

1 **Ecological traps for large-scale invasive species control: Predicting settling rules by**
2 **recolonising American mink post-culling.**

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20 **Summary**

21 1. Management programs worldwide seeking to reduce the density of invasive species must
22 overcome compensatory processes, such as recolonisation by dispersers from non- or
23 partially-controlled areas. However, the scale and drivers of dispersal in such context are
24 poorly known.

25 2. We investigated the dispersal patterns of American mink reinvading 20,000 km² of their
26 non-native range following a culling programme led by citizen conservationists. Using
27 multinomial models, we estimated the contributions of density dependence, proxies for patch
28 quality and distance from the natal patch on mink settlement.

29 3. Seventy seven percent of mink dispersed and settled in non-natal patches. Dispersal
30 distances were large with settlement probabilities only reduced by half at ~60 km, and 20%
31 of mink dispersing > 80 km.

32 4. Females were more attracted to patches of high quality mostly found at low altitudes.

33 Males favoured patches with intermediate current densities and consistently high quality.

34 *Synthesis and applications.* We predicted post-culling recolonisation by a non-native mobile
35 carnivore over a large spatial scale using information obtained during management
36 interventions largely implemented by citizen conservationists. This was made possible by a
37 monitoring component of the project designed to feed into the adaptive management process.
38 High mink mobility dictates management should take place on very large spatial scales to
39 minimise reinvasion from un-controlled areas. Both males and females were attracted to
40 patches that were previously consistently occupied, providing a degree of predictability to
41 patterns of recolonisation. Targeting control to patches attractive to immigrant mink requires
42 knowledge of current mink density. Creating so-called ecological traps in the face of ongoing
43 immigration from peripheral areas provides a promising tool to effectively control mobile
44 invasive species.

45

46 **Keywords:** invasive species, dispersal, settlement, compensation, immigration, adaptive
47 management, ecological traps

48 **Introduction**

49 Understanding the ecological processes governing invasive species population dynamics and
50 mitigating their threat to native ecosystems is a focus of much research (e.g. Simberloff *et al.*
51 2013, Hastings *et al.* 2005). Efforts to reverse the spread of invasive mammals have become
52 more rigorously designed and implemented, achieving eradications of e.g. rats, mice, cats and
53 rabbits on islands of increasingly large size (Bester *et al.* 2002; Barun *et al.* 2011; Kessler
54 2011). Where eradication is not feasible, the management objective is suppressing numbers
55 to near-zero density or to densities sufficiently low to allow the recovery of affected native
56 species (Norbury *et al.* 2015; as with red foxes and feral cats in Australia, Moseby & Hill
57 2011; stoats in New Zealand, Veale, Clout & Gleeson 2011). However, management
58 interventions focused on control must contend with compensatory recolonisation through
59 dispersal from adjoining uncontrolled areas.

60 Reducing densities of invasive species by culling typically produces density
61 dependent compensatory responses in surviving individuals, such as increased fecundity and
62 survival (Boyce, Sinclair & White 1999; Pöysä 2004; Melero, Robinson & Lambin 2015).
63 Reduced competition for resources may also stimulate dispersal from adjoining high-density
64 areas towards culled low-density areas. If individuals are able to detect variations in resource
65 availability, both residents that have escaped culling as well as immigrants may settle in
66 productive low-density areas and partially or completely negate culling efforts through
67 reinvasion (e.g. Matthysen 2005; Lieury *et al.* 2015). While such dispersal patterns would
68 tend to accelerate the recovery of the culled population, they can be harnessed so as to create
69 ecological traps in attractive but vacant areas where targeted ongoing culling would
70 effectively prevent population recovery through immigration (Delibes, Ferreras & Gaona
71 2001; Robinson *et al.* 2008; Lieury *et al.* 2015; e.g. Gervasi *et al.* 2015; Oliver *et al.* 2016).
72 Accordingly, understanding the drivers of dispersal, including settlement rules used by
73 dispersers at low density, may be central for optimising the management of invasive species
74 by spatially targeting control efforts (Glen, Pech & Byrom 2013).

75 Most studies of individual dispersal decisions have hitherto focused on emigration
76 (Clobert *et al.* 2012; Altwegg *et al.* 2012; Furrer & Pasinelli 2015; but see Turgeon &
77 Kramer 2012; Glen, Pech & Byrom 2013). The factors that determine settlement decisions
78 are comparatively poorly known, even for the best-studied model organisms. Theoretical
79 investigations predict that a disperser's settling decision should depend on its ability to access
80 information on the quality of potential patches (Ruxton & Rohani 1999; Vuilleumier &
81 Perrin 2006). This in turn may be influenced by the perceptual range and mobility of
82 dispersers and by the properties of the landscapes through which they move (Miller *et al.*
83 2011; Hovestadt, Mitesser & Poethke 2014). Most problematic predatory mammalian
84 invasive non-native species are highly mobile (e.g. red fox, cats, stoats, mink and mongoose;
85 Genovesi *et al.* 2012) and hence can acquire information about settlement opportunities over
86 large areas. A fundamental question is therefore: how do individuals make decisions in
87 relation to their settlement choices (Sutherland *et al.* 2013; Gilroy & Lockwood 2016).

88 Habitat quality and conspecific density are known to influence the attractiveness of
89 potential settlement areas to dispersers (e.g. Turgeon & Kramer 2012; Glen, Pech & Byrom
90 2013). Therefore, the balance between quality and the positive and negative influences of
91 density (due to e.g. conspecific attraction and competition for resources, respectively) might
92 also shape individual decisions. Generally, relatively more individuals are expected to settle
93 in poor quality sites at high-density than in low density populations (e.g. Gunnarsson *et al.*
94 2005). Indeed, in harvested cougar populations (*Puma concolor*), dispersers settled
95 preferentially in high quality habitats where conspecific density was reduced by harvest
96 (Robinson *et al.* 2008; Wolfe *et al.* 2013) and their settlement probability declined with
97 distance from the location of birth (Morrison, Boyce & Nielsen 2015). Performing studies at
98 sufficiently large scale relative to the large dispersal ability of predatory mammals is
99 particularly challenging (Glen, Pech & Byrom 2013), consequently, little is known about the
100 dispersal and settling rules they (Glen, Pech & Byrom 2013; Oliver *et al.* 2016).

