

Exotic lagomorph may influence eagle abundances and breeding spatial aggregations: a field study and meta-analysis on the nearest neighbor distance

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The introduction of alien species could be changing the food source composition, ultimately restructuring demography and spatial distribution of native communities. In Patagonia, Argentina, the exotic European hare has one of the highest numbers recorded worldwide and is now a widely used resource for many predators. We examine the potential relationship between abundance of this relatively new prey and the abundance and breeding spacing of one of its main consumers, the Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*). First we analyze the abundances of individuals of a raptor guild in relation to hare abundances through a correspondence analysis. We then estimated the Nearest Neighbor Distance (NND) of the Black-chested Buzzard-eagle abundances in the two areas with high hare abundances. Finally, we performed a meta-regression between the NND and the body masses of Accipitridae raptors, to evaluate if Black-chested Buzzard-eagle NND deviates from the expected accordingly to their mass. We found that eagles abundances were highly associated with hare abundances, more than any other raptor in the Patagonian guild. Their NND deviate from the value expected, which was significantly lower than expected for a raptor species of this size in two areas with high hare abundances. The presence of a new and abundant resource may have changed the abundances and distance between breeding areas of a large predator, potentially altering other interspecific interactions, and thus the entire community.

1 **Title**

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14 Abstract

15 The introduction of alien species could be changing the food source composition,
16 ultimately restructuring demography and spatial distribution of native communities. In
17 Patagonia, Argentina, the exotic European hare has one of the highest numbers recorded
18 worldwide and is now a widely used resource for many predators. We examine the potential
19 relationship between abundance of this relatively new prey and the abundance and breeding
20 spacing of one of its main consumers, the Black-chested Buzzard-Eagle (*Geranoaetus*
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26 expected accordingly to their mass. We found that eagles abundances were highly associated
27 with hare abundances, more than any other raptor in the Patagonian guild. Their NND deviate
28 from the value expected, which was significantly lower than expected for a raptor species of this
29 size in two areas with high hare abundances. The presence of a new and abundant resource may
30 have changed the abundances and distance between breeding areas of a large predator,
31 potentially altering other interspecific interactions, and thus the entire community.

32 Short title

33 Exotic prey effects on eagles abundances

34 **Introduction**


35 The spatial distribution of a species is determined by extrinsic and intrinsic factors.
36 Resource availability is the main extrinsic factor that may influence spatial distribution of
37 organisms (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). Changes in food sources
38 could be modifying consumers' spatial distribution. Ecosystems are composed of different
39 species that consume resources that are naturally limited (Chase & Leibold, 2003). Within a
40 given trophic level, interspecific and intraspecific interactions emerge in order to use these
41 resources. These include agonistic interactions as direct competition and spatial exclusion and
42 intraguild predation (Amarasekare, 2003; Sergio & Hiraldo, 2008) as well as resource
43 partitioning that favors species' coexistence (Martin & others, 1996; McDonald, 2002; Griffin et
44 al., 2008). At the individual level, the exclusion of conspecifics leads to territoriality, eventually
45 reaching a spatial configuration that maximizes the number of territories in a given area as a
46 function of resource availability (MacLean & Seastedt, 1979; Schoener, 1983).

47

48 One of the main intrinsic factors limiting the spatial distribution of species is animals'
49 body mass, as larger species require more energy to fulfill their energetic metabolic requirements
50 (Damuth, 1981; Peters, 1986; White et al., 2007). In any guild (e.g., carnivores, raptors), the
51 difference in body mass of the various species, is the main factor driving resource partitioning
52 (Aljetlawi, Sparre-Andersen & Leonardsson, 2004; Brose, 2010), as consumers select prey that provides
53 a positive energetic balance between food intake and handling time (Brose et al., 2006; Allhoff
54 & Drossel, 2016). This process of prey selection is directly linked to competing species
55 coexistence (Loreau & Hector, 2001; Amarasekare, 2002). On the other hand, this energetic
56 constraint also implies that larger species may require larger territories to provide enough

57 resources, therefore spacing their territories more widely than smaller species (Schoener, 1968;
58 Peery, 2000).

59

60 In the current global change scenario, humans are responsible for altering the ecosystems
61 in several ways and these changes are occurring in an accelerated way (Barnosky et al., 2012).
62 The introduction of species is among of the main factors of global change, which is not only
63 homogenizing biodiversity at a global scale but also has the potential of alteergy fluxes
64 (McKinney & Lockwood, 1999; Newsome et al., 2015). The introduction of exotic species may
65 profoundly impact the relative abundance of native species and therefore community structure
66 (Vitousek, 1990; Vitousek et al., 1997; Tilman, 1999; Newsome et al., 2015), which may be in
67 favor of some native species over others, improving their population parameters. However, this
68 change in structure can lead to unbalanced ecological situations (e.g.: Tablado et al. 2010;
69 Speziale & Lambertucci 2013).

