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1 **The role of colonization in the dynamics of patchy populations of a cyclic**
2 **vole species**

3 **Petter Glorvigen • Gry Gundersen • Harry P. Andreassen • Rolf A. Ims¹**

4 P. Glorvigen • H. P. Andreassen

5 Faculty of Applied Ecology and Agricultural Science, Campus Evenstad

6 Hedmark University College,

7 NO-2480 Koppang, Norway.

8 Telephone: +4795431269

9 Fax: +4762430851

10 e-mail: petter.glorvigen@hihm.no

11 G. Gundersen

12 Centre for Ecological and Evolutionary Synthesis,

13 Department of Biology,

14 University of Oslo

15 P.O. Box 1066, Blindern, 0316 Oslo, Norway

16 R. A. Ims

17 Department of Arctic and Marine Biology,

18 University of Tromsø,

19 NO-9037 Tromsø, Norway.

¹ Author contributions: RAI, GG and HPA conceived and designed the experiment. RAI, GG and HPA conducted the experiment. PG analysed the data and wrote the manuscript. RAI and HPA provided statistical and editorial advice.

20

21 **Abstract**

22 The crash phase of vole populations with cyclic dynamics regularly leads to vast areas of
23 uninhabited habitats. Yet although the capacity for cyclic voles to re-colonize such empty
24 space is likely to be large and predicted to have become evolved as a distinct life history trait,
25 the processes of colonization and its effect on the spatio-temporal dynamics have been little
26 studied. Here we report from an experiment with root voles (*Microtus oeconomus*)
27 specifically targeted at quantifying the process of colonization of empty patches from distant
28 source patches and its resultant effect on local vole deme size variation in a patchy landscape.
29 Three experimental factors: habitat quality (1), predation risk (2) and inter-patch distance (3)
30 were employed among 24 habitat patches in a 100x300 m experimental area. The first born
31 cohort in the spring efficiently colonized almost all empty patches irrespective of the degree
32 of patch isolation and predation risk, but dependent on habitat quality. Just after the initial
33 colonization wave the deme sizes in patches of the same quality were underdispersed relative
34 to Poission variance, indicating regulated (density-dependent) settlement. Towards the end of
35 the breeding season local demographic processes acted to smooth out the initial post-
36 colonization differences among source and colonization patches, and among patches of
37 initially different quality. However, at this time demographic stochasticity had also given rise
38 to a large (overdispersed) variation in deme sizes that may have contributed to overshadow
39 the effect of other factors. The results of this experiment confirmed our expectation that the
40 space-filling capacity of voles is large. The costs associated with transience appeared to be so
41 low, at least at the spatial scale considered in this experiment, that such costs is not likely to
42 substantially constrain habitat selection and colonization in the increase phase of cyclic
43 patchy populations.

44

45 **Keywords**

46 dispersal, extinction, habitat selection, immigration, population cycle

47

48 **Introduction**

49 Colonization – dispersal events leading to settlement of individuals in empty habitat (*sensu*
50 Ims and Yoccoz 1997) – is a key population process in species with violent spatio-temporal
51 density variation, such as small rodents with cyclic population dynamics. In such species vast
52 tracts of habitat are regularly empty (extinct) after cyclic population crashes, and extensive
53 colonization from spatially scattered founder demes is needed for the propagation of a new
54 cycle (Charnov and Finerty 1980; Stenseth 1978; Stenseth and Lomnicki 1990; Warkowska-
55 Dratna and Stenseth 1985; see also Andreassen et al. 2002). Indeed, it has been predicted that
56 that a pronounced drive and ability for effective colonization should have evolved as an
57 important life history trait in patchily distributed voles with cyclic dynamics (Ebenhard 1990).
58 Although an extensive potential for colonization is likely to be an adaptation to and premise
59 for cyclic dynamics (Bondrup-Nielsen and Ims 1988), as associated phenomena such as
60 spatial synchrony and period length (Ims and Hjermann 2001; Le Galliard et al. 2012), there
61 is yet actually little empirical knowledge about the spatial component of population growth in
62 cyclic rodents.

