Analyzing the proximity to cover in a landscape of fear: A new approach applied to fine-scale habitat use by rabbits facing feral cat predation on Kerguelen archipelago

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Although proximity to cover has been routinely considered as an explanatory variable in studies investigating prey behavioral adjustments to predation pressure, the way it shapes risk perception still remains equivocal. This paradox arises from both the ambivalent nature of cover as potentially both obstructive and protective, making its impact on risk perception complex and context-dependent, and from the choice of the proxy used to measure proximity to cover in the field, which leads to an incomplete picture of the landscape of fear experienced by the prey. Here, we study a simple predator-prey-habitat system, i.e., rabbits *Oryctolagus cuniculus* facing feral cat *Felis catus* predation on Kerguelen archipelago. We assess how cover shapes risk perception in prey and develop an easily implementable field method to improve the estimation of proximity to cover. In contrast to protocols considering the "distance to nearest cover", we focus on the overall "area to cover". We show that fine-scale habitat use by rabbits is clearly related to our measure, in accordance with our hypothesis of higher risk in patches with smaller area to cover in this predator-prey-habitat system. In contrast, classical measures of proximity to cover are not retained in the best predictive models of habitat use. The use of this new approach, together with a more in-depth consideration of contrasting properties of cover, could help to better understand the role of this complex yet decisive parameter for predator-prey ecology.

1   Analyzing the proximity to cover in a landscape of fear:

2   A new approach applied to fine-scale habitat use by rabbits facing feral

3   cat predation on Kerguelen archipelago

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20   **Abstract**

21   Although proximity to cover has been routinely considered as an explanatory variable in studies

22   investigating prey behavioral adjustments to predation pressure, the way it shapes risk perception

23   still remains equivocal. This paradox arises from both the ambivalent nature of cover as

24   potentially both obstructive and protective, making its impact on risk perception complex and

25   context-dependent, and from the choice of the proxy used to measure proximity to cover in the

26   field, which leads to an incomplete picture of the landscape of fear experienced by the prey.

27   Here, we study a simple predator-prey-habitat system, i.e., rabbits *Oryctolagus cuniculus* facing

28   feral cat *Felis catus* predation on Kerguelen archipelago. We assess how cover shapes risk

29   perception in prey and develop an easily implementable field method to improve the estimation

30   of proximity to cover. In contrast to protocols considering the "distance to nearest cover", we

31   focus on the overall "area to cover". We show that fine-scale habitat use by rabbits is clearly

32   related to our measure, in accordance with our hypothesis of higher risk in patches with smaller

33   area to cover in this predator-prey-habitat system. In contrast, classical measures of proximity to

34   cover are not retained in the best predictive models of habitat use. The use of this new approach,

35   together with a more in-depth consideration of contrasting properties of cover, could help to

36   better understand the role of this complex yet decisive parameter for predator-prey ecology.

37   **Introduction**

38

39   Cover, hereafter defined as any tangible feature in the habitat that impairs the prey's

40   and/or the predator's ability to see and/or move [i.e., the definition of "structural cover" by

41   Mysterud and Østbye (1999), restricted to the "landscape of fear" context of Laundré et al.

42   (2010)], has often been considered as an explanatory variable in field studies investigating prey

43   behavioral adjustments to predation risk (Caro 2005). Yet, the way cover shapes risk perception

44   in prey species and their subsequent antipredator tactics still remains equivocal (e.g., Burger et

45   al. 2000, Tchabovsky et al. 2001, Caro 2005). This may be due to the ambiguity inherent to the

46   use of a single word to refer to multiscale habitat objects (e.g., a prey may have its visual field

47   impaired by a tree line hundreds of meters away and by a tuft of vegetation near its eyes when

48   feeding head down) or to the paucity of studies considering simultaneously these different scales

49   (e.g., Pays et al. 2012). Two additional reasons may explain why the role of this parameter

50   remains ambivalent.

51   First, cover is a (visual/physical) barrier for the focal individual prey but also for its

52   predator(s). Hence, the ratio between its contrasting obstructive (i.e., prevents the prey from

53   seeing or escaping the predator) and protective (i.e., prevents the predator from seeing or

54   attacking the prey) properties (Lazarus and Symonds 1992, Mysterud and Østbye 1999) and thus

55   the overall risk perception is highly specific to a predator(s)-prey system. This

56   obstructive/protective ratio depends on the intrinsic physical properties of the cover itself (e.g.,

57   dimensions, opacity), in relation to characteristics such as the body size, sensory capabilities, and

58   hunting/escape tactics of particular predator and prey species (e.g., Lima 1990, Murray et al.