70

71 Patagonia is one such region, at the southern tip of South America, to have suffered
72 multiple species introductions (Rodríguez, 2001). One of the most conspicuous invaders has
73 been the European hare (*Lepus europaeus*) which reached the region in the early 1900's (Grigera
74 & Rapoport, 1983). European hare had no other similar species in the region and became
75 extremely abundant in number over a short period of time (Bonino, Cossíos & Menegheti, 2010).
76 As such, this introduced species may potentially alter energy fluxes, trophic interactions and
77 indirectly change community structure (Simberloff & Von Holle, 1999; Simberloff et al., 2013).
78 In fact, there is evidence that many predators in Patagonia have already shifted their diets to

79 include this new and abundant source of food (Montserrat, Funes & Novaro, 2005; Zanón
80 Martínez et al., 2012; Barbar, Hiraldo & Lambertucci, 2016).

81

82 Top predators that depend upon scarce resources are adequate to explore the resource
83 availability-territory size relationship, as their territories cover greater areas than herbivorous
84 species (Schoener, 1968) and any change can be easily quantified with simple metrics such as the
85 Nearest Neighbor Distance (NND, Clark & Evans, 1954). This includes raptor species that
86 generally behave as central place foragers and whose territory sizes are determined by resource
87 abundance (Sonerud, 1992; Newton, 2010). Their fidelity to nesting areas means that the
88 geographical distance between breeding sites can be used to quantify the relationship between
89 resource availability and territory size and location.

90

91 Here we aim to explore how the increased abundance of an exotic species (the European
92 hare) may influence the raptor guild at the higher trophic level, paying particular attention to the
93 Black-chested Buzzard-eagle (*Geranoaetus melanoleucus*; hereafter BCB eagle), which is the
94 species that consumes it the most (Barbar, Hiraldo & Lambertucci, 2016). For this we first
95 quantified and compared the abundance of different raptor species to the abundance of hares in
96 Northwestern Patagonia. We then, determined the Nearest Neighbor Distance (NND) for the
97 BCB eagle in an area of high exotic hare population density. Finally, we compared our NND
98 results with similar species of the Accipitridae family, conducting a meta-analysis on the NND
99 reported for these species worldwide. Our hypothesis is that the abundance of BCB eagles and
100 the spacing of their territories will be strongly influenced by the abundance of its principal prey,
101 the exotic European hare. We predict that 1) the abundance of BCB eagles will be more closely

102 linked to the abundance of hares, than will the other raptor species in the guild, and 2) that the
103 distance between BCB eagle territories will be smaller than expected for an eagle of this size
104 where there is a high abundance of its main prey.

105

106 **Methods**

107 *Study area*

108 Fieldwork was conducted in northwest Patagonia, Argentina; in an area of approximately
109 15,000 km² (Fig. 1). The climate is temperate-cold (annual mean 6°C), with a marked west-to-
110 east precipitation gradient, varying from 1000 mm to 400 mm annually (Paruelo et al., 1998).
111 The predominant habitat is an open herbaceous steppe (*Festuca pallescens*, *Stipa speciosa*), with
112 scattered shrubs (*Mulinum spinosum*) and with a frequent distribution of ecotonal forest
113 incursions (*Austrocedrus chilensis*, *Maytenus boaria*, Cabrera, 1976). The region is comprised of
114 undulating hills and frequent rock outcrops, used by the raptors as roosting and nesting sites
115 (Coronato et al., 2008; Lambertucci & Ruggiero, 2016). The presence of rock cliffs, shrubs and
116 trees are fairly evenly distributed in this area, ensuring that all species studied have plenty of
117 choices at the time of placing their territories and nests. Field work permits for this study were
118 granted by the National Park Administration, Argentina (project 1360) and Ministry of
119 Territorial Development, General Direction of Fauna Resources.

120

121 *Study species*

122 In the Patagonian raptor guild, the most abundant species are two facultative scavengers
123 and three hunters. The Southern crested caracara (*Caracara plancus*) and the Chimango caracara
124 (*Milvago chimango*) are medium sized scavenging raptors that consume European hare mainly as

125 carrion (Travaini et al., 1998). From the hunting raptors, the American kestrel (*Falco sparverius*,
126 ~125 g.), a small falcon, is too small to hunt or scavenge on hares, and the medium sized Red-
127 backed hawk (*Geranoaetus polyosoma*, ~950 g.) predaes only on young hares, contributing to <
128 10% of their diet (Monserrat, Funes & Novaro, 2005; Travaini, Santillán & Zapata, 2012).
129 Whereas the BCB eagle (*G. melanoleucus*, ~2450 g.) commonly predaes on the hare, consuming
130 between 15 to 90% of its diet (Iriarte, Franklin & Johnson, 1990; Hiraldo et al., 1995;
131 Bustamante et al., 1997; Trejo, Kun & Seijas, 2006).