63 The setting of enclosed vole populations in experimentally manipulated patchy habitats
64 have proven to give detailed insights about population processes, including dispersal (Barrett
65 and Peles 1999; Ims and Andreassen 2005; Stenseth and Lidicker 1992). However, a
66 challenge in such experiments is to invoke a combination of factors that may be important in a
67 natural setting and at relevant spatial scales. In the present study we assess by means of a
68 factorial experiment three factors that are likely to affect colonization of habitat patches and
69 spatial population dynamics of the root vole (*Microtus oeconomus*) - habitat quality, predation

70 risk (by raptor exclusion nets) and distance from source patches. The root vole is an adequate
71 experimental model for the purpose of the present study. It is known to inhabit patchy habitat
72 and to exhibit violent population cycles (Henden et al. 2011; Lambin et al. 1992; Tass 1966)
73 with large amplitude in habitat occupancy between the low phase and the peak phase of the
74 cycle (Henden et al. 2011). It is sensitive to both predation (Ims and Andreassen 2000) and
75 habitat quality (Henden et al. 2011), however it is not known to what extent such factors
76 influence the population dynamics through the processes of colonization. Although the
77 species is known to be quite mobile (Andreassen et al. 1996; Steen 1994), and many factors
78 effecting its rather flexible social system (Andreassen et al. 1998) and dispersal behaviour
79 (Andreassen and Ims 2001) is well explored, the role of habitat patch isolation on population
80 dynamics has not been analysed experimentally beyond 50 m inter-patch distances (e.g. Aars
81 and Ims 2000). To our knowledge there are presently no experiments on any vole species
82 exhibiting cyclic population dynamics that have focused explicitly on colonization. In the
83 present study we extended the spatial scale considerably as to specifically target colonization
84 in an overall experimental design that we believe is more realistic than previous experiments
85 for assessing the role of colonization as a determinant of spatio-temporal dynamics of patchy
86 populations (*sensu* Hanski 1999). We predicted voles to preferentially colonize high quality
87 patches and hence that the deme sizes should become largest in high quality patches (Lin and
88 Batzli 2004; Lin et al. 2006). In line with more small-scale, previous experiments showing
89 evidence for distance-dependent inter-patch movements in hostile matrix habitats (Ims and
90 Andreassen 2005) coupled with predation-inflicted mortality rates associated with such
91 movements (Aars et al. 1999; Ims and Andreassen 2000), we predicted both the colonization
92 rates and the post colonization deme sizes to decline with increasing inter-patch distance.
93 With regard to the effect of predation we expected the effect of raptor exclusion nets to be
94 conditional on whether voles are able to sense predation risk, for instance, in terms of fewer

95 strikes of raptors or mortality incidents among conspecific individuals. However, although the
96 raptor nets could potentially create a contrast in predation risk, the size of this effect was
97 beyond our experimental control due to the (uncontrolled) natural temporal dynamics of avian
98 predators in the general geographic region (Ims and Andreassen 2000).

99 **Material and methods**

100 Experimental design and animals

101 We conducted the experiment at Evenstad research station, South-east Norway, from spring
102 (May) to autumn (October) in two replicated years (2000 and 2001). The experimental
103 landscape was surrounded by a mammalian predator fence (1.5 m high chicken mesh fence
104 supplied with an electric wire) and consisted at the onset of the experiment of six plots (50 x
105 100 m) enclosed by steel sheet fences extending 0.4 cm below- and 0.6 cm above ground. Ten
106 days in advance of each replicate year all plots were emptied for all mammals that had been
107 able to inhabit the area through the previous winter. Each plot consisted of four habitat
108 patches (375 m² each) composed of grass dominated meadow vegetation located in pairs
109 (Figure 1).

110 To manipulate habitat quality one patch in each pair was burned, tilled and sown with
111 equivalent vegetation to the other patches in the spring just prior to the onset of the
112 experiment. By this treatment the two patches (in a pair) had different qualities: an untreated
113 “old grass” patch and a manipulated “new grass” patch. At the onset of each of the
114 experimental seasons in May the old grass patches had a dense cover of standing dead
115 vegetation and litter. In contrast, the “new grass” patch had very little cover at the onset of the
116 season while they developed new vegetation during the course of the summer and were
117 towards the end of each of the experimental seasons similar to the old grass patches in terms

118 of vegetation cover. Due to the lack of cover we expected the new grass patches be less likely
119 to be colonized early in the season than the old grass patches.

120 The second experimental factor was predation risk which was employed by excluding
121 avian predators from every second habitat pair by a net erected approximately 3 meters above
122 the ground (Figure 1). The net extended both horizontally (“roof”) and vertically (“walls”),
123 excluding all predatory birds. The area surrounding all habitat patches (i.e. the matrix) were
124 kept uninhabitable by regular mowing.