59   1995, Newberry and Shackleton 1997). Furthermore, intraspecific variability is expected in the

60   above described characteristics and also in other traits (e.g., sex, reproductive status, experience

61   or group size) that may also determine risk perception in relation to a specific cover type (e.g.,

62   Götmark and Hohlfält 1995, Bowyer et al. 1999, Stratmann and Taborsky 2014, Beauchamp

63   2014). Finally, time of day (e.g., Moreno et al. 1996) or season (e.g., Bowyer et al. 1999) may

64   affect the obstructive/protective ratio for a given cover type and individual. Hence, the

65   contrasting results of studies investigating the role of cover in shaping risk perception, even

66   those performed on the same species and type of cover (e.g., Jaksic and Soriguer 1981, Moreno

67   et al. 1996), may reflect natural heterogeneity.

68   The second reason why the role of cover for prey remains ambivalent is that field

69   measurements are often too basic to provide biologically relevant proxies. For any given time

70   and predator-prey system, the obstructive/protective ratio of cover may vary with proximity. For

71   instance, cover provided by drooping branches has a low obstructive/protective ratio when a prey

72   is close because the prey is less visible but its ability to detect a predator and flee is unaffected.

73   As distance from the branches increases, the ratio increases because the prey becomes more

74   visible and the branches provide a possible ambush site for a predator. Hence, field studies

75   classically consider the "distance to cover" (when mentioned, typically the "nearest" "principal"

76   cover) as a routine measurement (Caro 2005). We speculate that part of the variability in the

77   results of studies relating prey behavioral traits to cover is a consequence of using a single

78   distance measurement that leads to an incomplete picture of the landscape of fear experienced by

79   the prey. The problem with distance to nearest cover is that this measure ignores the dimension

80   of the edge of the cover the prey faces and the presence of additional cover. Yet, in a case of an

81   overall obstructive cover, a forest edge of 100 meters long provides more potential ambush sites

82   than a patch of trees of 10 meters long even if the shortest distance between the cover and the

83   prey is the same in both situations. Similarly, a prey surrounded by several shrubs is expected to

84   be at higher risk than if there is a single shrub in its vicinity in case of obstructive cover. Hence,

85   although the shortest distance to cover is of importance as this gives an indication of the shortest

86   time lag before being predated (or sheltered in case of overall protective cover), it is only part of

87   the information. There is thus a need for a measure of all distances between the prey position and

88   cover in the surroundings (see also Metcalfe 1984 and Gómez-Serrano and López-López 2014),

89   i.e., a need for an area to cover. We suggest that such a metric would provide a more reliable

90   measure of the proximity to cover and thus, of risk perception, than the commonly used

91   "distance to the nearest cover". In the present paper, our aims were to (1) develop such a metric,

92   from field measurements to their geometrical analysis and to (2) use this metric to investigate

93   habitat use of rabbits (*Oryctolagus cuniculus*) facing predation threat by feral cats (*Felis catus*)

94   on the Kerguelen subantarctic archipelago. We also considered classical proxies of proximity to

95   cover in order to allow comparisons.

96   In studies of responses to cover, there is a risk of circularity if the property of cover is

97   inferred from its effect on behavior (Lazarus and Symonds 1992). Instead, cover property, and

98   thus the way it is expected to trigger risk perception in prey, should arise from the knowledge of

99   the system. Hence, making a prediction requires assessing the risk perception (i.e., the

100 obstructive/protective ratio) inherent to the (different types of) cover(s), i.e., being able to relate

101 the physical characteristics of the cover such as opacity and size to the escape tactics of the prey

102 and the hunting tactics of the predator involved. Furthermore, it is important to recognize that

103 cover may be associated with foraging profitability (e.g., Morgantini and Hudson 1985), for

104 example if it directly provides food or affects food plants through shading or nutrients (e.g.,

105 Mysterud and Østbye 1999, Dellafiore et al. 2014). In the present paper, we took advantage of a

106 simple predator-prey-habitat system allowing us to hypothesize that predation threat was the

107 main driving force of habitat use by rabbits. Given the specific characteristics of the system, we

108 predicted that rabbits should avoid patches with high proximity to cover, i.e., with small area to

109 cover.

110

111 **Materials and Methods**

112

113 *Study site*

114   Introduced by sailors during the nineteenth century, rabbits are now widespread

115 throughout the Kerguelen archipelago (Chapuis et al. 1994). Domestic cats were introduced in

116 1951 to control invasive rodents (*Rattus rattus, Mus musculus*) and rabbits at the research station

117 of Port-aux-Français. Cats are now widely distributed over the main island (Grande Terre),

118 where the study took place (Pointe Morne area, 49°22'S, 70°26'E).

119   Our study was performed in December 2014. We focused on a ca. 100 by 700 m area

120 covered by mounds less than 2 m high, formed of earth and roots and covered by the perennial

121 herb *Acaena magellanica* (Rosaceae) (see Supplemental information file 1). The space between

122 the mounds was composed of *Acaena magellanica*, *Poa annua* and bare ground/rocks. The study

123 area is surrounded by open meadows with flat topography, covered with dense swards of *Acaena*

124 *magellanica*.