132

133 The BCB eagle is a large Accipitrid that inhabits a diversity of open habitats across South
134 America, from Venezuela to Tierra del Fuego (Ferguson-Lees & Christie, 2001). It nests mainly
135 in cliffs and rocky outcrops, although it can also use other substrates like trees, bushes and even
136 structures along power-lines including telegraph poles (Jiménez & Jaksić, 1989; Travaini et al.,
137 1994; Hiraldo et al., 1995; Pavez, 2001; Saggese & De Lucca, 2001; Ignazi, 2015). Adult BCB
138 eagles exhibit strong territoriality and nest site fidelity throughout the years (Saggese et al. in
139 press). Only juveniles are known to congregate in roosting places when a high resource
140 aggregation exists (Bustamante et al. 1997; López, Grande & Orozco-Valor, 2017). The breeding
141 season in Patagonia extends from September to February, during the austral spring/summer
142 (Hiraldo et al., 1995; Bustamante et al., 1997; Saggese & De Lucca, 2001). It is considered to be
143 a generalist species that feeds on small to medium sized mammals, birds, reptiles, carrion and
144 arthropods (Hiraldo et al., 1995; Bustamante et al., 1997; Galende & Trejo, 2003; Trejo, Kun &
145 Seijas, 2006).

146


147 *Raptors and hare densities*

148 During the austral late springs and summers of 2012-14, we conducted road transects
149 covering 1000 linear kilometers (Fig. 1) each year, evenly distributed (i.e. whole transects were
150 completed once each season). There, we counted the abundance of each of the five raptor species
151 as well as the abundance of hare. Raptors were surveyed from a car driving at an average speed
152 of 40 km/h, and during morning hours (from 1 hour after sunrise to 12:00 h) and hare surveys
153 were conducted at night (from sunset to 2 am) with a spotlight checking both sides of the road (to
154 a maximum distance of 50 m), at a constant speed of 8 km/h. The difference in schedule being
155 designed to maximize detectability associated with animal activities. For each observation we
156 registered GPS location, species, number of individuals and perpendicular distance to the road.
157 We later calculated species abundances per unit area in 13 a priori traced sections of the whole
158 transect (Fig. 1). We did not find significant differences in counts between years, allowing us to
159 pool data by site and using year as repetition. We conducted density analyses with the
160 “*Rdistance*” package in R-statistical software (R Development Core Team, 2012; McDonald,
161 Nielson & Carlisle, 2015). As abundances could be influenced by several factors, we first test if
162 environmental variables, abundance of the primary prey or abundances of other raptors had an
163 effect on the abundances of our focus species (the BCB eagle). For this we fit a GLM with the
164 abundances of BCB eagles by site as the response variable and hare and other raptors
165 abundances, year, nest availability (in three categories: low, medium, high) and dominant habitat
166 (in three categories: steppe, shrub, forest) as explanatory variables. We performed this analysis
167 with “*lme4*” package in R-statistical software (R Development Core Team 2012; Bates et al.,
168 2014). We then performed a Correspondence analysis to find relationships between abundances
169 of the raptors and hares per site. For this we organized a matrix with all 6 species (columns) and
170 the 13 transect per year (rows), where each cell contained the density, previously calculated from

171 counts in transects. For this analysis we used the “*vegan*” package in R-statistical software (R
172 Development Core Team, 2012; Oksanen, 2017).

173

174 *Nearest neighbor distance*

175 During the breeding seasons of 2012-13, in the austral late spring and summer, we
176 thoroughly searched 2 areas (of approximately 2000 km² and 5000 km², Fig. 1) to find active
177 BCB eagles nests. These areas were selected based on previous qualitative assessments showing
178 low degree of human disturbances (which may affect raptor distribution; Barbar et al. 2015), a
179 high abundance of eagles, hares and availability of cliffs (their most used nesting substrate,
180 Hiraldo et al., 1995). The two areas were selected because of i  homogenous and abundant
181 presence of potential nesting sites. There, the distances between cliff-shelves, trees and other
182 nesting substrates are small enough to consider these sites as a non-limiting resource for the BCB
183 eagles breeding pairs. Active nests were found either by direct observation (conspicuous stick
184 structure of 1-2 m diameter in rock cliffs) or by observing couples behaviors around nesting
185 areas (as they are highly territorial and spend most of the time in the vicinity). We confirmed that
186 each nest was active when BCB eagles were building (or repairing it), showing incubation
187 behavior or there was a fledgling at the nest. For each georeferenced nest site we calculated the
188 NND applying the nearest neighbor algorithm using “*geosphere*”, “*rgeos*” and “*mapproj*”
189 packages in R-statistical software (R Development Core Team, 2012; Bivand & Rundel, 2014;
190 Hijmans, 2016; Bivand et al., 2017).

