

Community-wide mesocarnivore response to partial ungulate migration

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1 **Community-wide mesocarnivore response to partial** 2 **ungulate migration**

3

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10 **Running head:** Mesocarnivore response to ungulates

11

12 **Author contributions:** RAI, NGY, AS and JAH designed the study, AS, BJB and JAH collected and processed
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19

20

21

22 **Summary**

- 23 1. Mesocarnivores have been found to increase in numbers and geographic ranges in human-
24 disturbed ecosystems with cascading negative impact on biodiversity. To mitigate such
25 impacts it is essential to identify the proximate causes of such mesocarnivore releases. Here
26 we assess to what extent increased partial migration in semi-domesticated tundra reindeer
27 induce a response in boreal and arctic mesocarnivores.
- 28 2. We used a large-scale and multi-year quasi-experimental study design with camera traps
29 deployed on coastal tundra peninsulas in northern Norway to estimate area occupancy of the
30 whole carnivore community. These peninsulas represent summer pastures for separate semi-
31 domestic reindeer herds that, owing to different degrees of partial migration, now display
32 spatially and temporally variable densities of year-round resident reindeer. We estimated
33 resident reindeer density by means of aerial surveys.
- 34 3. Area occupancy of all the recorded carnivore species increased strongly when resident
35 reindeer densities exceeded 1.5 deer per km².
- 36 4. Most of the increasing carnivore species were typical boreal forest species, implying range
37 expansions into tundra when provided with stable food resources (prey and carrion) in terms
38 of resident reindeer.
- 39 5. **Synthesis and application.** We found that boreal mesocarnivores, known to negatively
40 impact the productivity of reindeer and arctic wildlife of conservation concern, steeply
41 increased in tundra areas with many year-round resident reindeer due to increased partial
42 migration. To avoid such negative impacts actions should be taken to minimize residency in
43 tundra reindeer.

44

45 **Key-words:** arctic tundra, corvids, eagles, mesopredators, semi-domestication, reindeer, red fox,

46 wolverine.

For Peer Review

47 Introduction

48 Increased abundance and range expansions of medium-sized carnivores (mesopredators;
49 sensu Soulé et al. 1988) often become the unintended consequences of human interventions in
50 ecosystems, with potentially negative cascading impacts on biodiversity (Prugh et al. 2009;
51 Ritchie & Johnson 2009). While population declines and range contractions of apex predators are
52 the most highlighted proximate causes of such mesocarnivore increase, through relaxed top-down
53 regulation (Estes et al. 2011), also increased resource levels may provide bottom-up boosts of
54 mesopredator populations (Crooks & Soule 1999; Larivière 2004; Elmhagen & Rushton 2007).
55 When both top-down and bottom-up constraints on mesocarnivore populations become relaxed
56 simultaneously, the setting is expected to maximize mesocarnivore outbreaks (Prugh et al. 2009).
57 Rarely, however, are the effects of factors that may cause mesocarnivore outbreaks and range
58 expansion explicitly quantified (Prugh et al. 2009), especially considering the entire community
59 of carnivores that may respond (Sutherland et al. 2011). A community approach is important
60 because different species with different bottom-up and top-down constraints and/or functions in
61 the food web may be involved (DeVault et al. 2003; Finke & Denno 2004; Finke & Denno 2005;
62 Wilson & Wolkovich 2011).

63 Ungulates constitute important food resource in terms of prey for large predators, but also
64 as carrion for scavengers of all sizes (Selva et al. 2003; Wilmers et al. 2003a; Wilmers et al.
65 2003b). Ungulates are also important resources for humans. This leads to various management
66 strategies, including removal of competing large carnivores and ungulate domestication. For
67 instance, in large parts of the Arctic herds of tundra reindeer (*Rangifer tarandus*) – the
68 numerically dominant and most widespread northern ungulate - have been semi-domesticated by
69 native people (Jernsletten & Klokov 2002; Forbes & Kumpula 2009; Forbes 2010). Semi-

70 domestication of reindeer impacts many aspect of their ecology including range use patterns and
71 reindeer-predator interactions (Forbes & Kumpula 2009) and together with the removal of apex
72 predators this has led to increased reindeer abundance (Hausner et al. 2011; Næss & Bårdsen
73 2013). Large carnivores preying on reindeer are persecuted and often severely suppressed in
74 regions with reindeer herding (Ims & Ehrich 2013). Moreover, the original ranges and movement
75 patterns of the herds have become increasingly constrained by human infrastructure (Forbes
76 2010; Degteva & Nellemann 2013).

77 Throughout their circumpolar range most populations of *Rangifer* travel between boreal
78 forests in winter to coastal calving grounds in tundra in the summer (Gunn & Miller 1986;
79 Fauchald et al. 2007). These migrations represent some of the longest, and ecologically most
80 important, migrations documented for terrestrial mammals (Fancy et al. 1989). Generally, Fryxell
81 & Sinclair (1988) argued that animal migration causes resident predators to depend on alternative
82 resident prey for most of the year and are therefore less able to respond numerically to the
83 temporary superabundance of migratory prey. Hence, migration is expected to limit carnivore
84 abundance.

85 In northern Fennoscandia the original seasonal coast-inland migration pattern of wild
86 reindeer became altered already when the herds were semi-domesticated 3-400 years ago (Muga
87 1986). The migration became further restricted by closure of the borders between Norway and
88 Russia, Finland and Sweden from the mid 1800's (NOU 1984; Jernsletten & Klovov 2002),
89 preventing the use of the historical winter pastures in the northern boreal coniferous forest in
90 Russia and Finland (NOU 1984). More recently, the migration has become increasingly affected
91 by modern anthropogenic infra-structure causing migration barriers (Forbes 2010) as well as
92 malfunctioning governmental policies (Hausner et al. 2011). Finally, reindeer migration patterns
93 are likely to be affected by on-going climate change that alters the length of seasons (Tveraa et al.