101 In order to provide the necessary understanding to optimally counter recolonisation
102 through immigration, we sought to describe how dispersal distance, density dependence and

103 patch quality affect settlement probability of the invasive American mink (*Neovison vison*).
104 Mink is a globally widespread invasive species and the focus of much long-term control
105 efforts (Bonesi & Palazón 2007; Genovesi *et al.* 2012). They are solitary, territorial
106 carnivores inhabiting linear territories along watercourses. Mating occurs in February-March
107 in Scotland, when rutting males, but not females, abandon their territories, travelling tens of
108 kilometres in search of mating opportunities (Melero & Palazón 2011; Melero, Robinson &
109 Lambin 2015). Dispersal is thought to occur once, when juveniles of approximately 5 months
110 old leave the maternal territory seeking a vacant territory in which they typically settle by the
111 end of the year (Gerell 1970; Dunstone 1993).

112 We used multinomial models to analyse how recolonising mink selected settlement
113 locations amongst available patches where their conspecifics had been removed by a large-
114 scale citizen conservationist-based, project seeking to suppress mink populations in their
115 invasive range in NE Scotland (Bryce *et al.* 2011). We predicted a negative influence of
116 distance from the natal patch on settling probability (Oliver *et al.* 2016) and that dispersers
117 would preferentially settle in patches of relatively high quality that host a moderate number
118 of conspecifics, reflecting the dual influences of mate attraction and competition for
119 resources.

120

121 **Methods**

122 **STUDY AREA**

123 The mink control program started in 2006 in the Cairngorms National Park (57° 0'N, 3°
124 30'W, Fig. 1a) NE Scotland and gradually expanded spatially in a non-systematic manner,
125 reaching ~20,000km² by 2012 (Bryce *et al.* 2011). This area covers an heterogeneous
126 landscape mixing highlands up to 1300 m altitude dominated by acidic grasslands and bogs
127 with mean coverage 36.7% and 25.4% at 25 m-scale) and a coastal lowland plain partially
128 dominated by rough and improved grass (mean 8% and 30%, ranges 0-100%) respectively
129 (see Bryce *et al.* 2011) (Fig 1). The project area spanned 16 river catchments totalling 2,500
130 km of waterway, subdivided into 21 sections (patches hereafter) reflecting project

131 management units where mink control and monitoring were instigated at the same time (see
132 Bryce *et al.* 2011; Melero, Robinson & Lambin 2015). Patches had a mean waterway length
133 of 153 km (SD 26) and a mean maximum length of 40 km (SD 11, based on Euclidian
134 distances; Fig. 1a). The asynchrony in the inception of comprehensive control in each river
135 catchment led to a patchwork with different mink densities, each surrounded by variable
136 numbers of other patches not yet subjected to control and variably fuelling recolonisation of
137 adjacent patches. No mink were recorded or captured in one unit, so it was excluded from
138 analyses.

139

140 DATA COLLECTION

141 Project activities were undertaken by volunteers who detected, trapped and removed mink,
142 coordinated by three to four project officers. Mink were detected using mink rafts (Reynolds,
143 Short & Leigh 2004) deployed at regular intervals along waterways. A trap was placed on the
144 raft following detection, and left in place for a few days or until a mink was caught and
145 humanely dispatched. Sustained culling led to density reductions of 50% after the first year
146 of fully-comprehensive control, achieving overall density reductions of 80% after 6 years
147 (Melero, Robinson & Lambin 2015). The carcasses of 86% of 979 culled mink were
148 collected from ca. 400 volunteers for later dissection of which 387 were females, 452 were
149 males and 140 were of unknown sex (Fig. 1b). The carcasses of the remaining 14% mink
150 were not retained. Mink sex was determined and a canine tooth and muscle tissue samples
151 were removed for age determination and molecular analyses, respectively. Mink age was
152 estimated through X-ray of canines (Helldin, 1997) and using tooth cementum analyses for
153 non-juveniles performed by Matson's Laboratory LLC (Manhattan, USA).

154

155 CANDIDATE PREDICTORS OF SETTLEMENT DECISIONS

156 Dispersing mink are faced with a choice between multiple patches they could settle in. We
157 modelled the probability that an individual chooses a specific patch amongst all possible
158 candidates in relation to patch-level and individual-level covariates.

159

160 CHOICE-SPECIFIC VARIABLES

161 We were interested in understanding how the following environmental and population
162 covariates at the patch-level affected patch choice: patch quality (constant), natal dispersal
163 (individual-varying) and conspecific density (time-varying).

164

165 *Environmental covariates*

166 Estimating spatio-temporal variation in prey resources for generalist predators over
167 20,000 km² was unachievable, so we used the data available in the control project to derive
168 proxies of patch quality. First, we assumed that the most attractive patches would be those
169 with consistently high occupancy. Thus we used as proxy of patch quality, Q , the maximum
170 proportional length of a patch occupied by settled adult mink for the 6 year duration of the
171 study (cumulative total km occupied/total patch length in km) following the procedure
172 detailed in Melero, Robinson & Lambin (2015).

173 Calculations of Q did not exclude those mink focal to our inferences, which we
174 acknowledge may impose a degree of non-independence between the explanatory and
175 dependent variables. However, only 20% of the mink captures used to define Q were focal
176 mink, such as their contribution in Q was per patch was low. To overcome potential caveats
177 associated with using Q , we also used a set of habitat variables previously found to predict
178 mink occurrence in Scotland (Fraser *et al.* 2015) at 1 km buffer (reflecting mink home
179 ranges; Melero *et al.* 2008). These were mean altitude and proportion of improved grass, acid
180 grass, rough grass, and bog, mapped at 25 m resolution, derived from Land Cover Map
181 (LCM) 2007 data for the UK (Morton *et al.*, 2011) using ArcGis 10.1 (ESRI, 2014) at 1 km²
182 pixel. Because Q and candidate habitat descriptors were likely to be correlated, we fitted two
183 distinct models to ensure interpretability. Model-1 included Q and all population and
184 individual covariates described below but not the habitat covariates, whilst Model-2 included
185 all covariates except Q (see below).