191

192 *Bibliographic search and Meta-analysis*

193 To evaluate whether BCB eagles nearest neighbor distances differ from what is expected
194 in relation with their body mass we compared our results with other similar species through a
195 bibliographic search of studies disclosing NND worldwide and a meta-regression. We focused
196 our search on species similar to the BCB eagles (i.e., raptors from the family Accipitridae
197 inhabiting open areas) in order to reduce additional extrinsic variations in the NND measures.
198 We then excluded endangered species (e.g., *Aquila adalberti*), as their reduced populations
199 would not represent their true comparable NNDs. Later, we excluded gregarious foragers and
200 communal breeder species (e.g., Vultures, *Gyps* spp.), as their NNDs would not reflect their
201 spatial accommodation regarding to food resources. We also excluded specialist foragers (e.g.,
202 Fish-eagles, *Haliaeetus* spp.), as their NNDs would be conditioned to their not randomly
203 distributed resources, (for instance fish in certain rivers; Newton, 2010), while BCB eagles main
204 prey is considered to be randomly distributed across landscapes in our study area (Bustamante et
205 al., 1997). We ran a preliminary literature search using Scopus and Google Scholar with the key
206 words “nearest neighbor distance”, “nearest nest distance” and “NND” paired with the common
207 names of the raptors “eagle” and “hawk”. Then, to comprehensively complete our search, we
208 used the same first terms of the search, paired with the name of each raptor species previously
209 selected from Accipitridae family (e.g. “NND” AND “*Aquila verreauxii*”). All searches were
210 performed by Facundo Barbar and reviewed by the other authors. From each study found we
211 extracted the name of the first author and its year of publication (combined to form a study ID),
212 as well as the raptor species, NND metric, its standard deviation (SD) and the number of nearest
213 used to calculate the NND (n).


214

215 With this data we first performed an individual meta-analysis for each species using a
216 random-effects model, a method used to estimate the effect size of the entire population (Hunter
217 & Schmidt, 2000). In this way we obtained an outcome measure (hereafter NND_{avg}) for each
218 species depending on their NND, SD and n (Supporting information S1). We used this approach
219 as preliminary exploration of the data showed high variability between studies (I^2 always
220 exceeding 90%). This statistic estimates if the variability is due to heterogeneity between studies
221 ($I^2 > 75\%$) or due to sampling variability within each study ($I^2 < 30\%$) (Higgins & Thompson,
222 2002). Thus, analyzed as a whole, heterogeneity would be masking the actual effects and giving
223 unrealistic average values for each species. With the NND_{avg} outcome for each species we
224 perform a meta-regression with a fixed-effects model (used to estimate the effect size among the
225 sampled studies, Hunter & Schmidt, 2000), using the species specific NND_{avg} as the dependent
226 variable and the average weight of each species as the independent variable. We scaled the
227 weights by $\exp -0.75$ to account for the nonlinear change in metabolic rate (Damuth, 1981,
228 2007), which has been used for raptor species and proved to follow this nonlinear relationship
229 (Palmqvist et al., 1996). For all these calculations we used the “*metafor*” package on R-statistical
230 software (Viechtbauer, 2010; R Development Core Team, 2012).

231

232 **Results**

233 *Raptor and hare densities*

234 We found that the only significant variable affecting eagles abundances was the
235 abundance of hares ($\beta = 0.038 \pm 0.012$; $p = 0.047$), while nest availability and the dominant habitat
236  not any significant effect on its abundances ($\beta = 0.079 \pm 0.216$, $p = 0.719$; $\beta = 0.263 \pm 0.177$,
237 $p = 0.149$, respectively). The abundances of other raptor species did not have any significant effect

