

Analyzing the proximity to cover in a landscape of fear: A new approach applied to fine-scale habitat use by rabbits facing feral cats' 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 largely equivocal. This paradox arises from both the ambivalent nature of cover, making its impact on risk perception complex and highly context-dependent, and from the inaccuracy of the proxy commonly used in the field to measure this important variable, leading to a partial 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 cats *Felis catus* predation on Kerguelen archipelago, allowing to assess how cover shapes risk perception in prey and develop an easily implementable and inexpensive field method to index proximity to cover: while protocols classically consider the “distance to the closest cover item”, we focus on the overall “surface to the cover items” from a focal point. We show that rabbits' fine-scale habitat use is clearly related to our measure, in accordance with our hypothesis of cover being a source of risk in the specific case of this predator-prey-habitat system. In contrast, classical measures of proximity to cover are not retained in the final models. Hence, the use of this new simple approach, together with a more in-depth consideration of multiple scales and contrasting properties of cover, could help to better understand the role of this complex yet decisive parameter for prey ecology in a landscape of fear context.

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20 **Abstract**

21 Although proximity to cover has been routinely considered as an explanatory variable in
 22 studies investigating prey behavioral adjustments to predation pressure, the way it shapes risk
 23 perception still remains largely equivocal. This paradox arises from both the ambivalent
 24 nature of cover, making its impact on risk perception complex and highly context-dependent,
 25 and from the inaccuracy of the proxy commonly used in the field to measure this important
 26 variable, leading to a partial picture of the landscape of fear experienced by the prey. Here, we
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 28 cats *Felis catus* predation on Kerguelen archipelago, allowing to assess how cover shapes risk
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 31 cover item”, we focus on the overall “surface to the cover items” from a focal point. We show
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 34 system. In contrast, classical measures of proximity to cover are not retained in the final
 35 models. Hence, the use of this new simple approach, together with a more in-depth
 36 consideration of multiple scales and contrasting properties of cover, could help to better
 37 understand the role of this complex yet decisive parameter for prey ecology in a landscape of
 38 fear context.

39 Introduction



40 Cover, hereafter defined as any **habitat tangible feature** that impairs the prey **and / or** the
 41 **predator ability** to see **and / or** move (i.e., Mysterud and Østbye 1999's definition of
 42 "structural cover", restricted to Laundré et al. 2010's "landscape of fear" context), has been
 43 classically considered as a routine explanatory variable in field studies investigating prey
 44 behavioral adjustments to predation risk (Caro 2005). Yet, the way cover shapes risk
 45 perception in prey species and their subsequent anti-predator tactics still remains **largely**
 46 **equivocal** (e.g., Burger et al. 2000, Tchabovsky et al. 2001, Caro 2005). In addition to (1) the
 47 ambiguity inherent to the use of a single word to refer to **a multitude of multi-scales habitat**
 48 **items** (e.g., a prey may have its visual field impaired by a tree line hundreds of meters away
 49 and by a tuft of vegetation nearby its eyes when feeding head down) and (2) the paucity of
 50 studies considering simultaneously these different scales while they may interact (e.g., Pays et
 51 al. 2012), two main reasons may explain why the role of this well studied parameter remains
 52 ambivalent.

53 First, cover is a (visual / physical) barrier for the focal individual prey but also for its
 54 predator(s). Hence, the ratio between its contrasting obstructive (i.e., prevents the prey to see
 55 or escape from the predator) and protective (i.e., prevents the predator to see or attack the
 56 prey) properties (Lazarus and Symonds 1992, Mysterud and Østbye 1999), and thus the
 57 **associated risk perception, is highly specific to a predator(s) – prey system**. Obviously, this
 58 obstructive / protective ratio depends on the intrinsic physical properties of the cover itself (its
 59 dimensions, opacity etc.), in relation to, among others, the physical characteristics (body size,
 60 visual acuity etc.) and escape / hunting tactics of the focal prey and its predator(s) (e.g., Lima
 61 1990, Murray et al. 1995, Newberry and Shackleton 1997). However, intra-specific variability
 62 in risk perception **associated to** a given cover is also further expected because individuals
 63 differ in physical characteristics and escape tactics / skills but also in sex, reproductive status,

previous predation experience and other parameters (such as group size) that may determine risk perception (e.g., Götmark and Hohlält 1995, Bowyer et al. 1999, Stratmann and Taborsky 2014, Beauchamp 2014). Finally, time of the day (e.g., Moreno et al. 1996) or season (e.g., Bowyer et al. 1999) may affect the obstructive / protective ratio for a given cover and a given prey individual. Hence, the contrasting results in studies investigating the role of cover in shaping risk perception, including those performed on the same species and type of cover (e.g., Jaksic and Soriguer 1981, Moreno et al. 1996), probably reflects at least in part natural heterogeneity.