125 The third experimental factor - colonization distance - was implemented by employing the
126 two old grass patches in the two most distant plots in the experimental system (plot 1 and 6;
127 see figure 1) as source (founder) patches. Each of the source patches received same sized vole
128 founder deme consisting of 3 adult root vole females (mothers) with their newly weaned
129 litters (i.e. 16-18 days old) at the onset of each of the two experimental seasons. This
130 amounted to total founder populations (at the level of the entire experimental system)
131 composed of mothers:sons:daughters equal to 12:30:27 in year 2000 and 12:29:26 in year
132 2001. Patches of the old grass quality were chosen as the source patches to ensure that
133 sufficient vegetation cover was present for initial establishment of voles.

134 The founder animals originated from a wild root vole population known to exhibit violent
135 multi-annual cycles in Valdres, South Norway (Ims 1997). Voles were captured in Valdres the
136 previous falls (1999 and 2000) and kept at the Animal Division of the University of Oslo,
137 Norway. The founder animals used in the field experiment were first (mothers) and second
138 (litters) generation descendants of the wild animals brought to the Animal division from
139 Valdres. To secure initial familiarity between the animals in each source patch, the three
140 mothers and their litters were kept together (visual and olfactory contact, but in separate
141 netting cages) in advance of introduction. Animals were released from the cages by opening
142 one of the walls, so that the animals could move freely in and out of the cages. The animals

143 were thereafter given 9 days to habituate within the source plots (i.e. plot 1 and 6; cf. Figure
144 1) before gaps (10 cm wide) in the fences between all six plots were opened so animals were
145 free to settle in any of the 24 patches contained in the experimental system. The general initial
146 setting of the experiment was thus meant to simulate an aggregated distribution of surviving
147 animals and a predominance of empty habitat in the spring after a population crash (Aars and
148 Ims 2002).

149 Monitoring of voles

150 All 24 patches were monitored by live-trapping at 18 days after the opening of the fence gaps
151 and with the same intervals (i.e. 18 days) until the final trapping session in October (i.e. in
152 total 8 trapping sessions). Each trapping session lasted for 3 days and consisted of two trap
153 checks each day (i.e. in total 6 trap checks). Traps were activated at 24⁰⁰ and checked at 06⁰⁰
154 and 12⁰⁰, and left open until they were reactivated at 24⁰⁰. We used Ugglan multiple capture
155 live traps (12 traps per patch distributed in a uniform grid system) and one supplementary
156 pitfall trap at every second trap station. All traps were baited with carrots and wholegrain oats.
157 At any given capture we recorded identity (all animals were marked by toe-clipping), sex,
158 weight and reproductive status (open/closed vagina, pregnancy and lactation for females and
159 sexual maturity, i.e. visible testis for males) and also recordings of trap location and time of
160 capture. Previous studies with an identical trapping protocol applied to root voles yield
161 capture rates close to 100% in each trapping session (Aars et al. 1999). In our study none of
162 the voles missing in one session were captured in later sessions, thus we assume that all
163 animals present in a patch to be captured during each trapping session. Previous experiments
164 with comparable habitat patch geometry (distance and patch size) conducted at our research
165 station have shown that the home range of settled voles rarely confine more than one patch
166 (e.g. Gundersen and Andreassen 1998). The same pattern was evident in this study as 89%

167 (95% C.I.: 85-92%) of the voles were trapped exclusively in one patch within trapping
168 sessions. If an individual had been captured in more than one patch during a trapping session
169 it was designated the patch in which it was caught most frequently.

170 Statistical analyses

171 Data from the two replicated experimental years were analyzed together after first verifying
172 that there was not any treatment effect that was dependent on year. At the level of individual
173 animals, we estimated colonization probability with logistic regression and colonization
174 distance with linear regression. In consistence with previous studies of dispersal in root voles
175 (Aars and Ims 1999; Aars and Ims 2000; Andreassen and Ims 2001) permanent patch shifts
176 occurred predominantly in the first cohort - i.e. in this experiment before trapping session 1.
177 So the analyses of colonization rate and distance were restricted to the founder animals and
178 their dispersal from the source patches in plots 1 and 6. The colonization distance for animals
179 that left their source patch to settle in any of the other patches in the system (i.e. the
180 colonization patches) was measured as the number of plots between the source patch and the
181 patch of designation (i.e. taking values ranging from 0 – 5) for each of the surviving
182 individuals in trapping session 1.