238 on the abundance of BCB eagles; the estimates were: *G. polyosoma* ($\beta = -0.086 \pm 0.185$), *C.*
239 *plancus* ($\beta = 0.083 \pm 0.090$), *M. chimango* ($\beta = 0.042 \pm 0.067$) and *F. sparverius* ($\beta = 0.128 \pm$
240 0.081), all with p-values > 0.1 . Correspondence analysis showed that the abundance of *G.*
241 *melanoleucus* was closely linked to that of the hare, while for other species the relationship was
242 weaker (Fig. 2). The abundances of the two facultative scavengers, *C. plancus* and *M. chimango*,
243 were similar to each other at all sites. On the other hand, the most dissimilar species was *G.*
244 *polyosoma*, which although did not present extremely low abundances (average density of 0.16
245 ind./km²) tended to be negatively linked to the abundance of hares and BCB eagles (Fig. 2). In
246 the two areas where we later actively searched for BCB eagle nests, hare densities were high.
247 Hare density in the northern area was 202.09 ind./km² (± 25.26), while in the southern area was
248 249.25 ind./km² (± 22.65). Moreover, BCB eagle density mirrored those abundances with a mean
249 density of 0.71 ind./km² (± 0.18) in the north and 0.83 ind./km² (± 0.27) in the south.

250

251 *Nearest neighbor*

252 We found a total of 55 active nests within the two areas that were intensively searched. In
253 the northern area, we found 13 nests in the 2000 km² covered, while in the southern area we
254 found 42 nests for the 5000 km² scoped (Fig. 1). NND calculations (m \pm SD) were 3797 m
255 (± 2477) for the northern region and 3723 m (± 2594) for the southern area.

256

257 *Body mass and NND relationships in raptors*

258 We found 77 studies reporting NND for 13 species meeting our criteria obtaining a total
259 of 130 NND measures (Supporting information S1). We found a positive relationship between
260 the Weight^(-0.75) and NND_{avg} (Estimate = -1087044 ± 224387 , $p < 0.0001$) in the meta-regression

261 ($r^2 = 67.96\%$; $I^2 = 95.77\%$; Fig. 3). Of all species included in the meta-regression, only three
262 had NND_{avg} measures that deviated significantly from the NND expected value. *Aquila*
263 *chrysaetos* presented higher values ($NND_{avg} = 8242$ m. vs. NND estimated= 6013m), while
264 *Clanga pomarina* ($NND_{avg} = 2147$ m. vs. NND estimated= 3662m) and our focus species *G.*
265 *melanoleucus* presented lower values ($NND_{avg} = 4838$ m vs. NND estimated= 6013m; Fig. 3)
266 indicating that in our field area, BCB eagles tended to reduce their distances between nesting
267 areas.

268

269 Discussion

270 In this study we found one of the highest abundances recorded for an eagle of more than
271 2 kg (e.g., Pedrini & Sergio, 2001; Newton, 2010). Furthermore, eagle density was also reflected
272 in their nest spacing, since they have lower NND values than expected for raptors of this size.
273 We propose that these results can be explained by the extremely high abundances of the main
274 food source for the BCB eagle, the exotic European hare. In our study area hares reached one of
275 the highest abundances recorded for this species (up to 249 ind./km²), only matched by the
276 abundances recorded inside a fenced airfield in France, an area with no known predators (240
277 ind./km²; Flux & Angermann, 1990). Thus, our results highlight how an introduced and abundant
278 food source may enhance spatial distribution and abundance of a top predator, even when the
279 introduction is relatively recent (during the last century).

280

281 The fact that from the raptor guild of Patagonia BCB eagle was the species most closely
282 linked to the high abundances of this new exotic food resource, this may be related to the fact
283 that this species is the only one, in the studied raptors guild, capable of hunting hares of all age

284 classes (Hiraldo et al., 1995; Bustamante et al., 1997). This is something which could be a
285 challenge for the two facultative species (*C. plancus* and *M. chimango*) that depend mostly on
286 carrion only, scavenging on hares (Travaini et al., 1998). Therefore, their abundance will depend
287 on other environmental and anthropogenic factors that increase the density of carrion and waste,
288 such as the presence of settlements (which produce resources as house wastes) or high traffic
289 roads (producing high rates of road kills) (Lambertucci et al., 2009; Barbar et al., 2015). As
290 expected the abundance of the smallest raptor (*F. sparverius*) did not show any relationship with
291 hare abundance, but surprisingly, within the same areas they were less abundant than the BCB
292 eagles. This could indicate that hare presence is enough to override the theoretical energetic
293 constraint for larger species (Peters, 1986). Finally, the Red-backed hawk (*G. polyosoma*) was
294 negatively related to the abundances of hares and eagles. Their similar food habits and
295 nesting sites make the Red-backed hawk and the BCB eagle direct competitors (Schlatter, Yáñez
296 & Jaksić, 1980; Jiménez, 1995). However, being larger in size, the eagles may be at a
297 competitive advantage, ultimately limiting the abundance of the smaller hawk species. The lower
298 abundance of other raptors where BCB eagles abundance is high, could be influenced by
299 intraguild predation (Sergio & Hiraldo, 2008; Treinys et al., 2011). In fact, there is evidence of
300 predation of some of these species (e.g., *M. chimango*, *F. sparverius*) by the BCB eagles
301 (Hiraldo et al., 1995) and also frequent agonistic interactions with other raptors (mostly with *G.*
302 *polyosoma*; Jiménez & Jaksić, 1989).