Second, field measurements related to cover are probably usually too basic to provide biologically relevant proxies of risk perception experienced by the prey. At any given time and for a given predator(s) – individual prey system, the obstructive / protective ratio of a given cover item is expected to depend on its proximity to the point of interest (e.g., a focal animal, an index of presence, a birth site, a random point etc.). For instance, a discontinuous cover (i.e., tree foliage provided by drooping branches) is expected to display a low obstructive / protective ratio if the prey stands close to it as it breaks its body shape (i.e., protective properties against predator visual detection) but its own visual field may be unimpaired (depending on the exact position of the eye in respect to the branches and leaves) and its movements unaffected in case of attack (i.e., no visual / physical obstructive properties). With the distance between the focal point and the cover item increasing, the obstructive / protective ratio is expected to increase as the above rationale progressively shifts from the prey to the predator side (in particular for stalk-and-ambush predators), as long as the cover item remains in the “domain of risk” of the prey, i.e., where the prey is at risk if the predator starts hunting from the cover. Accordingly, field studies, and in particular those focusing on ground cover, classically consider the “distance to cover” (when mentioned,

typically the “closest” “principal” cover item) as a routine measurement (Caro 2005). We speculate that part of the variability in the results of studies relating prey behavioral traits to “cover” is the consequence of the use of this measure that may lead to a partial picture of the landscape of fear experienced by the prey. This because:

(1) A “distance” alone says nothing about a parameter as important as the stretch of the cover the prey faces. Although the shortest distance to cover is of importance as this gives an indication of the shortest time lag before being predated / sheltered, it is only part of the information: overall risk is not expected to be the same 10 meters away from a patch of trees or 10 meters away from a tree line of hundreds linear meters.

(2) The other cover items present in the surroundings are not considered in this approach. Yet, risk perception is not expected to be the same 10 meters away from a shrub with no other shrubs in the surroundings or 10 meters away from a shrub with another shrub 11 meters away.

We suggest that instead of the commonly used “distance to the closest cover item”, an overall “surface to the cover items” would provide a more reliable measure of the “proximity to cover” and thus, of risk perception. In the present paper, our aims were to (1) develop such a method, from field measurements to its geometrical aspects and (2) use this new measure to investigate habitat use of rabbits (*Oryctolagus cuniculus*) facing predation threat by feral cats (*Felis catus* L.) on the Kerguelen subantarctic archipelago. We also considered classical proxies of “distance to cover” in order to allow comparisons.

Predicting the effect of proximity to cover in habitat use by prey is usually complex, for two main reasons. First, it requires assessing the risk perception (i.e., the obstructive / protective ratio) inherent to the different (types of) cover item(s), i.e., being able to relate the

physical characteristics of the cover(s) (opacity, size) to the escape / hunting tactics of the prey / predator(s) involved in the system. Second, beside predation risk, patch choice by prey is also shaped by foraging profitability (Lima and Dill 1990). This leads to complex situations as cover may in turn be closely related to foraging profitability (e.g., Morgantini and Hudson 1985). This because (1) cover may impact food resources characteristics (e.g., plants growth / composition impacted by the amount of shade or the presence of specific plants), (2) a given soil may impact both cover and food characteristics (e.g., plants growth / composition or invertebrates community) or (3) in the case of herbivores, cover may be food (e.g., Mysterud and Østbye 1999, Dellafiore et al. 2014). For rabbits, several studies reported that cover shaped habitat use in a predation context (Moreno et al. 1996, Lombardi et al. 2003, Dellafiore et al. 2014). However, as expected given (1) the worldwide distribution of rabbits and thus the variety of predators and habitats they experience (Courchamp et al. 2003), and (2) the use of the classical approach to measure distance to cover (e.g., Moreno et al. 1996, Villafuerte and Moreno 1997), results are contrasted (e.g., over- or underuse of cover, Moreno et al. 1996, Banks et al. 1999). In the present paper, we took advantage of a simple predator-prey-habitat system allowing to predict risk perception and thus habitat use by rabbits in relation to proximity to cover, thereby avoiding the pitfall of qualifying the nature of cover based on animal behavior. Key characteristics of this system are:

- Food resources. We selected patches of a single preferred (Chapuis et al. 1994) plant species (*Poa annua*) in order to disentangle the effects of cover and foraging profitability. Moreover, rabbits face no interspecific competition for feeding resources in this habitat (in particular, reindeer *Rangifer tarandus* have not been observed in the study area), which may also have affected their foraging patch choice as well as our interpretation (see Discussion).