183 At patch level the number of individuals per patch (i.e. hereafter termed deme size) was
184 analyzed with log-linear models. We focused on deme size at two moments in the
185 experimental season. The first was in trapping session 1 just after the major colonization event
186 in the founder animals was completed and before the recruitment of new cohorts. At this
187 moment we could highlight how experimental factors (colonization distance, habitat quality
188 and predation risk) affected deme size through the colonization process. The second analysis
189 was conducted on the final deme sizes (session 8) in the autumn. At this final stage in the
190 season we could highlight to what extent the experimental factors (including their effect on

191 the colonization processes and local demographic processes) had affected deme size just
192 before the onset of the winter. For both of these time-specific deme sizes (i.e. in session 1 and
193 8) two separate analyses was conducted. One simple analysis compared the size of demes in
194 the source patches vs. all colonization patches. The other analysis considered the effect of the
195 three experimental variables. Colonization distance was in this case categorized in three
196 distance classes defined as the number of plots away from the source patches (i.e. taking
197 values in the range 0 – 2; cf. Figure 1). Predation risk was categorized as predator exclusion
198 or not and habitat quality as new or old grass patches. The fit of the models relative to the
199 assumed Poisson distribution were evaluated by means of the ratio between the sum of
200 deviance residuals and residual degrees of freedom. In case of overdispersion this was
201 corrected for by a quasi-likelihood approach before significance tests were applied. Model
202 terms (including interactions) were tested by the backward procedure ($p > 0.05$). All statistical
203 analyses were conducted in SAS 9.3.

204 **Results**

205 Colonization process

206 Of total 136 founder animals introduced to the source patches over the two experimental
207 seasons 114 individuals (84%) survived the four weeks until the first trapping session. Of
208 these survivors 81 individuals (71%) had emigrated from the source patches (i.e. 18 days after
209 the opening of fence gaps). Only 8 individuals (4 young females and 4 young males)
210 emigrated in later periods. Six emigrants immigrated into one of the other source patches (1
211 mother, 1 young female and 4 young males), whereas the rest colonized empty patches.
212 Young males had the highest probability to emigrate (mean [95% C.I.]: 0.85 [0.71, 0.93]),
213 young females intermediate (0.68 [0.53, 0.80]) and adult mothers the lowest probability to
214 emigrate (0.48 [0.28, 0.68]; $F_{2,111} = 4.60$, $P = 0.012$). Young males also emigrated the longest

215 distances (mean number of plots from source demes [95% C.I.; 2.74 plot [2.26, 3.22])
216 compared to young females (2.22 [1.69, 2.75] and mothers (1.00 [0.06, 1.94]; $R^2 = 0.12$, $F_{2,78}$
217 $= 5.52$, $P = 0.006$).

218 There were only four cases (of 40 possible) where patches were empty following the initial
219 colonization (period 1) of the experimental systems (Figure 1). At this time the deme sizes of
220 the founder patches were 1.95 times larger (95% C.I.: [1.22, 3.10], $P = 0.007$) than the old
221 grass colonization patches (Figure 2A). Moreover the old grass colonization patches had
222 demes that were 1.71 times larger (95% C.I.: [1.10, 2.70], $F_{1,38} = 5.42$, $P = 0.025$) than the new
223 grass patches (Figure 2A). There was however no effects of distance from source patches nor
224 of the predator exclusion treatment (all $P > 0.202$). Interestingly, among the colonization
225 patches of the same habitat quality deme sizes were less variable (underdispersed) than
226 expected from a random (i.e. Poisson) distribution (residual deviance/residual DF = 28/38 =
227 0.74).

228 Final deme size

229 In the final trapping session (i.e. session 8) four month after the initial colonization wave (i.e.
230 before period 1) recruitment of new cohorts had resulted in an average deme size that had
231 become 6.80 times larger than in period 1. However, at this stage there were no differences
232 among the demes that could be attributed to initial difference between source and colonization
233 demes or any of the experimental factors (Figure 2B, all $P > 0.194$). For the purpose of
234 providing a valid comparison to the analysis of the dispersion of post colonization deme sizes
235 (i.e. that indicated underdispersion; see above), habitat quality was retained in the Poisson
236 model applied to final deme sizes. There was now clearly more variation (overdispersion)
237 between the demes in same quality patches than expected from a random (i.e. Poisson)
238 distribution (residual deviance/residual DF = 120/38 = 3.16).