303


304 BCB eagles spaced their territories more closely than expected given their body size
305 showing that there is not only simply a spatial aggregation of foraging individuals, but of
306 breeding territories. From our meta-regression *C. pomarina* was the only other raptor to show

307 decreased territory size, spacing more closely together than expected. The most influential study
308 to examine NND_{avg} described a case study that found enhanced breeding parameters were
309 associated with synchronicity and super abundance of their main prey (*Myxotus* spp.; Treinys,
310 Bergmanis & Väli, 2017); thus supporting the resource availability-territory size hypothesis. On
311 the other hand, the Golden eagle (*A. chrysaetos*) was the only species to have a greater NND
312 than expected. This could be related to their huge size variability. The species average weight is
313 about 4600 g, however there are individuals that exceed 6700 g (Ferguson-Lees & Christie,
314 2001), representing a much greater energetic constraint. However this species also responds to
315 the presence and abundances of their main prey (Clouet et al., 2017), where the presence of
316 rabbits is enough to reduce their NND from 12.9 to 8.6 km.

317


318 In Patagonia the NND for the BCB eagle was smaller than expected for its body size and
319 in comparison to that of the two closest species in weight, the lighter *T. ecaudatus* and *A. rapax*.
320 Given that the latter species and *A. heliaca* all fall into the expected values we are confident that
321 the difference is not due to any statistical construct on the meta-regression, but rather the
322 biological mechanism we are testing. Moreover, our own field NND estimates were slightly
323 higher than those found for this species in the same region 20 years ago (with a mean of 2522 m,
324 Hiraldo et al., 1995 vs. 3760 in this study). This could be related to the fact that the abundances
325 of hare have showed a slight decline over the last two decades, therefore limiting the resources
326 for breeding eagles (Ignazi et al., submitted).

327

328 It is worth to mention that NND can be influenced by extrinsic factors not directly
329 assessed by this study  For instance, previous to hare introduction spatial arrangement of BCB


330 eagles. Unfortunately studies on these matters have started when hares were already abundant
331 and conspicuous participants of the ecosystem (Grigera & Rapoport, 1983). Here we found that
332 BCB eagles show lower NNDs than expected, at the same time that its main resource is in
333 extremely high abundances. This suggests that large eagles may aggregate more closely under
334 high resource abundances.


335

336 There are also intrinsic specific factors influencing the NND. Some behavioral traits can
337 make  some cases NND estimations impervious to food resource changes. For instance,
338 previous research on BCB eagles showed that adults tend to favor nesting areas rather than rich
339 resource patches (Bustamante et al., 1997). In this case, nest fidelity and the costs associated
340 with the relocation and defense of a new territory could be masking the effect of a shortage in
341 food (Saggese et al., in press). Although our meta-regression between NND and body masses of
342 predators allowed us to identify that BCB eagles are spacing their territories closer than
343 expected, future research on breeding parameters and shifts in the eagles' diets are necessary to
344 fully understand the relation between this predator and disparate abundances of its main prey
345 (Ignazi et al., submitted).

346

347 **Conclusions**

348 Overall, the enhanced population of a top predator caused by the presence of an exotic
349 prey could create important conservation issues for the invaded communities and the surrounding
350 environments. A shift in the diet of a top predator to an alien species could reduce the per capita
351 intake of native prey. However, as this exotic prey increases, the predator abundance  could
352 create apparent competition interactions (Holt, 1977; Oliver, Luque-Larena & Lambin, 2009).

353 This is particularly concerning when considering that  populations are already prone to
354 great natural variations, and also used as game species in several regions (Flux & Angermann,
355 1990; Wilson, Lacher Jr & Mittermeier, 2016). Even if this is not the case, the sole change in
356 spatial use by a predator could change the activity and distribution patterns of the prey, changing
357 their landscape of fear (Willems & Hill, 2009) or making native prey underperform (Lyly et al.,
358 2015). Furthermore, within the same trophic level, high abundance of the largest species in the
359 guild could lead to an increase in the intraguild predation (Sergio & Hiraldo, 2008). All of these
360 factors lead to an unbalanced structure of the invaded food web (Simberloff & Von Holle, 1999;
361 de Ruiter et al., 2005). Conservation biologists should therefore be cautious when planning
362 invasive species management, in order to reduce further and sudden changes in the invaded
363 communities (Myers et al., 2000).