125   We censused active rabbit burrows as indicated by fresh pellets or evidence of animal

126 passage in a 0.73 km^2 area including the patches (see below) used in this study. We found 51

127 active burrows, all outside our 70,000 m^2 study area. Although we do not know the relationship

128 between the number of active burrows and the population size in this habitat, previous published

129 relationships suggest about 22 rabbits (i.e., about 30 rabbits/km^2) (Ballinger and Morgan 2002).

130 Fifteen additional active burrows were present outside the 0.73 km^2 area, 800 m away from the

131 study area.

132

133 *Predicting the effect of area to cover on habitat use by rabbits*

134   The following characteristics of our system allowed us to reliably assess the role of cover

135 in shaping risk perception in rabbits.

136   — Food resources. We selected patches of a single preferred plant species, *Poa annua*

137 (Chapuis et al. 1994). This highly nutritious alien grass represents most of rabbit diet in our study

138 area (over 90% of the plant fragments found in fecal pellets at the time of the year our study took

139 place, Boussès et al. 1988). As the study area is relatively restricted, meteorological and edaphic

140 conditions are very similar. Moreover, *Poa annua* was heavily grazed (1 – 2 cm high) throughout

141 the study area. Because patches were likely to be similar in food quality and quantity, the effect

142 of cover was not confounded by foraging profitability. Finally, rabbits face no interspecific

143 competition for feeding resources in this habitat (in particular, reindeer *Rangifer tarandus* have

144 not been observed in the study area).

145   — Predators. Predation by brown skua (*Catharacta lonnbergi*) on rabbits occurs on the

146 Kerguelen archipelago, but mostly on small islands (Chapuis et al. 1994) and on young/sick

147 rabbits (the myxomatosis virus was introduced in 1950's to control populations). Given that our

148 study site was on the main island, that no skuas nested nearby, that no rabbits were observed or

149 killed (as part of other protocols) with apparent signs of myxomatosis, that our study took place

150 before the rabbit birth period, that cats were observed daily in our study area and finally that

151 rabbits are the primary prey of cats in Kerguelen archipelago (Pontier et al. 2002), we believe

152   that predation pressure experienced by rabbits in this habitat is mostly due to cats. This contrasts

153   with other studies on rabbits and other prey where predators are often diverse. Our field

154   observations of hunting bouts revealed that cats are stalk-and-ambush predators (although they

155   also visit burrows). A foraging rabbit is clearly at risk if surprised by a cat, while early visual

156   detection of the cat allows escape, especially in open areas.

157   — Cover types. We focused on a habitat with a single type of cover, earth mounds (i.e.,

158   visually opaque and physically impenetrable, see Supplemental information file 1), and

159   considered as "cover object" any mound higher than 20 cm (i.e., capable of hiding an ambushing

160   cat from a rabbit, even in an upright posture, and of hiding a rabbit from a cat, unless the rabbit

161   was in an upright posture). Most mounds were taller than 1 m. Cats may attack directly from a

162   side of a mound, but also from behind a smaller mound or possibly from the top of a larger

163   mound.

164   The characteristics of this predator-prey-habitat system allowed us to consider cover as a

165   source of risk for rabbits, i.e., far more obstructive (total opacity in a context of stalk-and-

166   ambush predator threat and complete physical barrier when escaping, with no intrinsic refuge

167   property – once potential burrows (see below) are statistically accounted for) than protective

168   (rabbits hidden from cats). Accordingly, we predicted that rabbits would favor patches with

169   larger areas to cover, i.e., with larger unobstructed areas.

170

171   *"Patch" characterization and data collection*

172   We defined a "patch" as a circular area with a 2 m diameter, covered exclusively with

173   *Poa annua*, whose center was at least 20 m away from the center of another patch. The studied

174   area was fully searched for patches, which numbered 32.

175   We used total dry weight of pellets per patch as a measure of patch use. In every patch,

176   we made a one-time collection of all the fecal pellets, thereby assuming that the disappearance

177   time of pellets was not related to the variables we considered. We also kept the pellet collection

178   time very short (2 days) to reduce the occurrence of additional pellets during the study period.

179   Pellets were subsequently dried for 4 days at 40°C (i.e., until their weight stopped decreasing)

180   and weighed. Pellet quantity is a reliable method to assess rabbit abundance at the habitat scale

181   (Palomares and Delibes 1997, Palomares 2001, Cabrera-Rodriguez 2006). At a finer scale, pellet

182   quantity has been shown to index the frequency of rabbit visitation of the patches (Bakker et al.

183   2005).

184   In every patch, a single observer took the following measurements:

185   — The GPS coordinates. This allowed us subsequently to investigate statistically the

186   spatial structure of our response variable, the pellet total dry weight.

187   — The total number of old burrows within a 20 m of diameter circle around the center of

188   the patch. This parameter was recorded because we observed that old burrows represented

189   potential refuges. We considered the hypothesis that there were more rabbits closer to active

190   burrows (all localized outside our study area, see above) as part of our investigation of spatial

191   structure. The number of burrows is classically part of rabbit habitat selection studies (e.g.,

192   Palomares and Delibes 1997).

193   — The terrestrial distance (m) to the nearest old burrow, bypassing a mound if present.