239 **Discussion**

240 Detailed analyses of the colonization processes in cyclic small rodent populations in their
241 natural habitats are lacking due to logistic difficulties of monitoring such phenomena.
242 However, it could be assumed that the potential for spatial expansion and colonization is large
243 given how fast the low habitat occupancy in the spring of low density years is turned into near
244 100% occupancy in the autumn of cyclic peak years (e.g. Henden et al. 2011; Löfgren 1995;
245 Sundell et al. 2012). The present study provided an experimental demonstration of the large
246 capacity of root voles to rapidly fill empty habitat space by means of colonization. Patch
247 isolation by >100m of barren matrix had no effect on the probability of dispersing voles to
248 find and settle on colonization patches in the experimental system. That the source patches
249 had higher deme sizes just after the main colonization is likely to be attributed to a tendency
250 for philopatry of some animals (Boonstra et al. 1987; Le Galliard et al. 2006); in particular the
251 adult mothers of the founder cohort (Andreassen and Ims 2001). Moreover, the more animals
252 that colonized the old grass than the new grass patches is likely to be attributed to the
253 perceived quality differences between the two types of habitats early in the season. At this
254 time the new grass patches had visibly less vegetation cover than the old grass patches. Also a
255 study of colonization in bank voles pointed to the importance of habitat quality as a key
256 determinant of settlement probability in empty habitat (Glorvigen et al. 2012). The lack of any
257 effect of predator exclusion on the other hand is likely to be due a low predation pressure in
258 the two years of this study as indicated by generally high survival rate. Previous studies at
259 Evenstad have shown that the effect of avian predators varies strongly between years
260 depending on the phase of the rodent cycle in the general region (Ims and Andreassen 2000).

261 Apart from the difference due to habitat quality the deme size distribution after the
262 colonization of patches was underdispersed (i.e. less variable than expected from a random

263 distribution). This suggests there was a tendency for colonists to actively distribute
264 themselves evenly over the patches of the same quality. Also previous studies using root vole
265 in patchy habitat as a model system have shown that dispersal processes (emigration and
266 immigration onto patches) are density dependent and contribute to regulate spatial population
267 dynamics (Aars and Ims 2000; Andreassen and Ims 2001; Gundersen et al. 2002). However,
268 these previous studies were conducted on much smaller spatial scales and in simpler systems
269 (e.g. fewer patches) than in the present study.

270 While partial philopatry caused initially larger demes in the source patches than in the
271 colonization patches, and habitat selection (during colonization) caused initially larger demes
272 in patches with old grass than new grass, these differences had vanished by the end of the
273 experimental period in the autumn. This is likely to be caused by combination of density
274 dependent local demography (in particular recruitment; cf. Andreassen and Ims 2001) and the
275 quality difference between the old grass and the new grass patches disappearing over the
276 summer. Interestingly, the underdispersed initial distribution of deme sizes after the
277 colonization event in the spring had by the autumn turned into a highly overdispersed
278 distribution. This is likely to be attributed local demographic stochasticity among the rather
279 small demes. In particular, reproductive failures for instance due to incidental episodes with
280 infanticide (this appears to be common in the root vole; Andreassen and Gundersen 2006) will
281 have a large effect in species in which the single litter size is as large as in the root vole (Ims
282 1997). It is possible that such a stochasticity may to some extent have overshadowed habitat
283 quality differences between old grass and new grass patches late in the season. One
284 implication of this result is that local habitat quality and local predation may only be distinct
285 sources of spatial density variation in certain seasons (e.g. spring) and phases (e.g. peak) of
286 the multi-annual population vole cycle.

287 Conclusion

288 The present study has demonstrated the large capacity of small rodents for colonizing
289 spatially scattered habitats – a capacity that explains the fast reclaim of empty habitat space
290 following crashes in cyclic populations. In particular, the first born cohort in early summer
291 actively search out vacant habitats and settle in them conditional on habitat quality and
292 population density. When the predation pressure is low the cost of the transient stage of the
293 colonization process (*sensu* Ims and Yoccoz 1997) appears to be low for such a mobile
294 species as the root vole (Steen 1995). This implies that in the increase phase of the small
295 rodent cycle, when the predation pressure indeed is very low (Ims and Andreassen 2000) and
296 there is lots of vacant space, habitat selection at the scale of patchy populations (*sensu* Hanski
297 1999) is not likely to be substantially constrained by such costs. There is however, a need to
298 study colonization processes in natural (meta)populations of voles where habitat geometry
299 may be more challenging for dispersing voles both in terms of habitat isolation and quality
300 than it is possible to mimic in an experimental setting.