- Predators. Predation by subantarctic skua (*Catharacta skua lönnbergi*) on rabbits occurs on the Kerguelen archipelago, but mostly on small islands (Chapuis et al. 1994) and on young / sick rabbits (myxomatosis virus introduced in 1950's to control populations). Moreover, the hunting bouts by skuas we observed were performed using low flight approaches, typically in wide open areas (authors pers. obs.). Given that our study site was on the mainland and in a closed area (i.e., covered by mounds, see below and Supplemental information file 1), that no skuas nested around, that no rabbits were observed or killed (as part of other protocols) with apparent signs of myxomatosis, that our study took place before the birth period, that cats were observed daily in our study area and finally that rabbits are the primary prey of cats in Kerguelen archipelago (Pontier et al. 2002), we believe that predation pressure experienced by rabbits in this habitat is mostly due to cats. This contrasts with other studies on rabbits, and probably on other prey species, where predators are often diverse. Our field observations of cats hunting bouts revealed that cats are stalk-and-ambush predators (although they also visit burrows). A foraging rabbit is clearly at risk when surprised by a cat, while an early visual detection of the cat allows efficient escape, especially in open areas (i.e., with no physical barriers).
- Cover types. We focused on a habitat with a single type of cover: earth mounds (i.e., visually opaque and physically impenetrable, see Supplemental information file 1) and considered as "cover item" any mound higher than 20 cm (i.e., concealing an ambushed cat for a rabbit, even in an upright posture; and concealing a rabbit, except in an upright posture, for a cat), although most of them were taller than 1 m high.

Altogether, the characteristics of this predator-prey-habitat system allowed us to consider cover items as a source of risk for rabbits, i.e., far more obstructive (total opacity in a context of stalk-and-ambush predator threat and complete physical barrier when escaping, with no refuge property) than protective (rabbits hidden from cats by the cover). Accordingly, the overall “surface to the cover items”, i.e., the surface around the patch without visual /physical obstruction in our study-case, was referred to as a “domain of safety” in our study (while it could be interpreted as a “domain of risk” in a case of a protective cover). We thus predicted that rabbits should favor patches with large “domains of safety”.

Materials and Methods

Study site

Introduced by sailors during the nineteenth century, rabbits are now widespread throughout the Kerguelen archipelago (Chapuis et al. 1994). Domestic cats were introduced in 1951 to control invasive rodents (*Rattus rattus*, *Mus musculus*) and rabbits at the research station of Port-aux-Français. Rabbits and cats are now widely distributed over the main island (Grande Terre), where the study took place (Pointe Morne area, 49°22’S, 70°26’E).

Our study was performed in December 2014. We focused on a ca. 70,000 m² area covered by mounds lower than 2 meters high, formed with earth and roots and covered by the perennial herb *Acaena magellanica* (Rosaceae) (see Supplemental information file 1). The remaining soil, between the mounds, was composed of *Acaena magellanica*, *Poa annua* and bare ground / rocks. The study area is surrounded by open meadows with dense swards of *Acaena magellanica*, with flat topography.

180 “Patch” characterization and data collection

181 We defined a “patch” as a circular area with a 2 m diameter covered exclusively with very
 182 short sward (1-2 cm high) of grazed *Poa annua*, whose center was distant at least by 20 m
 183 from another patch. *Poa annua* is a highly nutritive alien grass which represents most of the
 184 rabbits’ diet in our study area (over 90% of the plant fragments found in pellets at the time of
 185 the year our study took place, Boussès et al. 1988). The studied area was fully searched for
 186 patches, which numbered 32.