194   — The number of "contact points" with Poa annua around the focal patch. Contact points

195   were located 1, 3 and 5 m from the center of the focal patch every 45° (i.e., n=24 in total for each

196   patch). A proxy of the isolation of the focal patch of *Poa annua* was then calculated as the

197   frequency of "contact points" without *Poa annua*. We included this parameter because we

198   hypothesized that the attraction of a patch could have been positively related to how isolated it

199   was from other patches of *Poa annua* or conversely, that patches surrounded by a high overall

200   *Poa annua/Acaena* ratio could have been more attractive for rabbits. Moreover, this measure

201   allowed us to investigate the hypothesis that risk perception would be increased if abundant

202   *Acaena* around the focal patch impaired the visual field of a rabbit feeding head down.

203   — The distances (m) from the center of the patch to the nearest mound and to the nearest

204   side of a mound visible from the patch, within a biologically relevant area (see below). In

205   addition to their biological relevance as an obstacle when escaping or a point from which a

206   hidden cat may attack, these distances allow us to compare our proposed measure with other

207   measures of risk.

208   — The total number of mound sides visible from the patch inside the biologically

209   relevant area (see below) and the mean distance (m) to these sides.

210   — Additionally, we recorded the unobstructed area for each patch. The description of this

211   measure is presented below.

212

213   *Measuring the unobstructed area*

214   From the center of the patch, the observer scanned 360° using a rangefinder with angle

215   display (Vector 1500 GMD). Each time the rectilinear edge of a mound (i.e., forming a straight

216   line as a whole) started and stopped, the distance from the center of the patch and the

217   corresponding angle were recorded. When a mound edge did not appear to be rectilinear, the

218   measurements were recorded for each of its rectilinear segments. This gave us a set of triangles

219   with an angle and the length of the two adjacent sides, allowing the calculation of their area.

220   However, the sum of these areas would provide a poor proxy of the unobstructed area

221   experienced by a rabbit because some mounds would be too far away to provide a cat with a

222   successful ambush position or to provide a physical barrier to escape. Furthermore, considering

223   such distant mounds may inflate the unobstructed area, potentially masking biologically relevant

224   effects at shorter distances. We thus calculated the unobstructed area within a circle. Considering

225   such a circle also allowed us to deal with cases where no cover occurred before the horizon (a

226   single sector in a single patch for our study area). We set the circle radius based on our field

227   observations of hunting behavior by cats. Because the longest cat run toward a feeding rabbit that

228   we observed was about 25 m, we first considered this distance. Then, in order to identify the

229   radius of the circle with the highest predictive power, we computed the squared coefficient of

230   determination between the observed and the fitted values for models built with values of

231   unobstructed areas calculated for circles with radiuses ranging from 1 to 150 m (with 1 m

232   increments).

233   Depending on whether the rectilinear edge of the mound the observer faced fell entirely

234   inside the circle, entirely outside the circle or was secant in one or two points, we used different

235   formulas to calculate the corresponding area, as explained Fig. 1A, B and C (see also the script

236   used to compute the unobstructed area, written in the R language and provided in Supplemental

237   information file 2). The sum of these areas provides the unobstructed areas, ranging from 25.3 to

238   1646.1 m^2 for the circle with a radius of 25 m.

239

240   *Statistical analyses*

241   The pellet total dry weight exhibited significant positive autocorrelation (Moran's I =

242   0.111, p < 0.001, Fig. 2). We used generalized least squares (GLS) models to account for

243   autocorrelation in model residuals (Selmi and Boulinier 2001). Different models of spatial

244   structure (assuming spherical, exponential and Gaussian structures) were fitted and the best

245   fitting model (exponential in all the cases) was defined using the Akaike Information Criterion

246   (AIC; Selmi and Boulinier 2001, Diniz-Filho et al. 2003).

247   We log transformed the pellet total dry weight to meet the assumptions of constant

248   variance and normality of the residuals. To avoid collinearity issues, we only considered models

249   including explanatory variables that were not significantly correlated (all p > 0.14). We did not

250   include interactions among explanatory variables because of the small sample size. For patches

251   with no burrows within a 20 m of diameter circle (n=7), the variable "distance to nearest burrow"

252   was missing. Hence, we first tested the effect of this variable on a subsample and then reran the

253   models without it to avoid artificially reducing sample size when testing the other explanatory

254   variables. We proceeded in the same way for "distance to nearest side" (n = 2 patches with no

255   visible side) and for "mean distance to sides" (same 2 patches). We selected the final model by

256   fitting the complete model and removing each term successively. The significance of each term

257   was determined by assessing the change in deviance (i.e., Likelihood Ratio Test – LRT) against a

258   chi^2 distribution with the appropriate degrees of freedom. For nonsignificant variables considered

259   in several models, we present the maximum LR value, the corresponding minimum p-value and

260   the estimates. Estimates were all computed on standardized variables (mean = 0, S.D. = 1) to

261   allow comparisons of effect sizes not dependent on measurement scale (Gelman and Hill 2007).