301

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306

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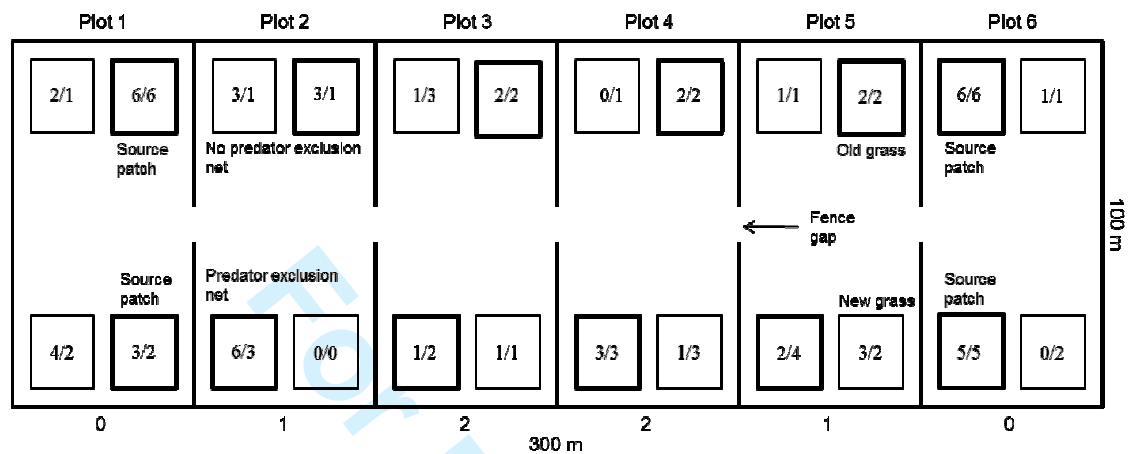
387 **Figure legends**

388 **Fig 1** Design of the experimental system. The six fenced plots contained each four habitat patches in a paired
389 design. Each patch pair consisted of one patch with old grass cover (thick lines) and one patch with new grass
390 (thin lines) constituting the habitat quality treatment. Every second patch pair was covered by avian predator
391 exclusion nets (shaded squares) constituting the predation risk treatment. Mammalian predation was excluded
392 from all plots by an electric fence surrounding the experimental area (not shown). Founder demes of root voles
393 (*Microtus oeconomus*) were introduced to the two old grass patches (source patches) in the two most distant
394 plots in the systems (plot 1 and 6). Nine days after the introduction of the founder demes fence gaps between the
395 6 plots were opened. Colonization distance classes from the source patches are given below the figure. Post-
396 colonization deme sizes in trapping period 1 (18 days after the opening of fence gaps) in the two replicate years
397 (year 2000/ year 2001) is given as numbers in each patch

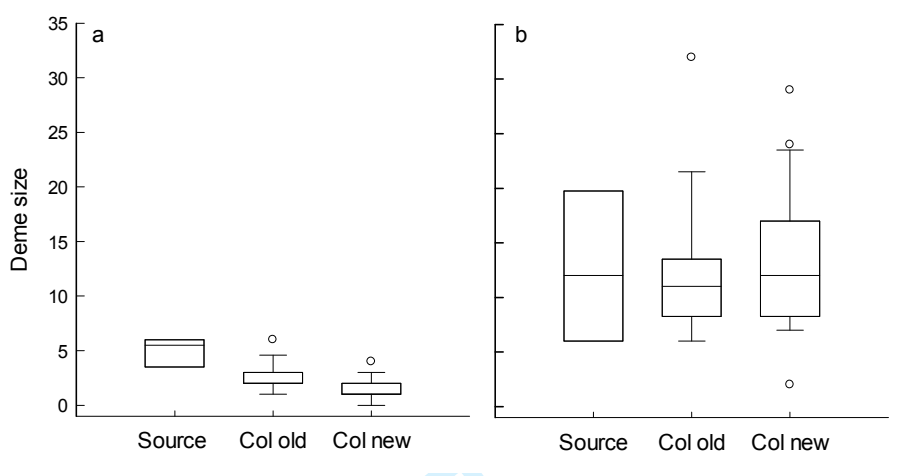
398 **Fig 2** Box plots showing deme size distributions for source patches (i.e. old grass patches receiving founder
399 demes at the onset of the experimental seasons) and colonization patches of the two habitat qualities: old grass
400 and new grass. Panel A shows the deme sizes after the initial colonization process was completed 4 weeks after
401 the onset of the experiment, while panel B shows the final deme sizes approximately 4 months later. Deme size
402 data from the two replicate years are pooled.

403

404 **Figure 1**



405 **Figure 2**



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