94 2013) and limits the access to winter pastures due to more ice-crusting snow (Bartsch et al. 2010).
95 Altogether, the cumulative effect of such emergent pressures on reindeer ranges may have
96 contributed to more partial migration (*sensu* Lack 1943), whereby a fraction of the population do
97 not migrate and become year-round resident in the summer habitat. Generally, global
98 environmental change is predicted to cause more partial migrations among animal species
99 (Chapman et al. 2011). In turn, a more partial migration (i.e. an increasing fraction of non-
100 migrant individuals) can have propagating ecological impacts, in particular, when the migrant
101 species are trophically important in food webs (Brodersen et al. 2008). Yet very few studies have
102 addressed the ecological consequences of such emergent partial migration patterns (Chapman et al.
103 2011).

104 By means of a large-scale study conducted over three years in coastal tundra of
105 northernmost Norway, our aim was to assess how the community of carnivores responded to
106 spatio-temporal variation in the degree of partial reindeer migrations across different
107 management districts. Partial reindeer migration implies that a fraction of the herd stays in their
108 summer pastures also in winter. In northern Norway the degree of partial migration varies among
109 different reindeer management districts and years, presumably owing to differences in
110 management/herding practices, range restrictions and climatic conditions. This particular setting
111 provided an opportunity to employ a quasi-experimental approach (cf. Ims et al. 2007) in which
112 spatio-temporal variation in density of resident reindeer in tundra was exploited to estimate the
113 response in the associated community of carnivores. If, as hypothesised by Fryxell & Sinclair
114 (1988), carnivore populations in coastal tundra are limited by access to reindeer prey or carrion
115 during winter, we predict that they will respond by increased species-level presence (i.e. area
116 occupancy) to increasing density of resident reindeer. Furthermore, we expected that such a
117 response would be strong (i.e. unconstrained) as the grey wolf (*Canis lupus*) – which was the

118 natural apex predator in low-arctic tundra - have been exterminated from the entire reindeer
119 herding region of northern Fennoscandia (Elmhagen & Rushton 2007; Hobbs et al. 2012). The
120 extant carnivore assemblage in the study region consists of species with widely different
121 ecological niches (Killengreen et al. 2012). They range from small-sized scavengers that never
122 prey on reindeer (e.g. corvids) to predators of calves (e.g. red fox *Vulpes vulpes* and golden eagle
123 *Aquila chrysaetos*) and adult reindeer (e.g. wolverine *Gulo gulo*). The various species in the
124 carnivore assemblage also differ with respect to ecosystem affinity (i.e. to which degree they
125 have strongholds in the boreal forest or the tundra), their mobility (e.g. birds and mammals) and
126 use of alternative prey. Thus we also aimed to assess whether the individual species within such a
127 functionally diverse community responded similarly or differently to increased residency of
128 reindeer in coastal tundra.

129

130 **Material and methods**

131 STUDY AREA

132 The study was carried out from 2009 to 2011 on four peninsulas along the coast of
133 Finnmark, northern Norway (Fig. 1); i.e. the peninsulas of Varanger (70–71° N and 28–31° E),
134 Nordkinn (70–71° N, 27–28° E), Sværholt (70° N, 25–26° E) and Porsanger (69–70° N, 24° E). The
135 northernmost parts of the four peninsulas are within the low arctic bioclimatic tundra zone
136 (Walker et al. 2005). The vegetated tundra areas are dominated by dwarf shrub heaths (Oksanen
137 & Virtanen 1995; Ims et al. 2007; Killengreen et al. 2007).

138

139 SAMPLING DESIGN

140 Carnivore monitoring at the two easternmost peninsulas (i.e. Varanger and Nordkinn) has
141 been conducted yearly since 2005, in relation to a conservation project on the regionally
142 endangered arctic fox (*Vulpes lagopus*) (Killengreen et al. 2012), while the monitoring at the two
143 western peninsulas (Porsanger and Nordkinn) was initiated in 2009 and continued through 2011
144 in connection with the present study. Within all four peninsulas, two-three study blocks were
145 selected (Fig. 1) in order to cover an anticipated spatial variation in the number of resident (i.e.
146 non-migrating) reindeer during winter based on their belonging to different herding districts with
147 different management practices (Ims et al. 2007). In each study block we selected 5 - 8 study
148 sites. The linear distance between two adjacent study sites within a block was minimum 4.5 km
149 with an average nearest distance of 5.8 km (SD = 0.88 km). At each study site we placed one
150 wildlife camera trap baited with a 15-20 kg block of frozen reindeer slaughter remains
151 approximately 3 m in front of the camera. Obviously the bait of these traps was intended to
152 function as a local carnivore attractant. However, as we here focus on analysing large-scale
153 variation in carnivore presence in relation to the density of resident reindeer among the study
154 blocks with the same baiting of traps, the use of bait is not expected to affect our results. The
155 cameras (Reconyx PC85/PC800 – Reconyx Inc., Wisconsin, USA) were set in a time-laps mode
156 with images taken at regular intervals of 10 min on Varanger and Nordkinn and at intervals of 15
157 min on Sværholt and Porsanger. On Sværholt and Porsanger the cameras was in use in 30-39
158 days (i.e. 28th of March to 26th of April in 2009, 25th of February to 25th of March in 2010 and
159 17th of February to 21st of March in 2011) and the bait was never replaced during this period. On
160 Varanger and Nordkinn the cameras were in use for between 53-64 days (i.e. 10th of March to
161 27th of April in 2009, 1st of March to 3rd of Mai in 2010 and 4th of March to 9th of April in 2011)
162 and the bait was replaced 2-3 times at each study site each year. The difference in camera settings
163 and bait maintenance was due to different logistic constraints in the two main regions (i.e. pairs

164 of peninsulas). However, the set-up was within the range of frequencies and duration of
165 recordings suggested by Hamel et al. (2013a). Moreover, the different bait-replacement schemes
166 are also taken into account in the statistical analysis (see below). The season in which the
167 recordings were made is bio-climatically the winter season at these high latitudes, with close to
168 100% snow cover, and before the return of migratory wildlife from their wintering areas further
169 south. It is important to note, however, that the sampling periods coincide with the period when
170 the carnivore species have established territories (e.g. corvids and eagles), are pregnant (e.g.
171 foxes) or have already given birth to young (e.g. wolverine) (Englund 1970; Persson 2005).
172 Hence, we expected that our recordings to a large degree reflect those carnivores that reside in
173 these areas year-round.