262   Analyses were performed in R 3.1.2 (R Core Team 2014) using the packages *ape* for spatial

263   analyses and *nlme* for developing the models. The French Polar Research Institute approved this

264   program (number 279).

265

266   **Results**

267

268   The unobstructed area within a 25 m radius circle around the patch positively affected the

269   pellet total dry weight (df = 1, LR = 9.264, p = 0.002; estimates: intercept = 1.41 ± 0.20 S.E.,

270   slope = 0.51 ± 0.16 S.E.; Fig. 3). When the unobstructed area increased from 500 to 1000 m^2, the

271   predicted pellet total dry weight increased from 3.38 to 7.02 g.

272   The mean distance to visible mound sides and, to a lesser extent, the distance to the

273   nearest visible side were also positively related to the pellet total dry weight (mean distance to

274   mound sides: df = 1, LR = 4.721, p = 0.030; estimates: intercept = 1.40 ± 0.23 S.E., slope = 0.39

275   ± 0.17 S.E.; distance to the nearest side: df = 1, LR = 3.776, p = 0.052; estimates: intercept =

276   1.39 ± 0.24 S.E., slope = 0.35 ± 0.18 S.E.). Finally, the total number of visible sides within a 25

277   m circle negatively affected the pellet total dry weight (df = 1, LR = 5.032, p = 0.025; estimates:

278   intercept = 1.42 ± 0.27 S.E., slope = - 0.37 ± 0.16 S.E.).

279   The other explanatory variables, including the distance to the nearest mound, were not

280   retained in the final models and had smaller effect sizes as measured by standardized regression

281   coefficients (distance to the nearest mound: df = 1, LR = 2.156, p = 0.142; estimates: intercept =

282   1.44 ± 0.27 S.E., slope = 0.25 ± 0.17 S.E.; total number of old burrows: df = 1, LR = 0.247, p =

283   0.619; estimates: intercept = 1.40 ± 0.19 S.E., slope = - 0.08 ± 0.14 S.E.; distance to the nearest

284   old burrow: df = 1, LR = 1.847, p = 0.174; estimates: intercept = 1.27 ± 0.51 S.E., slope = - 0.27

285   ± 0.18 S.E. ; isolation: df = 1, LR = 1.014, p = 0.314; estimates: intercept = 1.41 ± 0.31 S.E.,

286   slope = - 0.15 ± 0.15 S.E.).

287   The hypothesis that the proximity to active burrows partly explains the spatial pattern we

288   report (Fig. 2) might be relevant as active burrows were localized at about 100 meters northwest

289   from the patches, i.e., on the side of the highest values in pellet total dry weight.

290   Finally, the best radius of the circle ranged between 19 and 32 m (based on maximizing

291   the coefficient of determination between the observed and the fitted values), in line with our field

292   observations of cat hunting behaviors (Fig. 4).

293

294   **Discussion**

295

296   We took advantage of a study area with patches composed of a single preferred plant

297   species, displaying cover objects of a single type (i.e., a single intrinsic obstructive/protective

298   ratio) and where predation risk arose from only one species, feral cats. In this context, our results

299   strongly suggest that cats shape fine-scale habitat use by rabbits. Fewer pellets were present in

300   patches with smaller unobstructed areas, i.e., with smaller visible area from the center of a 25 m

301   radius circle around the patch, and thus closer potential danger, and with greater proximity of

302   physical barrier, and thus reduced escape possibilities.

303   The consideration of the area to cover helped to understand the role of cover in fine-scale

304   habitat use by rabbits. With classical approaches, i.e., with the distance to the "nearest cover"

305   (i.e., nearest mound or nearest visible side and thus shortest time to initiate an escape and

306   shortest distance before reaching a barrier to escape/an exit) as an explanatory variable, the

307   conclusion of an absence of (or weak) differences between the patches in the amount of pellets

308   according to the proximity of cover would have emerged (i.e., no or weak effect of nearest

309   mound or nearest visible side distance in our analyses, respectively). Yet, our results strongly

310   suggest that proximity to cover shapes habitat use by rabbits in this habitat.

311   Our method requires no particular expertise – we provide an R-script to calculate the

312   required areas (see Supplemental information file 2). Although a rangefinder with angle displays

313   may be expensive, this can be replaced by a basic model without angle displays (or even by a

314   tape measure) and a compass. A limitation of our method is the subjectivity in classifying a

315   portion of the cover object as rectilinear or not. However, this subjectivity is more pronounced

316   when the cover is far, i.e., when the rabbit also faces visual limitations.