187 In every patch, we collected all the faecal pellets (that were subsequently dried 4 days
 188 at 40°C – i.e., until their weight stopped decreasing – and weighed). Pellet count is a reliable
 189 method to assess rabbit abundance at the scale of the habitat (Palomares and Delibes 1997,
 190 Palomares 2001, Cabrera-Rodriguez 2006). At a finer scale, pellet counts index rabbits
 191 visitation level (Bakker et al. 2005). We thus expected more pellets (i.e., higher values of total
 192 dry weight) for patches displaying larger “domains of safety”, i.e., a larger surface without
 193 visual / physical barriers. In every patch, a single observer took the following measurements:

- 194 - The GPS coordinates. This allows us to subsequently statistically investigate the
 195 existence of a spatial structure in our dependent variable, the pellet total dry weight.
- 196 - The total number of burrows in a 20 meters diameter circle around the center of the
 197 patch. No fresh burrow (i.e., typically, with fresh pellets and / or clear evidence of
 198 passage) was present in the study area. Hence, we only considered these burrows as
 199 escape possibilities for the rabbit, as sometimes observed. The hypothesis that fresh
 200 burrows outside our study site (known as they were part of another protocol) may have
 201 impacted our results (namely, more rabbits closer to their inhabited burrows) was
 202 considered when we investigated the spatial structure of our dependent variable (see

below). The number of burrows is classically part of rabbit habitat selection studies (e.g., Palomares and Delibes 1997).

- The terrestrial distance (m) (i.e., bypassing a mound when applicable, as would do an escaping rabbit) to the closest burrow (as defined above).
- The number of “contact points” with *Poa annua* around the focal patch. Contact points were considered at 1, 3 and 5 m at every 45° around the center of the focal patch (i.e., n=24 in total). A proxy of the isolation of the focal patch of *Poa annua* was calculated as the frequency of contact points without *Poa annua*. We included this parameter because we hypothesized that the attraction of a patch could have been related to how it was isolated from other *Poa annua* spots.
- The distances (m) from the center of the patch to the closest mound and to the closest mound corner, inside the “domain of safety” (calculated as explained below). In addition to biological relevance (closest physical obstacle when escaping / closest terrestrial point a cat may hide), it allows us to compare the explicative power of our “domain of safety” with the one of the classical “distance to the closest cover” in explaining spatial variability in the pellet total dry weight.
- The total number of mound corners inside the domain of safety and the mean distance (m) to these corners.

Additionally, we recorded the “domain of safety” for each patch.

Measuring the “domain of safety”

From the center of the patch, the observer scanned exhaustively the 360° of the surroundings using a rangefinder including angle displays (Vector 1500 GMD). Each time a linear mound started and stopped, the distance from the center of the patch and the corresponding angle were recorded. When a mound did not appear linear, the measurements were recorded for

each of its linear segment. This gave us a set of triangles with an angle and the length of the two adjacent sides known, allowing the calculation of their surface. However, the sum of these surfaces would provide a poor proxy of the “domain of safety” experienced by a rabbit as above a certain distance mounds are not relevant proxies of danger anymore (e.g., too far away for a cat to ambush with a high chance of success or to represent a physical barrier when escaping). Further, considering such distant mounds may considerably increase the value of the “domain of safety”, thereby potentially masking biologically relevant differences between patches occurring at shorter distances. We thus calculated the “domain of safety” inside a theoretical circle. Considering such a circle further allowed us to deal with cases where no cover occurs before the horizon (a single case in our study area). We set the circle radius based on our field observations of hunting bouts by cats. Because the longest cat running bout towards a feeding rabbit we observed during this protocol and others was about 25 m, we first considered this distance. Then, in order to identify the radius of the theoretical circle with the highest explicative power, we computed the squared coefficient of correlation between the observed and the fitted values for models built with values of “domain of safety” calculated for theoretical circles of radiuses ranging from 1 to 150 m.

Depending on whether the mound falls entirely inside the circle, entirely outside the circle or was secant to it in one or two points, we used different formulas to calculate the corresponding surface, as explained Fig. 1A, B and C (see also the script allowing to compute the “domain of safety”, written in the R language and provided in Supplemental information file 2). The sum of these surfaces provides the “domain of safety”, expressed in m².

248 Statistical analyses

249 Since the pellet total dry weight exhibited significant **positive autocorrelation** (Moran's I =
250 0.111, $p < 0.001$, Fig. 2), we used generalized least squares (GLS) models to account for
251 spatial autocorrelation in model residuals (Selmi and Boulinier 2001). Different models of
252 spatial structure (assuming spherical, exponential and Gaussian structures) were fitted and the
253 best fitting model (exponential in all the cases) was defined using the Akaike information
254 criterion (Selmi and Boulinier 2001, Diniz-Filho et al. 2003).

