.10	0.52	0.60
Trap diversity	transect 1 - 2	0.24 ± 0.13	1.76	0.08
	transect 1 - 3	0.21 ± 0.14	1.55	0.12
	M - F	0.06 ± 0.11	0.54	0.59

542

543

544 **Table 2** Giving Up Density for each area, transect and season. Trays were filled with 2 l of sand
 545 and 30 g of sunflower seeds and checked every 12 hours (see methods for details).

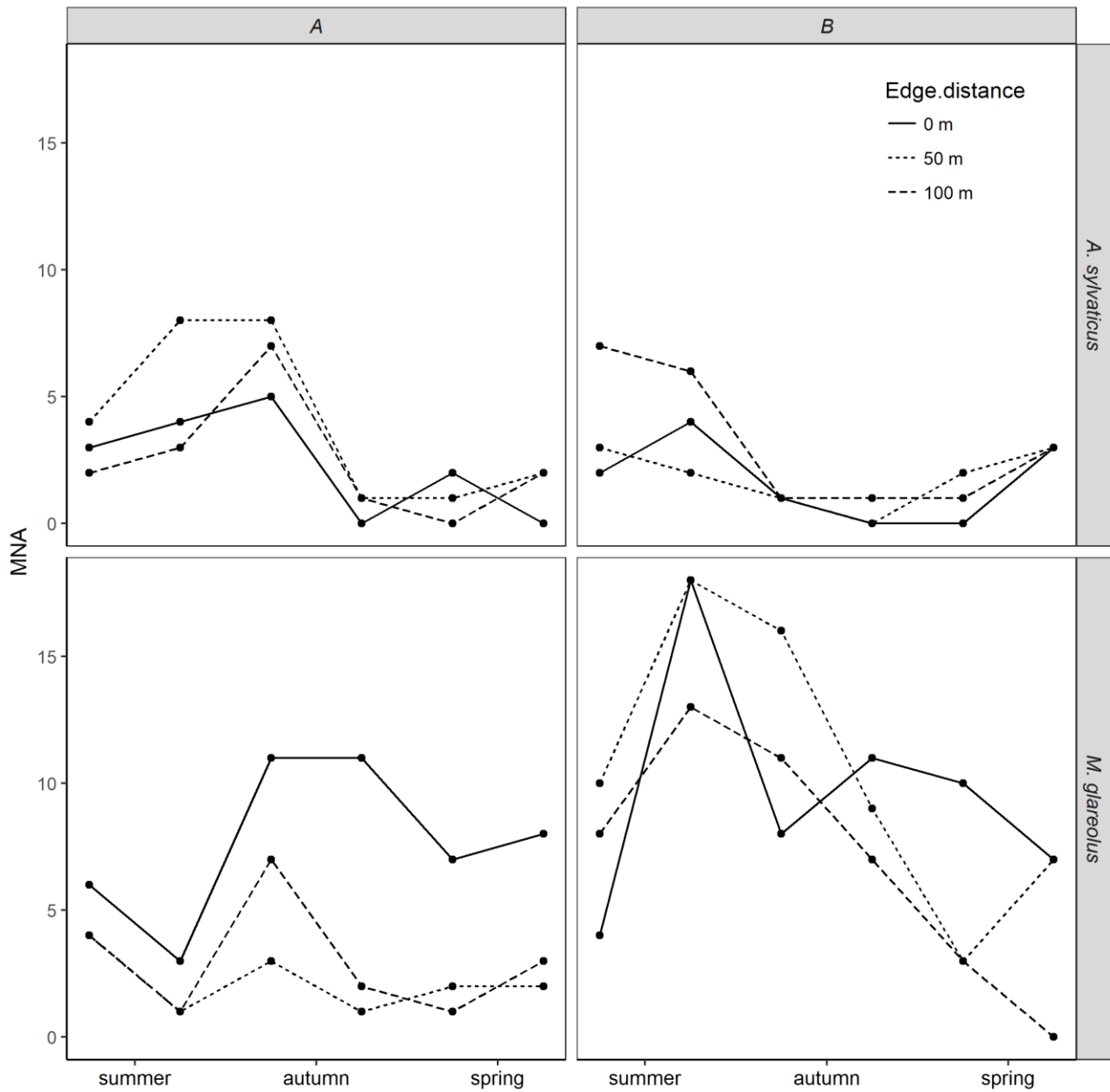
546

		area A		area B	
		mean (g)	± SD	mean (g)	± SD
transect	1	24.57	6.42	19.96	8.72
	2	25.84	8.54	25.91	7.76
	3	26.54	6.45	24.9	8.44
season	summer	21.55	4.05	14.85	11.71
	autumn	26.56	6.26	24.3	7.26
	winter	27.22	5.89	26.57	5.46
	spring	27.53	4.05	26.79	4.4

547

548

549 **Figure 1** Average Minimum Number of animals known to be Alive (MNA) per season for the
 550 species *Apodemus sylvaticus* and *Myodes glareolus* in each study area and at different distances
 551 from the edge.



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