174

175 COUNTS OF RESIDENT REINDEER

176 The numbers of resident reindeer were counted annually during February and March in
177 each study block by aerial surveys. The surveys were thus conducted before migrants returned to
178 the summer pastures towards the end of April. The aerial surveys were conducted according to a
179 strip transect sampling design (Buckland et al. 2001), with one dedicated and experienced
180 observer counting reindeer on both sides of the aeroplane. The area covered by the aerial surveys
181 was constant over years within the blocks, but varied between blocks due to variation in the
182 spatial extent of the tundra habitat within the blocks (range = 250 - 600 km², mean = 398.5, SD =
183 156.1, Table 1).

184

185 ANALYSES

186 For all the analyses we reduced the large sample of camera records (e.g. 33686 animal
187 records/pictures in Varanger/Nordkinn in 2009) of individual species each year to simple
188 “detection/nondetection” (1/0) for each day and site in the study. For the analysis of species-
189 specific occupancy and community richness we adopted a slightly modified version of the
190 multispecies hierarchical model presented in Zipkin et al. (2010). This modelling framework
191 allows true absence to be distinguished from non-detection by incorporating presence-absence
192 and detection-nondetection as two distinct components in the statistical model (MacKenzie et al.
193 2002; Kéry et al. 2009; Zipkin et al. 2010). Due to different length of the camera surveys and the
194 bait shifting regimes in the study blocks in the peninsulas of Varanger/Nordkinn and
195 Sværholt/Porsanger, respectively, we conducted separate analyses for these two regions (which
196 then were represented by 5 and 6 study blocks each (cf. Table 1). Moreover, we analysed each
197 year separately as the time of camera initiation varied between years as well as the length of the
198 recording period. We modelled the occurrence probability for species i at study site l by
199 incorporating site-specific covariates (c.f. Zipkin et al. 2010). We incorporated reindeer density
200 (i.e. count/survey area) in the occupancy estimates by assuming that the logit transform of the
201 occurrence probability (ψ) was a linear combination of a species effect (i) and the site-specific
202 reindeer density (l) as follows:

$$203 \quad \text{logit}(\psi_{i,l}) = u_i + \alpha_{li} * \text{ReindeerDensity}_l$$

204 Reindeer density was standardized (mean = 0, SD = 1), meaning that the inverse-logit of u_i is the
205 occurrence probability for species i in study sites with average reindeer density. Moreover, the α_{li}
206 is the slope parameter for the effect of reindeer density for species i . It is important to note that
207 models of species occupancy assume a closed system, i.e. that the occupancy of species does not
208 change over the time of the survey within a year. As this assumption is likely to be violated in

209 open systems like ours, with long surveys of highly mobile species inhabiting large home ranges,
 210 occupancy should be interpreted as the proportion of sites used by the species in a given time
 211 period (MacKenzie et al. 2004). Also note that the hooded crow was removed from the analysis
 212 of the carnivore assemblage in Porsanger/Sværholt in 2010 because it was not recorded.

213 The detection probability (p) for species i was assumed to vary based on slightly different
 214 variables for the study sites in the different peninsulas. This was done to account for the potential
 215 temporal heterogeneity in detection due to the bait replacements conducted on Varanger
 216 /Nordkinn. In both analyses we included reindeer density to account for the possibility that
 217 camera baits were used less when the density of reindeer and possibly the access to natural
 218 carcasses in an area was high. Finally, we included “day-of-the-year”, and its squared value, to
 219 account for seasonal changes in detection probabilities caused by changes in day length and
 220 predator activity levels. Thus for Varanger/Nordkinn:

$$221 \quad \text{logit}(p_{i,l}) = v_i + \beta_{1i} * \text{ReindeerDensity}_l + \beta_{2i} * \text{DayOfTheYear}_l + \beta_{3i} * \text{BaitReplacement}_l +$$

$$222 \quad \beta_{4i} * \text{DayOfTheYear}_l^2 ,$$

223 while for Sværholt/Porsanger:

$$224 \quad \text{logit}(p_{i,l}) = v_i + \beta_{1i} * \text{ReindeerDensity}_l + \beta_{2i} * \text{DayOfTheYear}_l + \beta_{3i} * \text{DayOfTheYear}_l^2 ,$$

225 where v_i denote the detection probability for average values of the covariates. As for the
 226 occupancy compartment of the model, all predictors for detection probability were standardized
 227 (mean = 0, SD = 1). Our analysis was performed using WinBUGS 1.4.3 (Spiegelhalter et al.
 228 2003), which uses Markov Chain Monte Carlo (MCMC) simulations to estimate posterior
 229 probability distributions. We estimated the model parameters by using naïve prior distributions
 230 for all the parameters in the model (Appendix B; WinBUGS model) (cf. Zipkin et al. 2010). We
 231 ran two parallel chains of length 25000 from random starting values, discarded the first 5000 as

232 burn-in, and retained 1 in 10 updates. Model convergence was assessed by the convergence factor
233 R_{hat} for each parameter in the model, where R_{hat} values close to 1 implies convergence (Gelman
234 & Rubin 1992).

235

236 **RESULTS**

237 REINDEER COUNTS

238 Reindeer aerial counts showed that the number of resident reindeer, and hence the degree
239 of partial migration, varied considerably among years, regions and blocks (Table 1). Resident
240 reindeer were more abundant in the first year (2009) of the study (reindeer presence in 9 out of 11
241 blocks) than in the two later years (5 blocks in 2010 and 4 blocks in 2011). Moreover,
242 Porsanger/Sværholt tended to have blocks with higher reindeer numbers than
243 Varanger/Nordkinn, except in year 2011 when there were no block with high reindeer numbers in
244 either of the two regions. Also among the blocks within a given year and region the counts
245 exhibited large spatial variation, often with neighbouring blocks having highly contrasting
246 numbers (Table 1). This provided a powerful setting for the quasi-experimental study design and
247 statistical analysis, in particular for those region and year combinations with the largest range in
248 reindeer densities.