186 Approximate natal dispersal distances were taken as the distance between natal and
187 culling patches. This distance was measured as the Euclidean distance between the arithmetic
188 means of the capture locations of all mink culled in each patch (i.e. from the centroid of the
189 natal to that of settlement patch) as mink appear unconstrained by waterways in their
190 dispersal (Oliver *et al.* 2016). This reduced the error due to mink mobility within the patch
191 (i.e., capture location does not necessarily relate to the location of activity), but reduced the
192 resolution reported using exact locations (e.g. Oliver *et al.* 2016 Natal patch was inferred
193 using a combination of information on pedigrees (Appendix S1, Supporting Information),
194 and dates and locations of capture and birth following Telfer *et al.* (2003). The natal patch
195 was deemed to be that of the capture location of an individual's mother. When the mother
196 was unknown, it was taken as the capture location of an individual's full- or maternal half-
197 siblings if siblings were captured prior to the seasonal initiation of natal dispersal (October).
198 Fathers and paternal half-siblings were not used because males roam widely during the rut
199 and their locations of capture poorly reflect the natal patch of their offspring (Dunstone,
200 1993). The settlement patch was taken to be the capture location of those individuals deemed
201 to be holding a territory at the time of capture (i.e. settled mink). Thus, we excluded those
202 mink likely to be transient (i.e. mink < seven months old, assuming all were born in June)
203 and rut males (i.e. male mink caught during the mating season, February-March).

204

205 *Population density covariates*

206 Due to the large scale of our study, it was unfeasible to estimate time-varying mink density.
207 Instead, we used relative density values taken as the ratio of the number of captured
208 territorial individuals in a calendar year relative to the maximum number of mink potentially
209 settling in that patch (using Q as denominator). We did so in the knowledge that not all mink
210 present in a given year and location were trapped but under the assumption that the number
211 of mink caught was proportional to the number of mink present, and therefore that the
212 estimate would capture biologically relevant variation in density. Relative density was
213 calculated pooling males, females and mink of unknown sex as the later account for 14 % of

214 979 mink caught. Both relative density (RD) and its quadratic term (RD²) were included as
215 candidate explanatory covariates in the analyses to allow for positive and negative influences
216 of density.

217

218 INDIVIDUAL-SPECIFIC COVARIATES

219 The influence of patch-specific covariates on settlement decisions is likely to differ between
220 classes of individuals. Accordingly, we included sex as an individual-level covariate within
221 all patch-specific covariates in our analyses. Dispersal distances inferred from pedigree
222 assignments are not error-free in partially sampled populations (Leonarduzzi *et al.* 2012;
223 Melero, Oliver & Lambin 2017). Hence, when considering dispersal distance, we first
224 included the inferred relationship type (mother-offspring, full- or (maternal) half-siblings)
225 used to infer natal patch as an individual-level covariate. We expected that the most error-
226 laden assignments would see the greatest shrinkage of the effect of distance, with errors
227 increasing from mother-offspring, to full- and half-sibling (Melero, Oliver & Lambin
228 2017). Relationships with the highest reliability (mother-offspring; Melero, Oliver & Lambin
229 2017) were then used to test the sex-distance interaction.

230 Finally, following Vardakis *et al.* (2015), we included a ‘home advantage’ variable in
231 the models. This allows the probability of staying in the natal patch to be independent of the
232 distance-to-travel effect.

233

234 All continuous variables were standardised by subtracting the mean and dividing by
235 the standard deviation to assess the relative contribution of each variable to settlement
236 probability.

237

238 MODELLING DISPERSAL DECISIONS

239 Dispersal movement data have recently been analysed using multinomial discrete choice
240 models (multinomial regression models), where the probability of settling in a particular
241 patch is a function of patch- and individual-level covariates (Vardakis *et al.* 2015). We used

242 multinomial probit models to describe individuals' choice from a finite set of mutually
243 exclusive alternatives.

244 The models assume that an individual i selects its preferred settlement patch from the
245 entire set of available patches $p = 1, \dots, P$. Relative preference by individual i is modelled
246 through a $(P - 1) \times 1$ latent variable vector Λ_i . The chosen patch is assumed to be the one
247 with the highest value of the latent variable:

$$248 Y_i(\Lambda_i) = \begin{cases} 0 & \text{if } \max(\Lambda_i) < 0 \\ p & \text{if } \max(\Lambda_i) = \Lambda_{ip} > 0 \end{cases}, \text{ for } i = 1, \dots, N \text{ and } p = 1, \dots, P-1$$

249 Where Y_i is the index of the chosen patch and $Y_i = 0$ is an arbitrarily chosen reference patch.

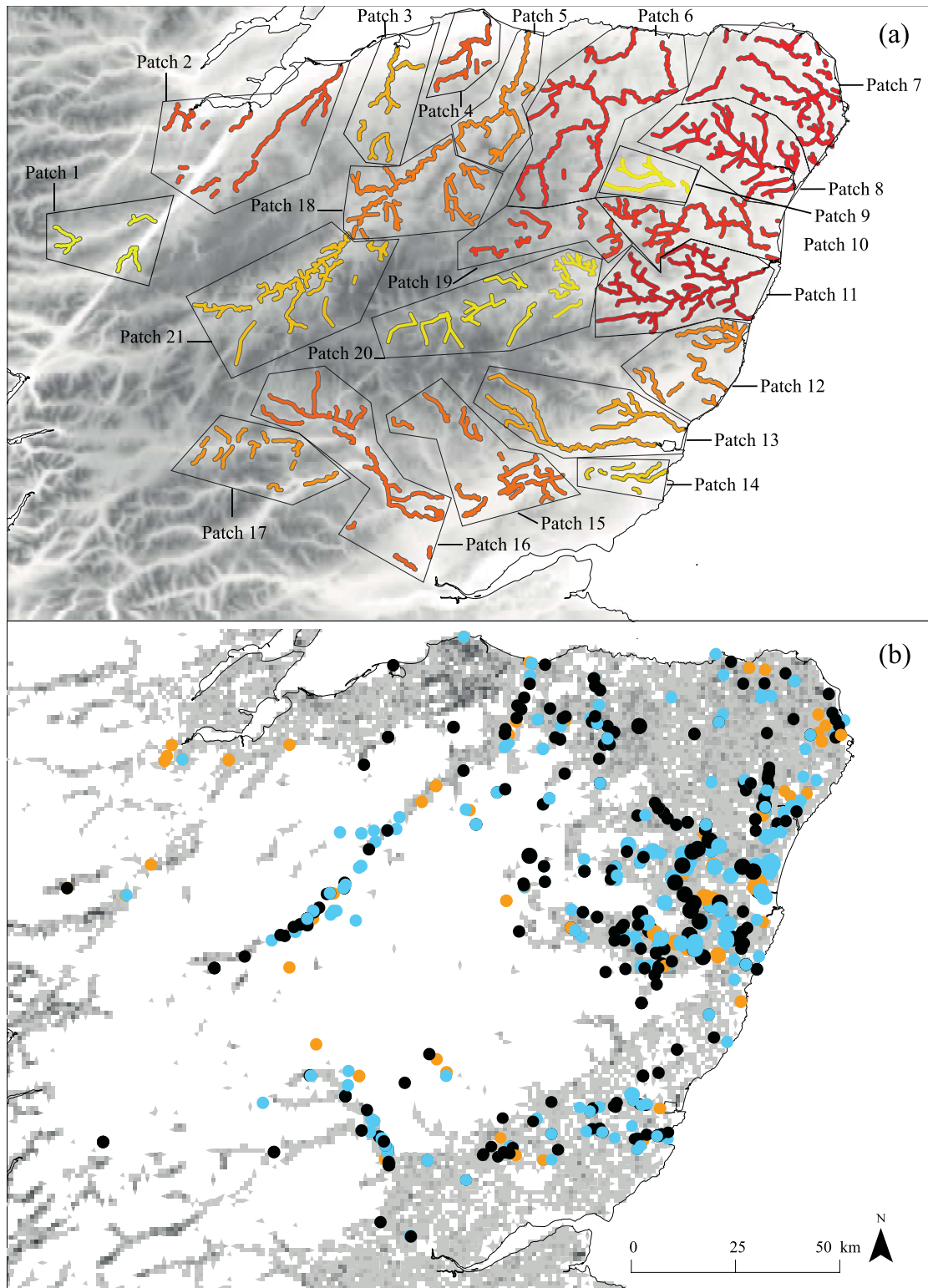
250 The latent variable vectors Λ_i are defined as a function of k covariates:

$$251 \Lambda_i = X_i\beta + \varepsilon_i$$

252 X_i is a $(P - 1) \times k$ matrix of choice-specific and individual-specific covariates (listed in the
253 previous section), and β is a $k \times 1$ vector of regression coefficients. ε_i is $(P - 1) \times 1$
254 multivariate normal vector of errors $\varepsilon_i \sim N(0, \Sigma)$ where Σ is a $(P - 1) \times (P - 1)$ positive-
255 definite matrix which allows for some redundancy between alternative choices (Ray 1973).

256 We made the simplifying assumption that our study area included all possible
257 alternatives, given the 20,000 km² size of our study area, even though not all patches were
258 covered at the start of the project, such that some individuals may have died of natural cause
259 undetected after settling. The models were fitted in a Bayesian setting using a Markov Chain
260 Monte Carlo (MCMC) procedure, using package MNP (Imai and Dyk, 2005) in R 3.0.2
261 software (R Core Team 2016). We used the default non-informative priors (Gaussian with
262 “infinite” variance) and drew 1,050,000 MCMC Gibbs samples, discarding the first 50,000
263 and retained one iteration in 100 for storage-saving purposes (for implementation see
264 Appendix S2). We ran five independent MCMC chains, starting from overdispersed values
265 and diagnosed their convergence with the Gelman-Rubin statistic (Table S1; Gelman &
266 Rubin 1992).

267



268

269 **Figure 1.** (a) The 21 patches coloured in yellow-to-red scale as per their gradient in quality Q

270 (1-41% past use). The white-to-grey scale background relates to the gradient of altitude

271 (spanning 0-1300 m). (b) Settled female (blue circles, $N = 387$), settled male (black circles; N

272 = 452) and mink of unknown sex (orange circles, N = 140). The grey scale background
273 relates to the gradient of rough grass (1-100%, white relates to zero rough grass).