317   Beside the role of predation risk as a driver of the pattern we report, we cannot rule out

318   the influence of nonexclusive additional pressures. Reduced visibility may also lead to decreased

319   opportunity to monitor conspecifics while foraging. This may again indirectly relate to predation

320   risk because of the concomitant loss of information about conspecifics' vigilance/escape

321   behavior and because of the decreased "confusion effect" (Beauchamp 2014), as other prey

322   individuals are also less visible to an attacking predator. However, reduced visibility is further

323   expected to decrease foraging and social opportunities (e.g., localization of high quality patches,

324   scrounging, gathering information about potential mates/competitors) (Beauchamp 2014 for a

325   review, Monclús and Rödel 2008 for rabbits). Smaller unobstructed area is also expected to

326   mechanistically lead to lower overall surface of edible plants (i.e., more mounds and thus less

327   accessible plants per unit area) and thus to increased foraging effort/gram of ingested grass/unit

328   time, i.e., to possible decreased attractiveness. Finally, we cannot rule out the possibility that

329   patches with small unobstructed areas are more difficult to find for rabbits.

330   Pellet weight suggests that rabbits spend more time in patches with larger unobstructed

331   areas. However, the similar height of grass suggests that different patches are foraged at similar

332   rates which would be expected to take similar amounts of time. Several hypotheses may explain

333   this apparent contradiction. First, because we did not measure grass height, we cannot rule out

334   the possibility that patches with larger unobstructed areas had slightly shorter grasses as a result

335   of more time spent foraging. Second, although we believe meteorological and edaphic conditions

336   are very similar over our restricted study area, we cannot rule out the possibility of fine-scale

337   variations. This could lead to higher *Poa annua* productivity in some patches, and thus to

338   increased foraging time despite similar height of grass. For instance, patches with larger

339   unobstructed areas may benefit from increased sunlight. Finally, under the hypothesis of similar

340   foraging rates among patches, behavioral explanations may be proposed. Rabbits may increase

341   grazing rate (through bite rate/size) and thus decrease exposure time in patches with smaller

342   unobstructed areas. Additional activities such as grooming, resting or playing may also occur in

343   safer places (e.g., Cowlishaw 1997, Blumstein 1998), leading to an increase in the overall

344   amount of time spent.

345

346   *Past and future studies*

347   The use of an incomplete measure of the proximity to cover may explain the absence of

348   significant results in studies investigating behavioral adjustments of prey in relation to cover

349   (e.g., Pays et al. 2014) while other studies in the same population report such an effect (e.g.,

350   Périquet et al. 2012), depending on which particular cover object is considered. Investigating the

351   predictive power of our proxy in these prey-predators-habitats systems, including large-scale

352   cover objects such as forest edges, may be informative. Previous studies on habitat selection by

353   rabbits in relation to cover reported contrasting results, possibly reflecting the ambivalent

354   properties of cover and the large range of predators rabbits face in their worldwide distribution

355   (Courchamp et al. 2003). While the importance of the protective function of cover in rabbit

356   habitat selection has been shown by several studies (Villafuerte and Moreno 1997, Dellafiore et

357   al. 2014), leading to a greater use of patches farther away from cover when predation pressure is

358   lower (Banks et al. 1999), cover may also be avoided when it reduces the visual field (Moreno et

359   al. 1996). Part of the variability among studies may further be explained by the use of the

360   distance to nearest cover, widespread in this species also (e.g., Moreno et al. 1996, Villafuerte

361   and Moreno 1997). Moreover, the obstructive/protective ratio of a given cover for a given

362   population may vary according to the period of the day (Moreno et al. 1996): rabbits have been

363   reported to preferentially feed closer to cover during the day (hiding from birds of prey) than at

364   night (avoiding stalking carnivorous mammals).

365   Cover presenting total visual and physical obstruction, as in our study, is probably

366   uncommon. Assessing the obstructive/protective ratio and thus the risk perception associated

367   with a cover may require consideration of its visual and physical properties (Schooley et al.

368   1996, Camp et al. 2012). Moreover, it is probably uncommon to have only a single type of cover

369   as in our study. The "area to cover" should thus be calculated separately for each cover type.

370   Cover objects can all be of the same nature (e.g., protective/obstructive properties > 1) but differ

371   in the relative intensity of protective and obstructive properties, or can be of opposite nature

372   (e.g., some with protective/obstructive properties > 1 and some others with a ratio < 1). For

373   example, a feeding patch for a mountain ungulate in the vicinity of a cliff and of several shrubs

374   and rocks may be characterized by the overall area to the shrubs and rocks (with a risk increased

375   for patches with smaller areas) and by the overall area to the cliff (with a risk decreased for

376   patches with smaller areas) if the individuals face stalk-and-ambush predators unable to reach

377   their prey on a cliff.