249

250 CARNIVORE AREA OCCUPANCY

251 Seven small to medium-sized carnivore species, with very different average levels and
252 spatio-temporal variation in estimated area occupancy, were present (Fig. 2). The raven (*Corvus*

253 *corax*) was by far the most common and least variable species, followed by the red fox. The
254 regionally endangered arctic fox was the least common species and only present on the Varanger
255 Peninsula. Although generally low for most species (< 0.5 : Appendix A), the estimated mean
256 detection probability showed substantial variation. Reindeer density, day-of-the-year and bait
257 replacement (the latter only for the Varanger/Nordkinn region) were all important for the
258 probability of detection of the carnivore species and therefore important to take into account in the
259 detection compartment of the model in order to obtain unbiased estimates of area occupancy rates
260 (Appendix A).

261 The estimated effect of the reindeer density on species-specific carnivore area occupancy rates
262 differed between years and study regions both in terms of strength (Fig. 3) and precision (see
263 Appendix A for estimates of model parameters and their credibility intervals). However, the sign
264 and strength of the estimated effect (i.e. the slope parameter α_1) depended on the range of
265 reindeer densities within regions and years (Fig. 3, Table 1). Specifically, all slope estimates were
266 consistently positive for the three year and region combinations where the range in reindeer
267 densities exceeded 1.5 deer per km² (Porsanger/Sværholt 2009 and 2010, Varanger/Nordkinn
268 2009; Fig. 4), indicating a community wide carnivore response to reindeer residency above some
269 threshold density. The responses were weaker and much less consistent for densities less than 0.5
270 deer per km², although the majority of the slope estimates were still positive (Fig. 4). This strong
271 community response was also evident with respect to estimated species richness, with a
272 significantly higher estimated species richness in areas of high vs. low reindeer density in years
273 where the range in reindeer densities was large and exceeded 1.5 deer per km² (Appendix B; Fig.
274 B1).

275

276 Discussion

277 During the long Arctic winter the tundra is climatically hostile and biologically
278 unproductive; an ecosystem where plants and invertebrates are dormant under a thick and hard
279 snow cover and where most mobile vertebrate prey species have escaped by migrating to lower
280 latitudes. This must, almost as a virtue of necessity, have “knock-on” effects on higher trophic
281 levels in terms of an impoverished carnivore community, in particular with few carnivores that
282 feed on large herbivores (Krebs et al. 2003). Increased residency of large herbivores is thus
283 expected to cause increased residency of carnivore species that would otherwise not find
284 subsistence in tundra. However, whether carnivores originating from other ecosystems actually
285 will increase in tundra also depends on their tolerance to other attributes of the tundra
286 environment, like open habitats without vegetation cover and harsh climatic conditions. Thus the
287 expectation of an increased presence of such carnivores is in need of an empirical test.

288 By using a large-scale study design that included samples of different reindeer herds over
289 three years, we found that carnivore area occupancy rates in tundra increased distinctly with
290 increasing density of non-migrating reindeer. This is, to our knowledge, the first empirical
291 confirmation of the expectation that increased tendency for partial ungulate migration may induce
292 a strong bottom-up boost in the mesocarnivore community, especially when the native apex
293 predator has been removed. It is notable how similar the response to high reindeer density was in
294 different carnivore species despite their different ecosystem origins. Several of the species found
295 to respond most strongly typically belong to neighbouring ecosystems. The hooded crow (*Corvus*
296 *corone*), red fox and the golden eagle are all mainly associated with forest ecosystems at high
297 latitudes, while the white-tailed eagle (*Haliaeetus albicilla*) mainly belongs to the marine food
298 web (Killengreen et al. 2012). This indicates that the increased presence of these predators is due

299 to an influx from neighbouring ecosystems and thus represents range expansions. This inference
300 is corroborated by the recent large-scale tendency for northwards expansion of boreal carnivores
301 and omnivores that are able to exploit increased amount of human-induced subsidies in the arctic
302 tundra (Ims & Ehrich 2013). On the other hand, forest-dwelling species such as the European
303 lynx (*Lynx lynx*) and the pine marten (*Martes martes*), which is known to inhabit the boreal forest
304 in the study region, was not recorded in tundra in this study. The lack of response in these species
305 may be due to smaller propensity for scavenging or stronger avoidance of open tundra habitats
306 than the boreal species we actually recorded by the camera traps baited with carrion.

307 The mammalian carnivores that prevailed in tundra in this study, as well as the eagles and
308 raven, start their breeding season already in February-March (Englund 1970; Persson 2005), prior
309 to the return of migrating reindeer in late April and early May. This suggests that increased
310 residency of reindeer may allow such carnivore species to reside and breed. The increased
311 presence of resident wolverine, golden eagle and red fox on reindeer calving grounds, all which
312 are important predators of new born calves (Fauchald et al. 2004; Norberg et al. 2006; Johnsen et
313 al. 2007; Nieminen 2010; Mattisson et al. 2011; Nieminen et al. 2011) is expected to negatively
314 affect the reindeer populations and cause significant losses to the owners of the herds (Hobbs et
315 al. 2012). Moreover, many of the carnivores that are subsidized by reindeer carrion in the critical
316 winter period (Killengreen et al. 2011) are also generalists predators (e.g. corvids and foxes) that
317 may negatively impact other species in the tundra food web, such as ground-nesting birds in the
318 spring (Fletcher et al. 2010). A recent study of nest predation rates in the study region showed
319 that corvids and red fox were the most influential nest predators on ground-breeding birds (Ims et
320 al. 2013). Notably, a high nest predation rate in the lesser white-fronted goose (*Anser erythopus*)
321 in the study region appears to be a key factor for its present red-listed status as critically

322 endangered in Norway (DN 2011). Finally, a species-enriched carnivore community may cause
323 intensified intra-guild interaction. Henden et al. (2010) showed how increased densities of the red
324 fox, due to increased access to reindeer carrion during the limiting winter period (Killengreen et
325 al. 2011), could negatively impact the subdominant and threatened arctic fox in Fennoscandia (see
326 also Angerbjörn et al. 2013; Hamel et al. 2013b). Hence, while partial migration patterns are
327 likely to feedback on the reindeer herds themselves through increased predation rates, increased
328 residency of reindeer may also work as a catalyst for many impacts that affects arctic biodiversity
329 negatively.