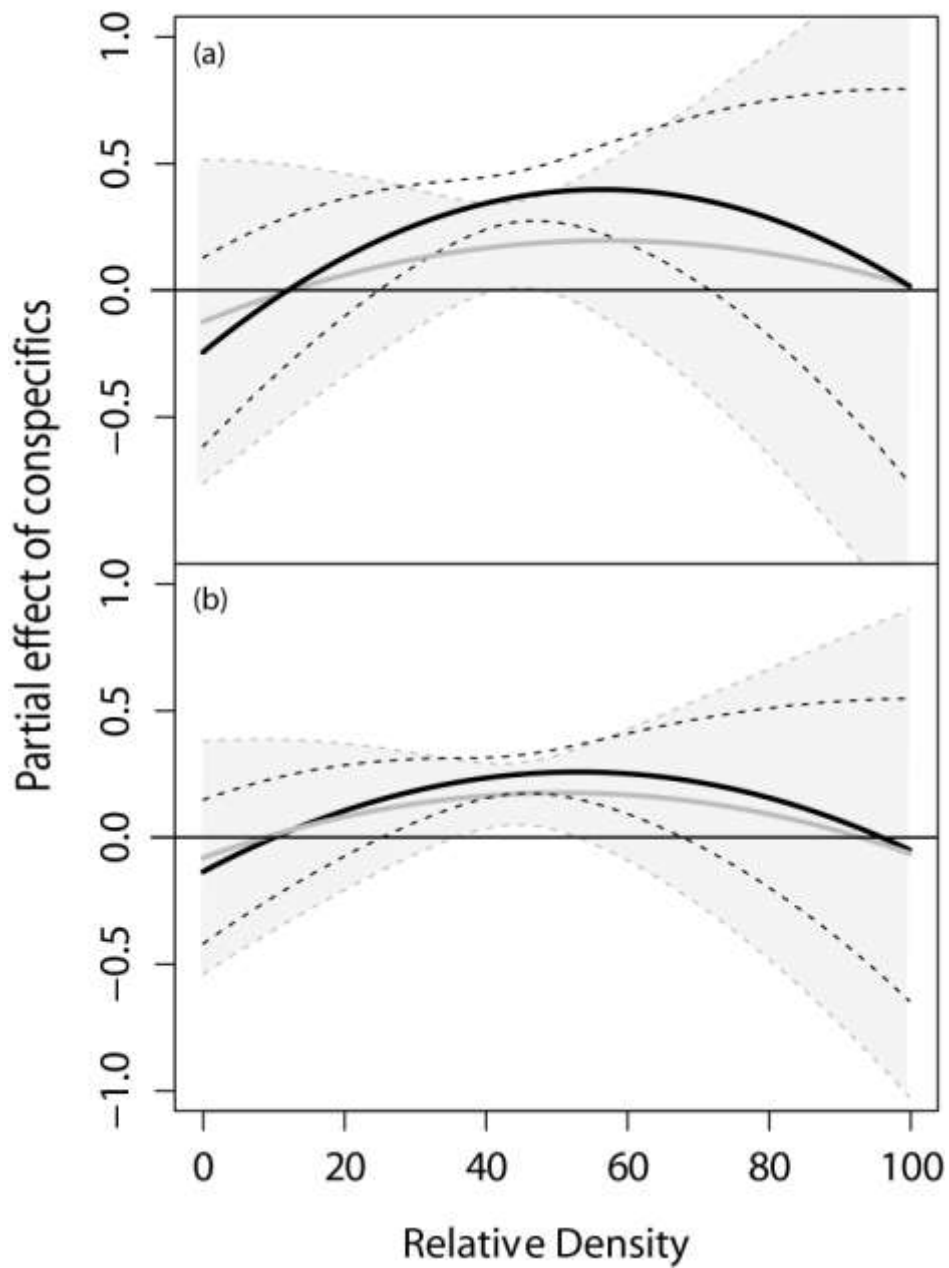
274

275 **Results**

276 All mink contributed to estimating the population density covariates, but only 479 out of 839
277 mink with known sex were successfully assigned to a relative (mother or pre-dispersal
278 sibling) from which we could infer the natal location. Of these, 76.7% and 77% of adult
279 females and males, respectively, were caught as outside their natal patch (Fig. S1).

280 Mink settlement decisions were influenced by both environmental and population
281 covariates. Conspecific density (RD and RD²) was a positive driver in both models, although
282 the strength of its effect was lower in Model-2 (Table 1). Male probability of settlement
283 increased with increasing conspecific density up to approximately 50% RD, but started to
284 decline when RD exceeded ~60% RD, without evidence of any effect at highest densities
285 (Fig. 2). The influence of density on female settlement was comparatively weak (Fig. 2).

286



287

288 **Figure 2.** Estimated marginal effect of relative density (i.e., proxy of the saturation by
 289 conspecifics) on mink settlement probability (i.e. the additive effect on the link scale of
 290 relative density on the probability of choosing a patch) and 95% credible intervals (dashed
 291 lines) for (a) Model-1 (using occupancy as an indicator of patch quality) and (b) Model-2
 292 (using habitat covariates as an indicators of patch quality), and for males (black lines) and
 293 females (grey lines and shadows). Solid horizontal lines represented no effect ($y = 0$).

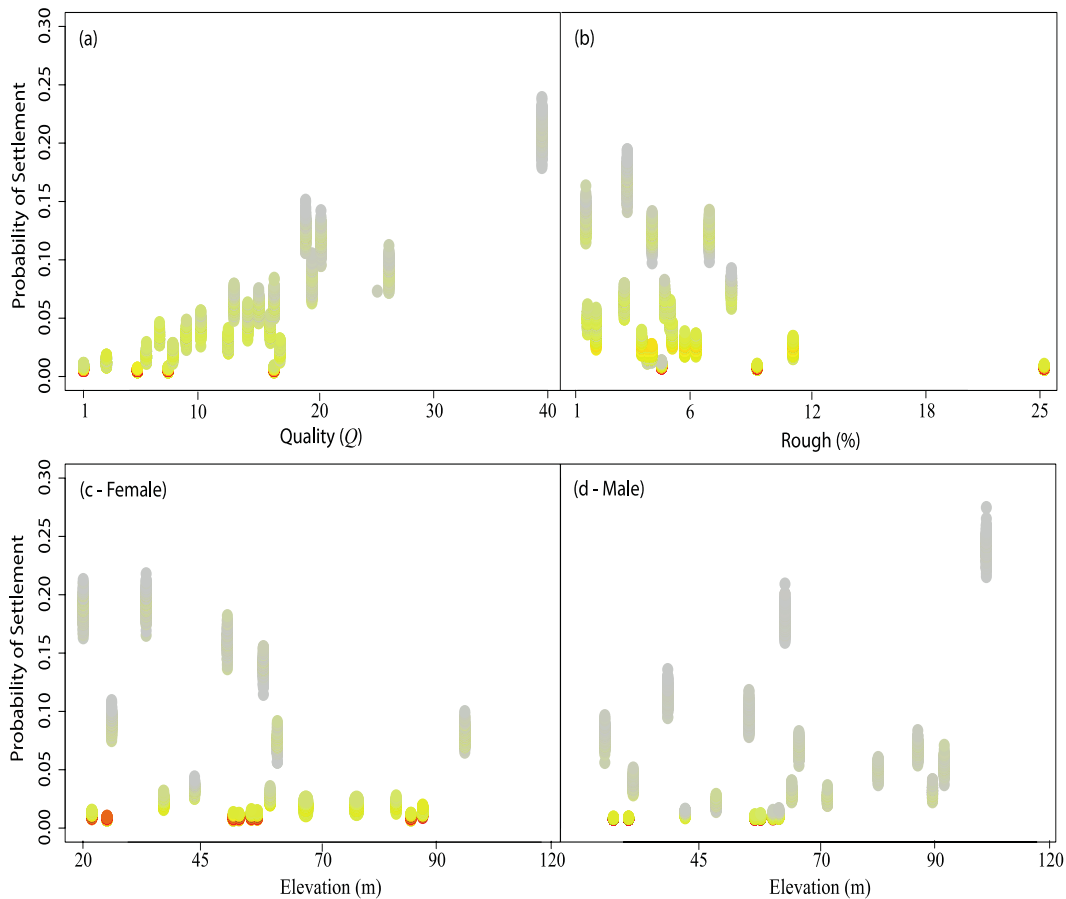
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295 **Table 1.** Posterior coefficient estimates for standardised patch-specific covariates (mean,
 296 standard deviation and 95% credible intervals bounds). Covariates with the “female”
 297 subscript (e.g. “RD_{Female}”) denote the difference between the effect of this covariate on
 298 females compared to its effect on the reference level, in this case, males. “D_{full sibling}” and
 299 “D_{half sibling}” are the difference between the effect of distance D for the reference level (D
 300 inferred from mother-offspring relationship) and the effect of D with D inferred from full and
 301 half sibling relationships respectively. *Q* relates to patch quality and RD to relative density.
 302 Bold indicates significant covariates.
 303