364

365 **Acknowledgments**

366 We wish to dedicate this work to Mikel Larrea, a young and enthusiastic raptor researcher
367 that left us way too soon. We thank the land managers of “El Cóndor”, “San Ramón”,
368 “Rinconada” and Lonco Audulio Pailallef for permissions to work in their lands. We thank to
369 Hannah Williams for comments on an early version of this manuscript.

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Figure 1

Map of the study area in the northwestern Patagonia Argentina.

The smaller dotted rectangle corresponds to the area where we conducted raptor and hare surveys. The roads used to perform the surveys are highlighted in green and each transect indicated with a numbered black circle. Red squares are the two regions where we actively searched for BCB eagle nests.

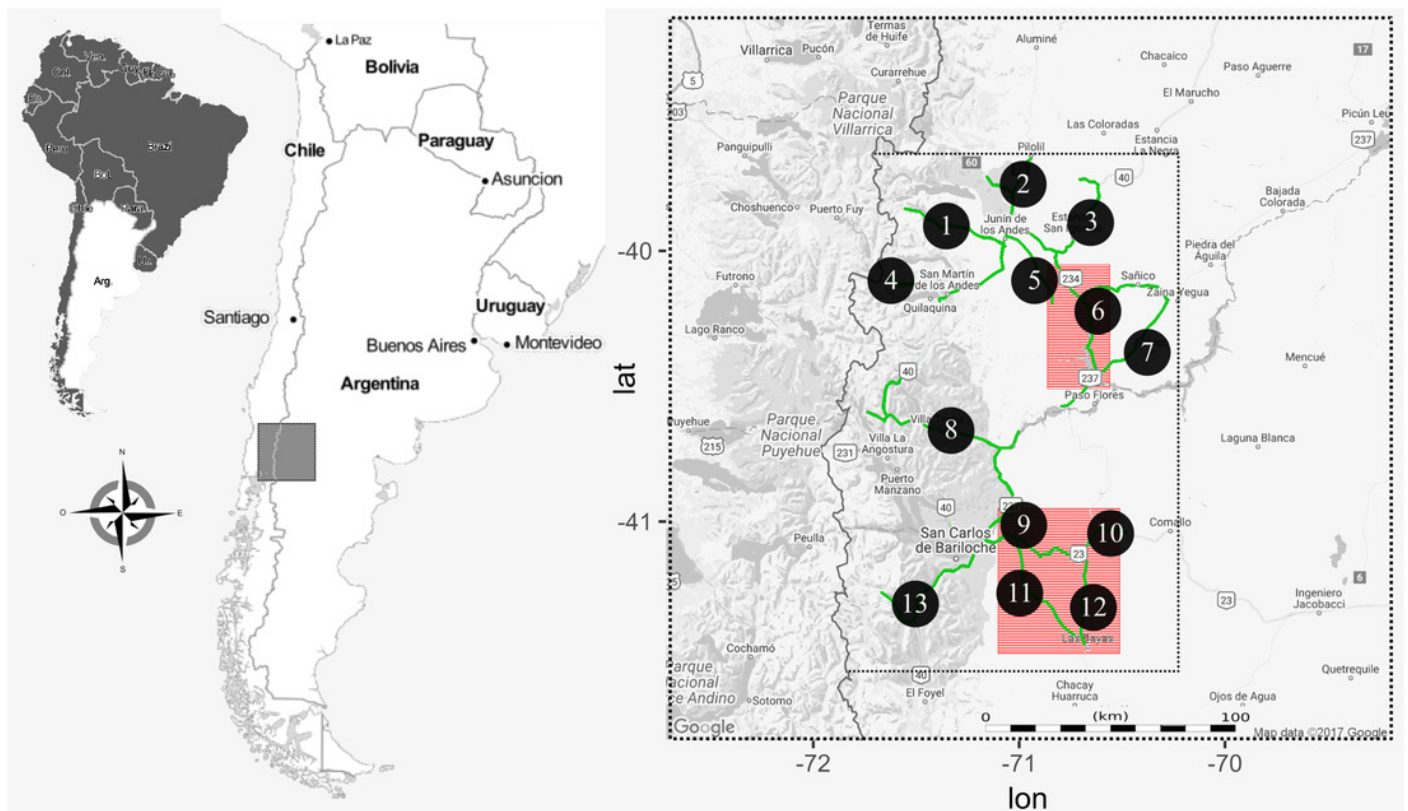


Figure 2

First two ordination axes form the correspondence analysis relating the abundances of the 5 raptor species and the abundances of European hare.