330

331 MANAGEMENT IMPLICATION

332 In light of increasing human impact on ecosystems through e.g. overharvesting,
333 anthropogenic barriers, climate change, removal of apex predators, habitat loss and degradation,
334 it is expected that the phenomenon of disrupted migration of many animal species will be
335 accentuated (Berger 2004; Berger et al. 2008; Bolger et al. 2008; Wilcove 2008; Wilcove &
336 Wikelski 2008). While this problem has also been raised earlier in the case of tundra reindeer
337 (e.g. Jernsletten & Klovov 2002), the present study is the first to present actual numbers that
338 quantifies the degree of partial migration for a sample of reindeer herds and management districts
339 at a regional scale in northern Fennoscandia. The implications of our study are, however, likely
340 so be substantially broader as there are in total 2.2 million semi-domestic reindeer distributed
341 over wide expanses of the Eurasian tundra (Huntington 2013).

342 By conducting aerial surveys we found that a substantial number of reindeer did not
343 migrate from their summer pastures and moreover that these numbers differed among herds and
344 years. Future studies should attempt to unravel the underlying cause of this variability in order to

345 identify management actions that could minimise the number of reindeer that reside in the
346 summer pastures during winter. Potential management actions could involve new herding
347 practices, mitigation of migration barriers, regulation of herd sizes and adjustments of
348 management district borders. Minimising residency on summer pastures, ought to provide a win-
349 win situation by being beneficial for the productivity of the herding industry which presently
350 struggles with high losses (Tveraa et al. 2003; Forbes & Kumpula 2009; Hobbs et al. 2012), for
351 the management of tundra small game species which show declining populations (Ehrich et al.
352 2011; Henden et al. 2011), for the restoration of threatened arctic fox populations (Henden et al.
353 2010) and for conservation of arctic ground nesting birds that experiences high nest losses
354 (McKinnon et al. 2010; Ims et al. 2013). Indeed, a common denominator of these issues may be
355 boreal mesocarnivores that expand into vulnerable tundra ecosystems (Ims & Ehrich 2013).

356

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548 Tables:

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550 **Table 1.** Reindeer counts (# individuals) and area covered (km²) during aerial surveys in 2009-2011 in each block and peninsula.

Peninsula	Block	Survey Area (km ²)	Count 2009	Count 2010	Count 2011
Porsanger	North	252	32	0	0
Porsanger	Middle	290	2	0	0
Porsanger	South	614	27	0	180
Sværholt	North	266	128	93	0
Sværholt	Middle	358	44	88	0
Sværholt	South	555	1585	1356	88
Nordkinn	North	283	289	0	0
Nordkinn	South	253	0	52	141
Varanger	North	318	0	35	42
Varanger	South-East	581	1102	0	0
Varanger	South-West	613	61	0	0

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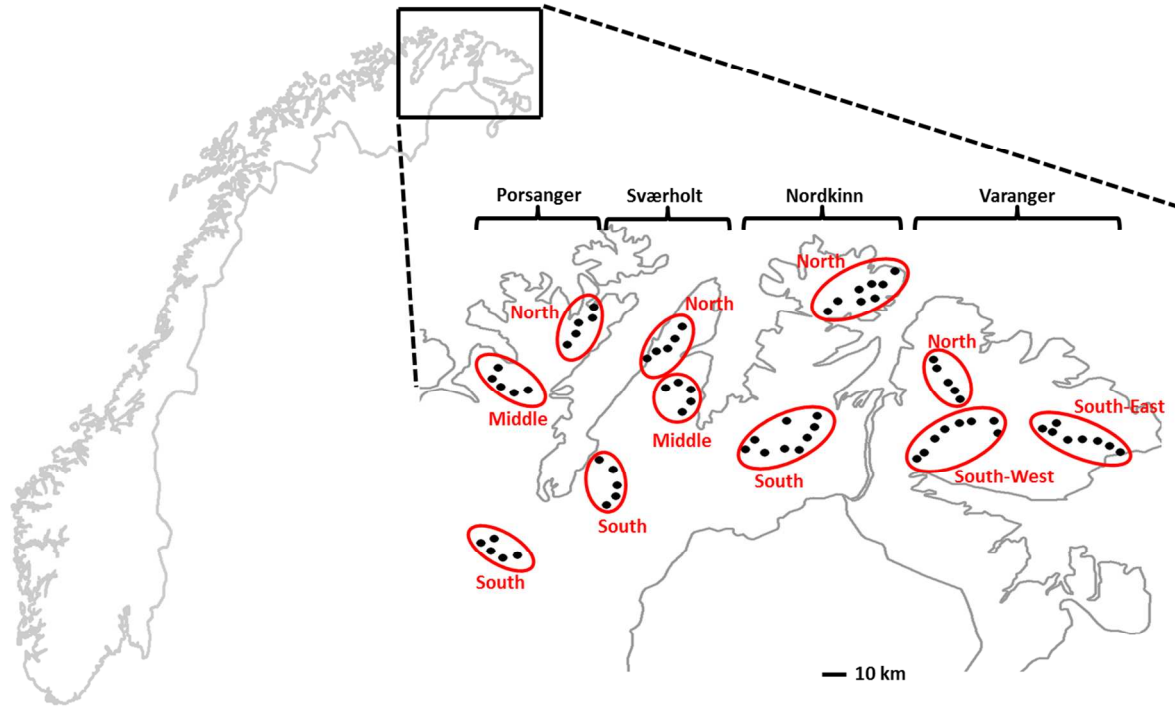
553 Figures:

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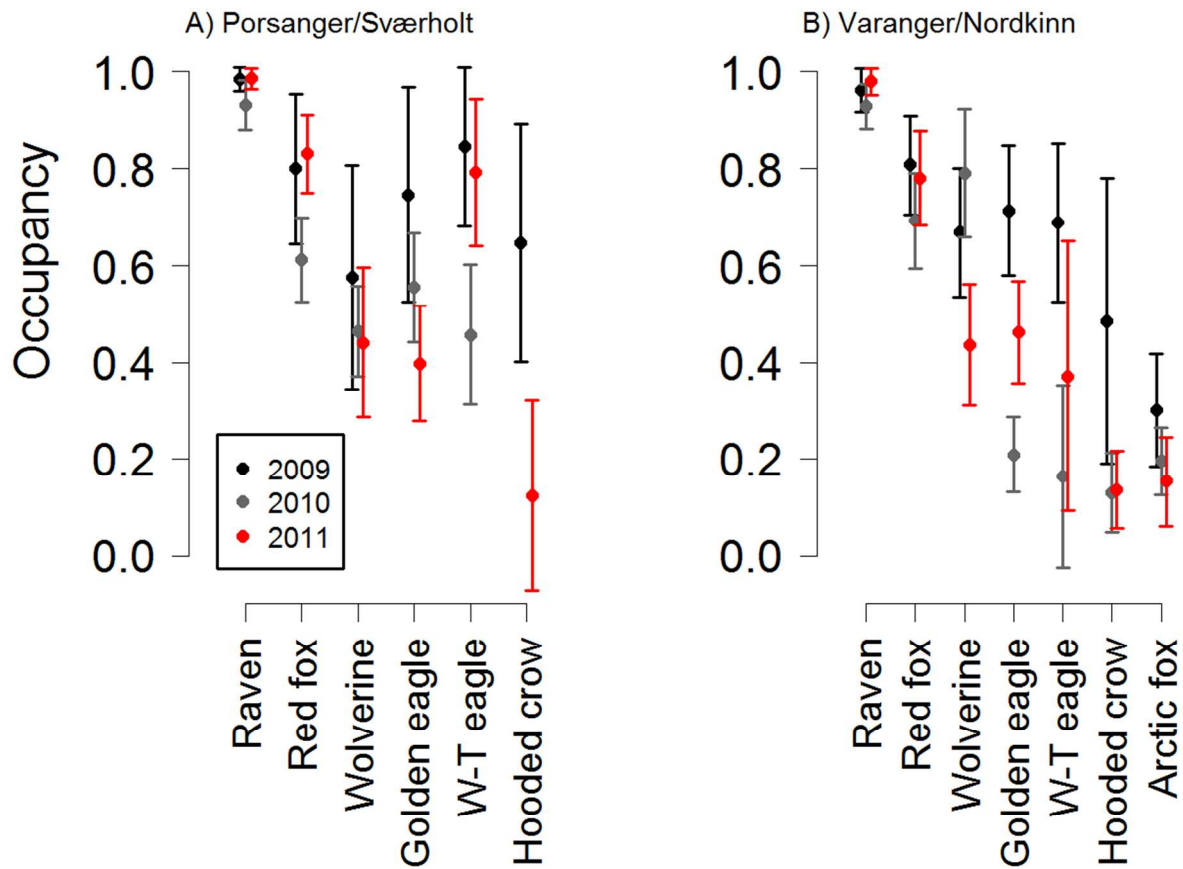
559 **Fig. 1.** Map giving the location of the four peninsulas (Porsanger, Sværholt, Nordkinn and Varanger) in
560 Finnmark County, northern Norway. Red circles enclosing black dots depict the different blocks within
561 each peninsula and the selected study sites within blocks, respectively. Note the scale of the inserted map.

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567 **Fig. 2.** Mean area occupancy rates with standard deviation for the different carnivore species over the

568 three years of the study and the two pairs of peninsulas (panel A and B) with somewhat different sampling

569 designs. Note that hooded crows are absent from the Porsanger and Sværholt peninsula in 2010 (no

570 recordings).