	(a) Model-1				(b) Model2			
	Estimate	SD	2.5%	97.5%	Estimate	SD	2.5%	97.5%
RD	0.86	0.17	0.54	1.20	0.60	0.13	0.35	0.87
RD _{Female}	-0.47	0.23	-0.94	-0.02	-0.19	0.17	-0.51	0.13
RD ²	-0.81	0.17	-1.15	-0.48	-0.61	0.14	-0.90	-0.35
RD ² _{Female}	0.46	0.24	-0.01	0.93	0.17	0.17	-0.15	0.51
Q	0.45	0.03	0.40	0.51				
Q _{Female}	0.03	0.03	-0.03	0.08				
D	-0.39	0.05	-0.51	-0.29	-0.31	0.05	-0.42	-0.22
D _{full-siblings}	0.14	0.08	-0.02	0.29	0.14	0.07	0.01	0.27
D _{half-siblings}	0.17	0.06	0.06	0.28	0.15	0.05	0.06	0.25
Home Adv	-0.18	0.07	-0.32	-0.04	0.07	0.06	-0.05	0.19
Altitude					-0.26	0.16	-0.61	-0.01
Altitude _{Female}					-0.10	0.05	-0.20	-0.02
Rough					-0.37	0.20	-0.80	-0.10
Rough _{Female}					0.09	0.07	-0.03	0.22
Bog					0.05	0.07	-0.05	0.21
Bog _{Female}					0.02	0.03	-0.04	0.08

304

305 In both models, patch quality positively influenced mink settlement probability.
 306 Settlement by both sexes strongly increased similarly with Q (Model-1, Fig. 3a). Mink
 307 settlement decisions followed a distinct spatial pattern since patches with highest Q (3rd
 308 quartile $Q = 19\%$, range 1-41; Fig. S2) were located in the coastal plain and along valleys
 309 floors. All patches had some coverage of rough grass (range 1-25%) but mink were attracted
 310 to those with lower than average cover and lower altitudes (both at 1 km-radius-scale), with
 311 lower altitude patches being more preferred by females relative to males (Table 1b, Fig. 3b-
 312 c). Other covariates either did not provide further explanation of habitat quality (Table 1 -
 313 Model 2) or were correlated with covariates already present in the model (Fig. S3).
 314



315
 316 **Figure 3.** Partial predicted settlement probability for each mink and for each patch (i.e. each
 317 of the 479 mink is confronted with a choice of 21 potential patches, giving a total of 9009
 318 probabilities) in relation to the patch variables (a) Q , (b) percentage of rough grass, (c)

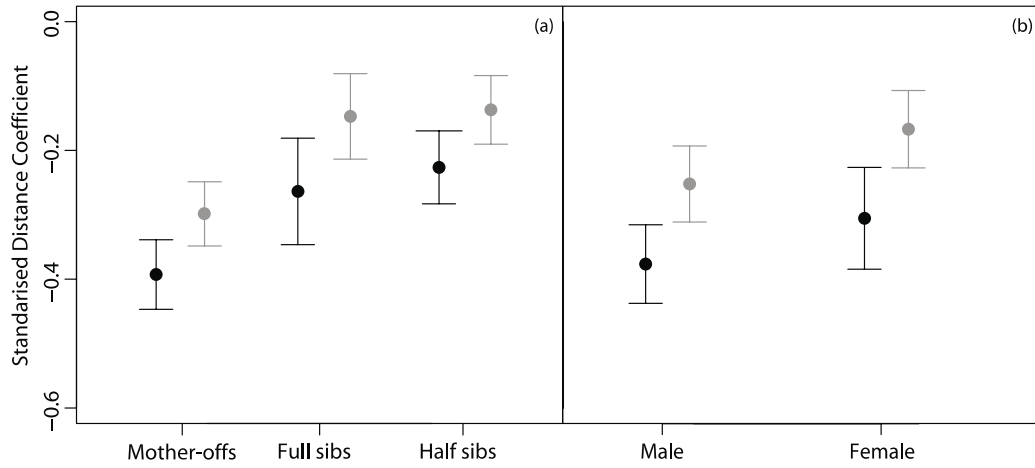
319 altitude for females and (d) altitude for males. A gradient of colour has been linked to the
320 density of predicted values (low to high: grey-to-yellow-orange-red). Predictions are based
321 on holding all other covariates at their mean value.

322

323 Mink settlement probability declined with the distance from the natal patch in both
324 models and for all three types of kin relationships used to infer natal location (mother-
325 offspring, full- and half-siblings). The estimated negative slope of the relationship with
326 distance was reduced by $\approx 33\%$, but not nullified, with assignment uncertainty levels, from
327 mother-offspring to full- and half-siblings (Table 1, Fig. 4a). Consistently, estimated
328 distances between centroids of natal and capture patches (Fig. S4) were longer when using
329 half-siblings (mean 26.31, 3rd quartile 58 km, N = 324) and full-siblings (mean 25.44, 3rd
330 quartile 55 km, N = 44) than when using mothers (mean 19.22 km, 3rd quartile 40 km, N =
331 112).

332 Considering only mother-offspring relationships, distance between patches had a
333 similarly negative effect for both sexes (Fig. 4b, Fig. S5), reducing settlement probabilities to
334 half (from approximately 0.20 to < 0.10) when patches were > 60 km distant from the natal
335 patch in both models and with 20% of males dispersing > 80 km (Fig. 5). The significant
336 effect of home advantage in Model-1 indicated that the probability of settling in the natal
337 patch was less than predicted solely using the distance effect at distance zero; Model-2 did
338 not capture this effect (Table 1).