378

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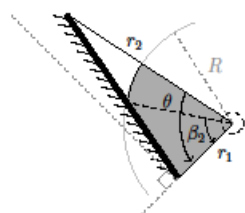
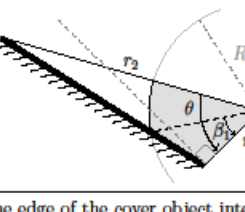
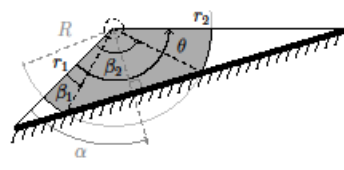
383   **Fig.1**

384   The different potential cases for the position of edges of cover objects in relation to a circle

385   around the patch and the corresponding formulas for the calculation of the area ("A" in (B))

386   between the center of the patch and the cover object or the circle. The unobstructed area is

387   calculated by summing all these areas (see also Supplemental information file 2). Cases

388   numbered (1) to (4) in (A) refer to the same numbers in (B). Dark grey areas in (B) refer to

389   subcases illustrated in (A); light grey is used for alternative subcases. Inequalities in (B) are not

390   strict: for limiting cases, the different corresponding formulas lead to the same results. All the

391   angles are counterclockwise. R is the radius of the circle. d, α, β_1 and β_2 are defined in (C). We

392   defined $r_1 \leq r_2$. The only required field measurements are r_1, r_2 and θ.

394   **Fig.1 (continued)**

395

396   **Fig.1 (continued)**

(3) The edge of the cover object intersects the theoretical circle in one point		
(3a)	Conditions: • $r_1 \leq R$ • $r_2 \geq R$ • $r_2 \cos\theta \leq r_1$	Area: $A = \dfrac{R^2(\theta - \beta_2)}{2}$ $\quad + \dfrac{Rr_1 \sin\beta_2}{2}$
(3b)	Conditions: • $r_1 \leq R$ • $r_2 \geq R$ • $r_2 \cos\theta \geq r_1$	Area: $A = \dfrac{R^2(\theta - \beta_1)}{2}$ $\quad + \dfrac{Rr_1 \sin\beta_1}{2}$

(4) The edge of the cover object intersects the theoretical circle in two points		
	Conditions: • $r_1 \geq R$ • $d \leq R$ • $\alpha \geq 0$	Area: $A = \dfrac{R^2(\theta - \beta_2 + \beta_1)}{2}$ $\quad + \dfrac{R^2 \sin(\beta_2 - \beta_1)}{2}$

(C) Notations and formulas

- Minimal distance (altitude length) between the center of the patch and the cover object:

$$d = r_1 r_2 \frac{|\sin\theta|}{\sqrt{r_1^2 + r_2^2 - 2r_1 r_2 \cos\theta}}$$

- Angle between the altitude and the border of the sector:

$$\alpha = \arctan \frac{r_1 - r_2 \cos\theta}{r_2 \sin\theta}$$

- Angle of the intersection between the cover object and the theoretical circle:

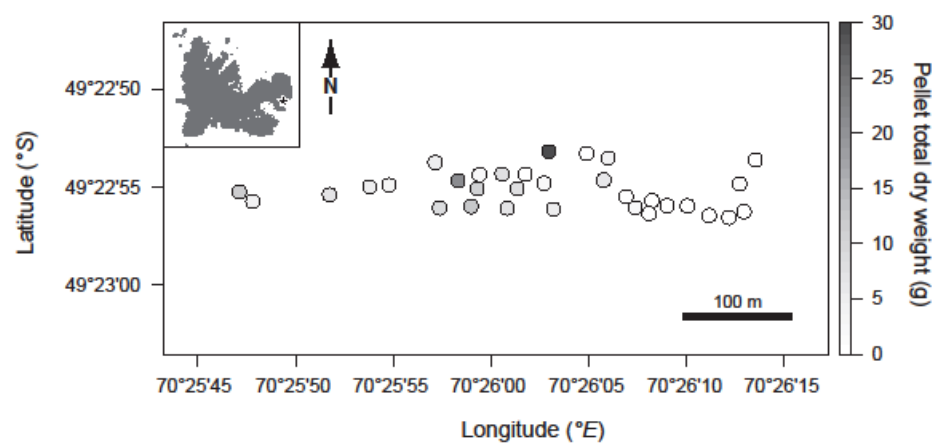
$$\beta_1 = \arccos \frac{r_1 r_2^2 \sin^2\theta + \sqrt{(R^2(r_1^2 + r_2^2 - 2r_1 r_2 \cos\theta) - r_1^2 r_2^2 \sin^2\theta)(r_2 \cos\theta - r_1)^2}}{R(r_1^2 + r_2^2 - 2r_1 r_2 \cos\theta)}$$

$$\beta_2 = \arccos \frac{r_1 r_2^2 \sin^2\theta - \sqrt{(R^2(r_1^2 + r_2^2 - 2r_1 r_2 \cos\theta) - r_1^2 r_2^2 \sin^2\theta)(r_2 \cos\theta - r_1)^2}}{R(r_1^2 + r_2^2 - 2r_1 r_2 \cos\theta)}$$