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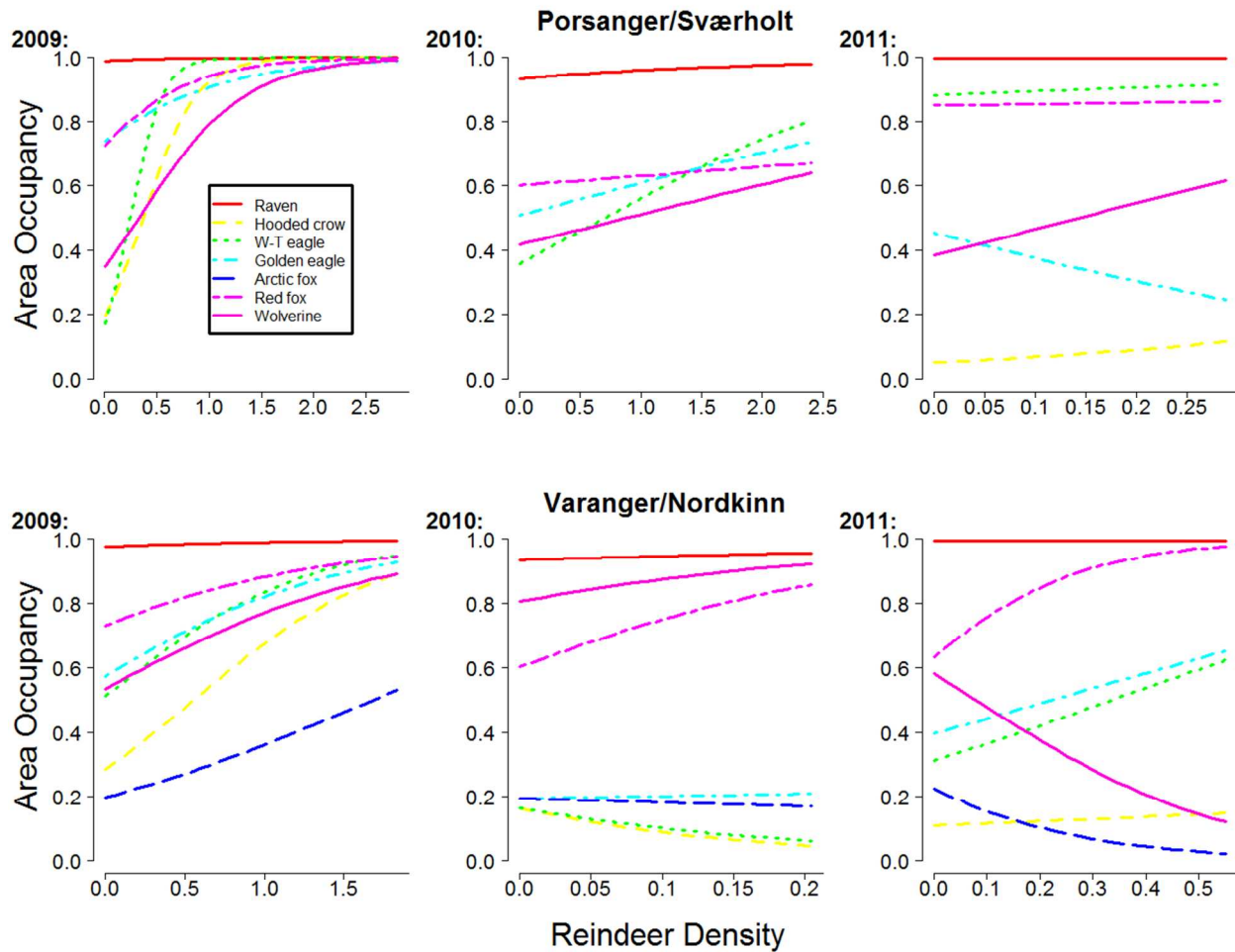
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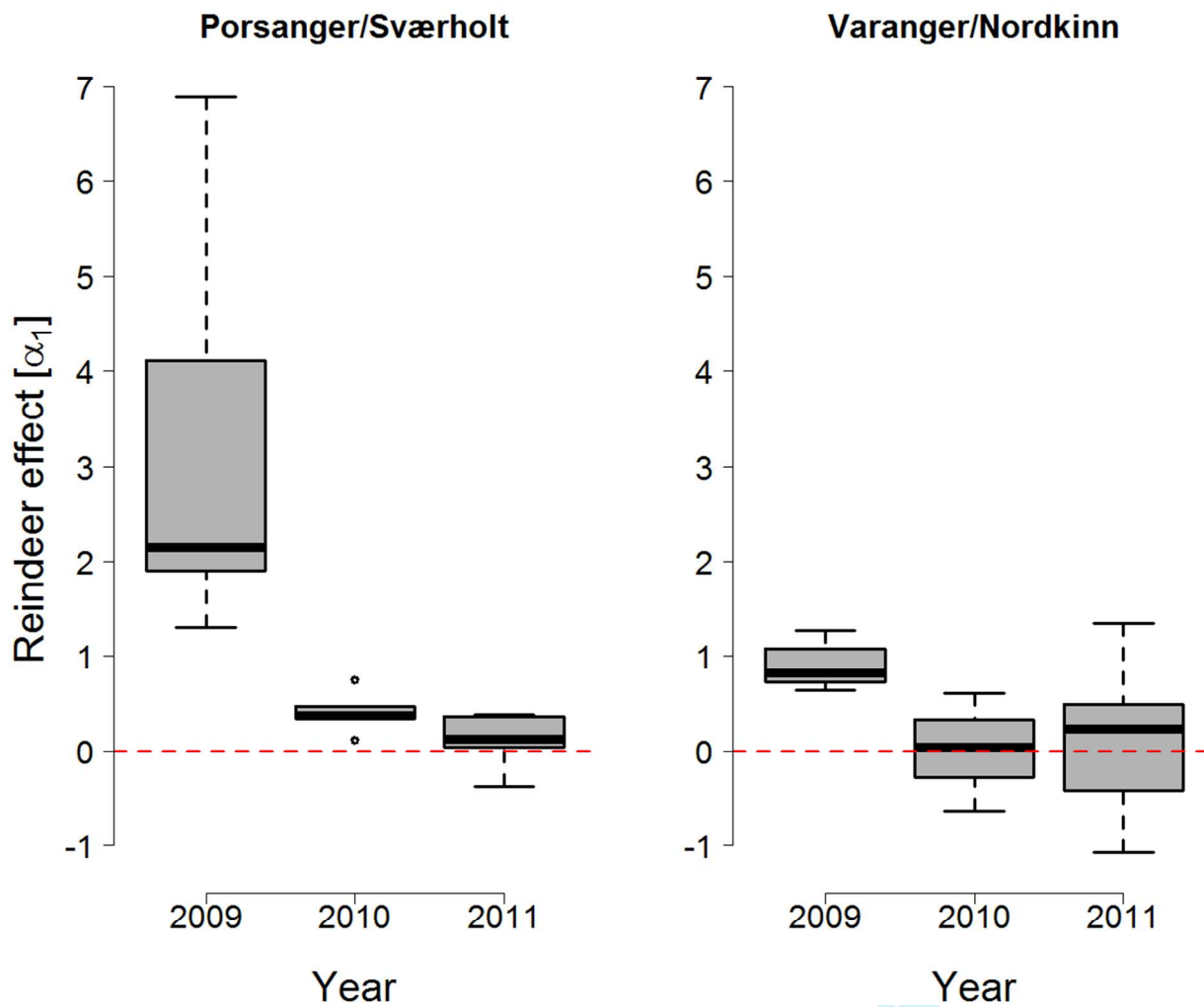
577

578 **Fig. 3.** Estimated species-specific area occupancy rates as a function of reindeer density for the two
 579 regions and the three years. Note that arctic foxes (blue stippled lines) are only present on Varanger
 580 Peninsula (right panel), that hooded crows are absent from the Porsanger/Sværholt region in 2010 (no
 581 recordings) and the distinctly different scale on the x-axes (i.e. reindeer density=animals per km²).

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586 **Fig. 4.** Distribution (boxplots) of reindeer density effects (i.e. slope estimates [α_1]; Appendix A) on
587 carnivore species-specific area occupancy for the two regions over the three years.

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Appendix B.