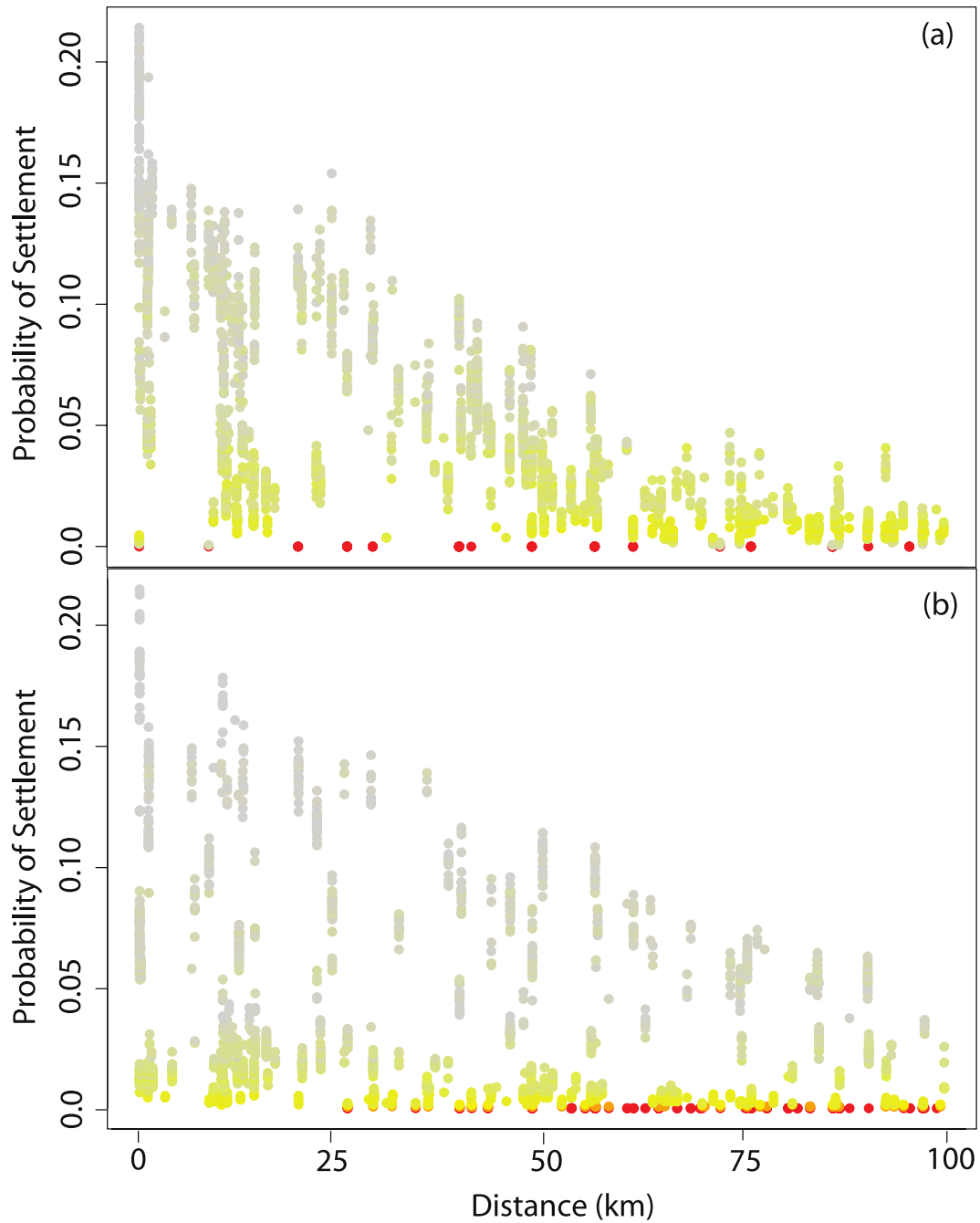
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340

341 **Figure 4.** Estimated effect of the standardised distance from the natal patch on mink
 342 settlement probability in relation to (a) the relationship type and (b) sex using only mother-
 343 offspring relationship for Model-1 (in black) and Model-2 (in grey).

344



345

346 **Figure 5.** Partial predicted settlement probability for each mink and for each patch (i.e. each

347 of the 112 mink using only mother-offspring relationship is confronted with a choice of 21

348 potential patches, giving a total of 2352 probabilities) in relation to the distance from the

349 capture to the natal patch for (a) Model-1 and (b) Model-2. A gradient of colour has been

350 linked to the increasing frequency of predicted values (grey-to-yellow-orange-red).

351 Predictions are based on fixing all other covariates values at their mean. Predictions at

352 distance zero include a “home advantage” effect.

353

354 **Discussion**

355 We used discrete choice models similar to Vardakis *et al.* (2015) for considering dispersal as
356 a choice process whereby individuals' decisions are ruled by the characteristics of the chosen
357 patch and of alternative choices. Using this relatively novel methodological approach, and
358 utilising dispersal data from mink recolonising a large area repeatedly depleted of
359 conspecifics by culling implemented by volunteers, we provided evidence of both density
360 dependence and habitat quality affecting mink settlement decisions. Mink selected high
361 quality patches to settle in. Probability of settlement decreased with distance from natal areas
362 in a similar way for female and male mink but the distances reached were long (mean 19 km,
363 max 100 km), therefore not constituting a strong limitation. Our findings indicate that large-
364 scale mink control could be optimized by turning preferential settlement areas in ecological
365 traps.

366

367 *Dispersal distances and mink settlement*

368 The precision of natal dispersal distances estimates using inferred pedigrees depends
369 largely on the type of kinship relationship between mother and descendants (Melero, Oliver
370 & Lambin 2017). We pragmatically ensured that our inferences were robust by accounting
371 for the influence of relationship type on the estimated effect of distance in the models. Not all
372 dispersers were detected and some mink immigrated and emigrated from our study area.
373 While these issues introduce a negative bias in estimations of dispersal distance in all studies
374 (Koenig, Van Vuren & Hooge 1996), their impact was likely minimal given the exceptionally
375 large size of the study area and the fact that it was bounded over roughly 75% of its periphery
376 by the North Sea and the semi-permeable Cairngorms Mountains (Fraser *et al.* 2013). Re-
377 invading mink of both sexes may have dispersed long distances. Both mean (19 km) and
378 maximum (100 km) dispersal distances are well in excess of values predicted for carnivorous
379 mammals of the size of mink (Sutherland *et al.* 2000) and may have contributed to mink's
380 success as an invasive species. Long-range dispersal by mink and other mobile invasive

381 species dictates that vast areas should be monitored and removal after an initial knock down
382 phase to prevent re-establishment of a breeding population (e.g. Oliver et al 2016; Lieury et
383 al. 2015). Given the range of natal dispersal in mink, the resource expenditure required
384 would be unmanageable without some way of targeting monitoring based on habitat
385 selection.

386

387 *Environmental quality and mink settlement*

388 We evaluated two sets of candidate proxies for patch quality, giving pragmatic consideration
389 to the challenges of characterising 2,500 km of waterways. Both indices similarly had a
390 positive influence on the settlement decisions of male and female mink. This provides scope
391 for targeting monitoring to intercept and removing dispersers settling in areas turned into
392 ecological traps through culling (Delibes, Gaona & Ferreras 2001; Delibes, Ferreras & Gaona
393 2001).

394 The proxies of quality in Model-2 were remotely-sensed properties of the riparian
395 habitat. Unlike Q , they have the benefits of being available from the outset of any control
396 project or in any future expansion area. Consistent with female mammals being constrained
397 by the energetic demands of lactation, they indicated that female mink settled preferentially
398 in river sections located in the fertile lowland plain of the North-East portion of the project
399 area where arable farming is the dominant land use. However, the level of discrimination
400 these proxies provided was limited, leaving 1,500 km of river with high quality scores, hence
401 with high priority for ongoing monitoring.