Distances between text labels represent the association among abundances of species by site. Shorter distances mean a more closely association between two species. Percentages show the total inertia explained by each axis.

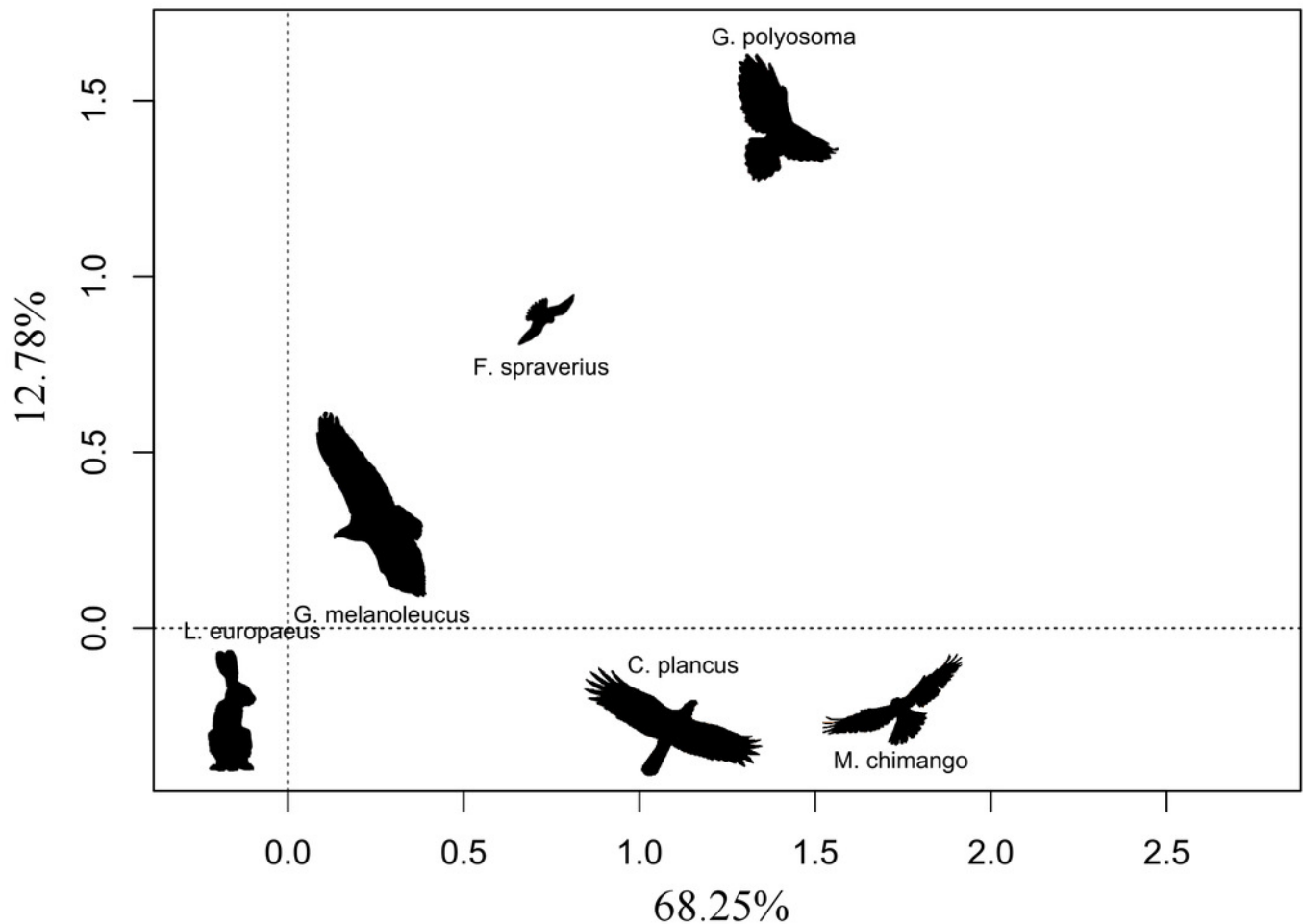


Figure 3

Meta-regression of the Nearest Neighbor Distance (NND_{avg}) for each Accipitridae raptor species in relation with their average weight.

Black diamonds are the model estimate (with a 95% CI) for each species. NND_{avg} (with a 95% CI) calculated from the measures extracted from each study are represented in squares.

Highlighted in red are species which NND_{avg} differed from the estimate.