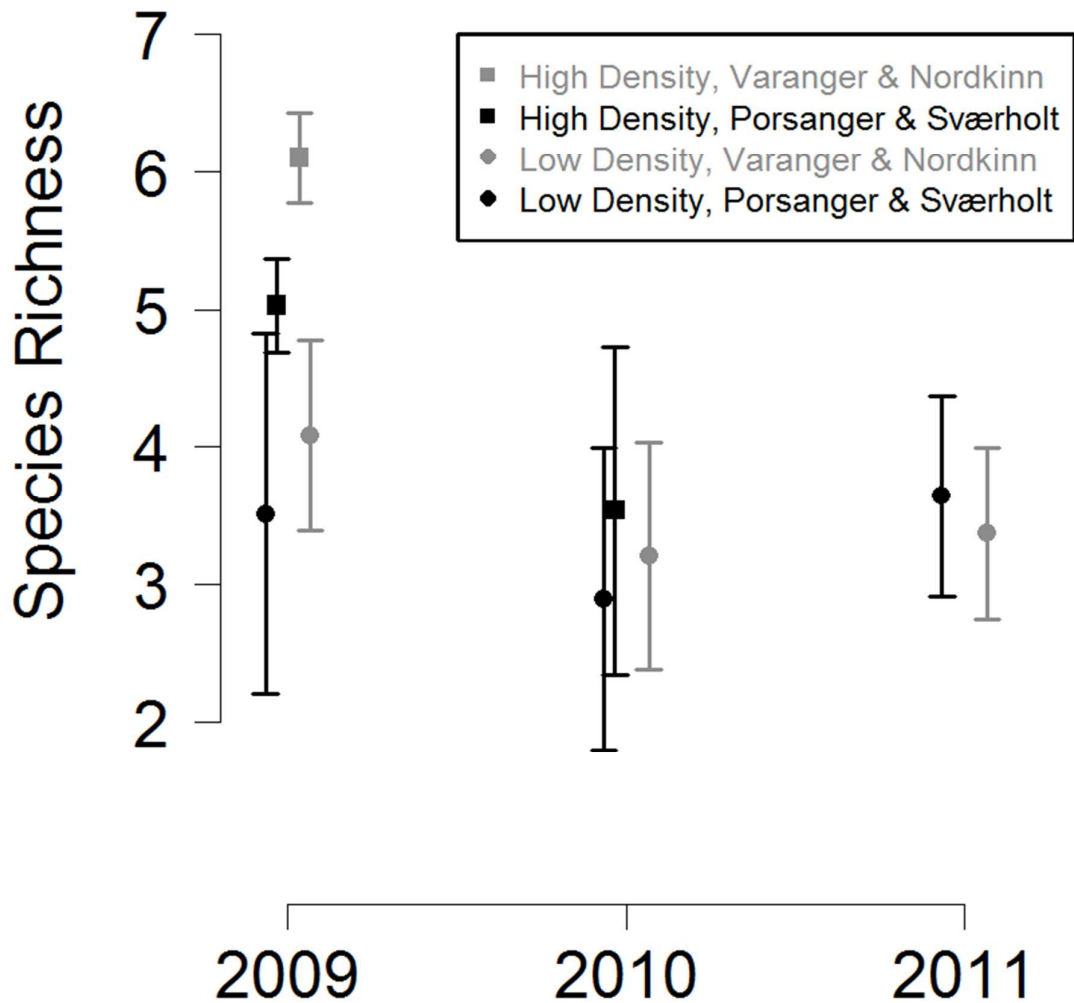


Fig. B1. Estimated mean site-specific species richness with standard error bars in relation to low and high reindeer density for the three years and two regions of the study. High density: >1.5 reindeer/km² and Low density: <0.5 reindeer/km². Note that species richness at a specific site is a derived quantity

in the model and represents the sum of occupancy rates for the different species estimated to be present (cf. WinBUGS model below).

*WinBUGS model: (model structure for the Porsanger/Sværholt analyses.)

```

model{
## Prior distributions for community-level parameters
omega ~ dunif(0,1)
v.mean ~ dunif(0,1)      ### Detection
mu.v <- log(v.mean) - log(1-v.mean)
u.mean ~ dunif(0,1)      ### Occupancy
mu.u <- log(u.mean) - log(1-u.mean)
tau.u ~ dgamma(0.1,0.1)
tau.v ~ dgamma(0.1,0.1)

mua1 ~ dnorm(0, 0.001)
mub1 ~ dnorm(0, 0.001)
mub2 ~ dnorm(0, 0.001)
mub3 ~ dnorm(0, 0.001)
tau.a1 ~ dgamma(0.1,0.1)
tau.b1 ~ dgamma(0.1,0.1)
tau.b2 ~ dgamma(0.1,0.1)
tau.b3 ~ dgamma(0.1,0.1)

## Create priors for species i from the community level prior distributions
for (i in 1:(n+nzeroes)) {
  w[i] ~ dbern(omega)      ## whether it belongs to the detected species or not
  u[i] ~ dnorm(mu.u, tau.u)  ## Occupancy
  v[i] ~ dnorm(mu.v, tau.v)  ## species-specific detection
  a1[i] ~ dnorm(mua1, tau.a1)  ## parameter for covariate of occupancy
}

```

```

b1[i] ~ dnorm(mub1, tau.b1)      ## parameters for covariates of detection:
b2[i] ~ dnorm(mub2, tau.b2)
b3[i] ~ dnorm(mub3, tau.b3)

## Create a loop to estimate the Z matrix (true occurrence for species i at site j.
for (j in 1:J) {
  logit(psi[j,i]) <- u[i]+ a1[i]*Reinab1[j]
  mu.psi[j,i] <- psi[j,i]*w[i]
  Z[j,i] ~ dbern(mu.psi[j,i])
  ## Create a loop to estimate detection for species i at point k during sampling period/replicate k.
  for (k in 1:K[j]) {
    logit(p[j,k,i]) <- v[i] + b1[i]*date1[j,k] + b2[i]*Reinabdet[j,k] + b3[i]*date2[j,k]
    mu.p[j,k,i] <- p[j,k,i]*Z[j,i]
    X[j,k,i] ~ dbern(mu.p[j,k,i])
  } }
  ## Derived quantities: ##
  ## Total estimated richness
  n0 <- sum(w[(n+1):(n+nzeroes)])
  N <- n + n0
  ## Site level richness estimates for the whole community.
  for(j in 1:J){
    Nsite[j]<- inprod(Z[j,1:(n+nzeroes)],w[1:(n+nzeroes)])
  }
} Model end

```