397

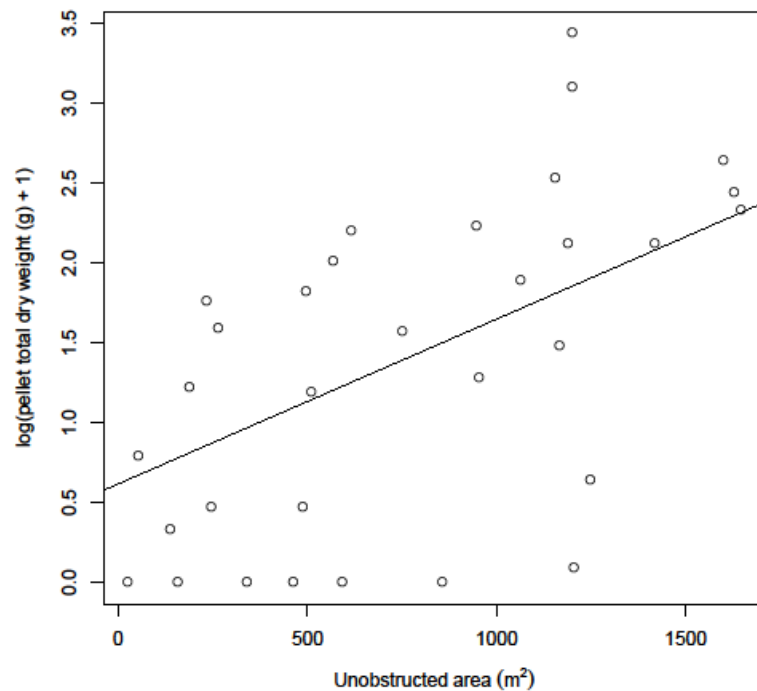
398   **Fig. 2**

399   Pellet total dry weight (indexed by grey levels shown on the right y-axis) measured in the studied

400   patches (dots) according to their spatial position (left y-axis and x-axis).

401

403   **Fig. 3**

404   The positive relationship between the log(pellet total dry weight (g) + 1) and the unobstructed

405   area (m²) computed for a circle with a 25 m radius.

406

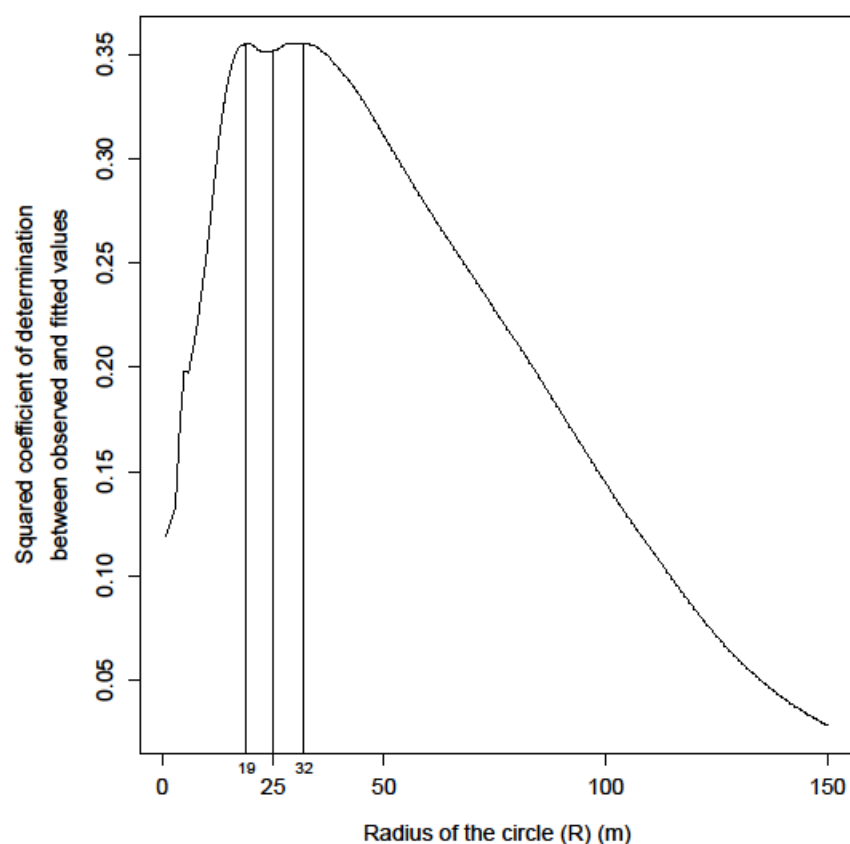
408 **Fig. 4**

409 Squared coefficients of determination between the observed and the fitted values for models built

410 with values of unobstructed areas calculated for circles of radiuses (R in Fig. 1, in m) ranging

411 from 1 to 150 m and plotted on x axis. The biologically relevant distance ranges between 19 and

412 32 m, in line with our field observations of cat hunting bouts.

413

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