402 The second proxy, the consistency of patch use as defined by mink occupancy (Q)
403 was a good predictor of settlement consistent with inference from remote-sensed covariates.
404 It was the main factor predicting female mink settlement, with greater influence than distance
405 to the natal patch. High quality patches were mostly at low altitudes ($Q_{lowlands}$ mean = 22.4,
406 $SD_{lowlands} = 10.1$; $Q_{highlands}$ mean = 8.8, $SD_{highlands} = 4.8$; Fig. S2) but not all lowland patches
407 had high Q values. Unlike remotely-sensed habitat proxies, Q is derived from the
408 management process and relies on mink captures gradually accumulating.

409 Using Q as proxy of patch quality as perceived by mink themselves to predict
410 settlement by immigrants and spatially prioritise management is a technique broadly
411 applicable to other species, even where detectability of settlers is <100%. It can be
412 particularly useful when measures of resources (e.g. food, shelter) are not attainable. Indeed
413 past occupancy is widely used as a proxy of quality where gradients of quality are steep, as in
414 metapopulation studies (Hanski & Gilpin 1991; Johnson 2007).

415

416 *Density dependence and mink settlement*

417 Our metric of density was a time-varying relative estimate based on the number of mink
418 culled reported by volunteers. As the ratio of the number of occupied inferred territories per
419 patch in a calendar year relative to the maximum potential number of mink settling in that
420 patch, it is as a pragmatic measure of saturation relative to a notional carrying capacity.
421 Averaged annual relative patch density ranged from 6-90.4%; median 20%, overall range 0-
422 100%). There was evidence of non-linear effect of conspecific density ($RD + RD^2$ effects)
423 with highest probability of settlement at intermediate densities; the effect being stronger for
424 male than for female. This density dependence supports the hypothesis of a trade-off between
425 the benefits of the presence of conspecifics, which may inform prospective immigrants about
426 patch quality and on the presence of females, and the costs of competition.

427 Detecting the dual influences of quality patches and conspecific density on
428 settlement probability was facilitated by the reduction in mink population density through
429 culling. Indeed density dependence in saturated conditions in the early stages of the project
430 likely contributed to some female mink settling in low quality patches in the upland reaches
431 of the river catchments (Bryce *et al.* 2011). Our analyses imply that mink settled
432 preferentially in the more productive lowland patches as relative densities decreased, and
433 adds to the evidence of compensatory immigration that is known to occur in other controlled
434 mammalian species (e.g. Loveridge *et al.* 2007; Lieury *et al.* 2015).

435

436 *Management implications*

437 Our results exemplify that engaging citizen-conservationists in a conservation project
438 makes it feasible to carry out adaptive management and collect data at an exceptionally large
439 spatial scale. These can be judiciously exploited for learning about ecological processes
440 affecting management despite partial reporting and imperfect detectability.

441 Where the objective of invasive-species management is control rather than
442 eradication, identifying and focussing control effort on attractive areas is an effective option
443 for preventing reinvasion of an area following an initial knock down of the population. These
444 attractive areas where individuals are more likely to settle, can be used as ecological traps by
445 managers (Delibes, Ferreras & Gaona 2001) by enhancing trapping effort via e.g. higher
446 volunteer deployment and renewal of rafts in priority river sections and, at a finer scale, in
447 the vicinity of previous mink captures within these. The approach of relying on habitat
448 selection to spatially focus invasive control is however not without risk, as it relies on
449 statistically defined settling rules being faithfully used by all individuals. As such, it may not
450 be suited to eradication attempts, where it is crucial to remove all individuals.

451 Remotely-sensed habitat variables identified clear gradients of attractiveness to
452 prospective immigrants but were not sufficiently discriminant to efficiently target long term
453 monitoring aimed at thwarting recolonisation of very large areas. Indeed, some priority
454 patches were large in our study, reflecting both historical management and sample size
455 limitations. A better characterization of habitat variables defining attractiveness of river
456 section within the productive lowlands would be beneficial and applicable in newly
457 controlled areas where mink resettlement information is lacking. Over time, as adaptive
458 management progresses, variation in patch quality inferred from historical settlement
459 decisions by previous individuals will help refine the ranking of attractiveness of potential
460 settling areas and more sharply focus monitoring and removal effort. Ideally, accurate
461 prediction of patch attractiveness to prospective immigrants requires knowledge of current
462 density, or an appropriate proxy thereof provided by adaptive monitoring by e.g. mink rafts
463 and volunteer vigilance, emphasising the importance of spatiotemporal predictions for
464 management (e.g. Baker 2017). In our long-invaded project area, the distribution of native

465 species most vulnerable to mink predation is largely restricted to upland low productivity
466 refuges (Bryce *et al.* 2011), precluding the need to intercept mink before they reach the
467 productive patches they prefer. Instances where areas attractive to invaders and native species
468 coincide require a rapid response to reinvasion, further emphasising the need for
469 prioritisation.

470 In an ongoing control program, evidence of variation in patch quality will become
471 increasingly valuable to refine knowledge of the location of potential attractive areas that can
472 be used as ecological traps as capture of immigrants accumulate and the predictive power of
473 models improve. Their scale, while increasingly become refined over time as data
474 accumulate, is nevertheless suitable for targeting control or volunteer staff deployment to
475 those portions of the overall project area most attractive to the immigrants and suppress
476 reinvasion.

477

478 **Authors' Contributions**

479 Y.M and XL conceived the study, all authors interpreted the results and wrote the
480 manuscript. Y.M. performed the genetic analyses and estimated dispersal distance with
481 M.K.O, and the statistical analysis with T.C. X.L. supervised the research and the
482 management project.

483

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489

490 **Data Accessibility**

491 Data of the culled American mink in NE Scotland (ID), their settlement choice and the
492 related covariates formatted for the multinomial model will be archived in Dryad.

493

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647

648 **Supporting Information**

649 Additional supporting information may be found in the online version of this article.

650 **Appendix S1.** DNA extraction, genotyping and pedigree analyses

651 **Appendix S2.** R code and dataset for the Bayesian multinomial probit model (Model-1)

652 **Table S1.** Convergence statistics of the five MCMC chains for each model

653 **Fig. S1.** Matrix of the accumulative number of settled mink from natal to settlement patch.

654 **Fig. S2.** Quality (Q) per patch.

655 **Fig. S3.** Correlations between habitat variables.

656 **Fig. S4.** Patches coloured as per Q and their centroid of mink captures.

657 **Fig. S5.** Histogram of distances between patches.

658

659