255 We log transformed the pellet total dry weight to meet **residuals constant variance** and
256 normality assumptions. To avoid collinearity issues, we only considered models including
257 explanatory variables that were not significantly correlated (i.e., all $p > 0.14$). We did not
258 include interactions among explanatory variables given the small sample size. For patches
259 with no surrounding burrows ($n=7$), the variable “distance to closest burrow” was missing.
260 Hence, we re-ran the models without “closest burrow” to avoid artificially reducing sample
261 size when testing the other explanatory variables. **For these variables, we present these latter**
262 results. We proceeded in the same way for “distance to closest corner” ($n = 2$ patches with no
263 corner inside the “domain of safety”) and for “mean distance to corners” (same 2 patches).
264 We selected the final model by fitting the complete model and removing each term
265 successively. The significance of each term was determined by assessing the change in
266 deviance (i.e., Likelihood Ratio Test – LRT) against a Chi^2 distribution with the appropriate
267 degrees of freedom. For non significant variables considered in several models, we present the
268 maximum LR value and the corresponding minimum p-value and estimates. Estimates were
269 all computed on standardized variables (mean = 0, S.D. = 1) to allow comparisons of effect
270 sizes not dependent on measurement scale (Gelman and Hill 2007). Analyses were performed

in R 3.1.2 (R Core Team 2014) using the packages *ape* for spatial analyses and *nlme* for developing the models. The French Polar Research Institute approved this program (n°279).

Results

The surface of the “domain of safety” in a 25 m radius circle around the patch positively impacted the pellet total dry weight ($df = 1$, $LR = 9.264$, $p = 0.002$; estimates: intercept = 1.41 $\pm$ 0.20 S.E., slope = 0.51 $\pm$ 0.16 S.E.; Fig. 3): when the “domain of safety” increased from 500 to 1000 m² (observed range: 25.3 to 1646.1 m²), the predicted pellet total dry weight increased from 3.38 to 7.02 g.

The mean distance to mounds corners and, to a lesser extent, the distance to the closest corner were also positively related to the pellet total dry weight ($df = 1$, $LR = 4.721$, $p = 0.030$; estimates: intercept = 1.40 $\pm$ 0.23 S.E., slope = 0.39 $\pm$ 0.17 S.E. and $df = 1$, $LR = 3.776$, $p = 0.052$; estimates: intercept = 1.39 $\pm$ 0.24 S.E., slope = 0.35 $\pm$ 0.18 S.E., respectively). Finally, the total number of corners in the theoretical circle negatively impacted the pellet total dry weight ($df = 1$, $LR = 5.032$, $p = 0.025$; estimates: intercept = 1.42 $\pm$ 0.27 S.E., slope = - 0.37 $\pm$ 0.16 S.E.).

The other explanatory variables, including the distance to the closest cover item, were not retained in the final models and had smaller effect sizes as measured by standardized regression coefficients (distance to the closest mound: $df = 1$, $LR = 2.156$, $p = 0.142$; estimates: intercept = 1.44 $\pm$ 0.27 S.E., slope = 0.25 $\pm$ 0.17 S.E.; total number of burrows: $df = 1$, $LR = 0.247$, $p = 0.619$; estimates: intercept = 1.40 $\pm$ 0.19 S.E., slope = - 0.08 $\pm$ 0.14 S.E.; distance to the closest burrow: $df = 1$, $LR = 1.847$, $p = 0.174$; estimates: intercept = 1.27

293 +/- 0.51 S.E., slope = - 0.27 +/- 0.18 S.E. ; isolation: df = 1, LR = 1.014, p = 0.314; estimates:
294 intercept = 1.41 +/- 0.31 S.E., slope = - 0.15 +/- 0.15 S.E.).

295 **Fig. 4 revealed** that the biologically relevant distance for the radius of the theoretical
296 circle ranged between 19 and 29 m, in line with our field observations of hunting bouts of
297 rabbits by cats.

298

299 Discussion

300 We took advantage of a study area **allowing to consider** patches composed of a single
301 preferred plant species, displaying cover items of a single type (i.e., a single intrinsic
302 obstructive / protective ratio) and where predation risk arose from only one species, feral cats.
303 Our results strongly suggest that cats shape fine-scale habitat use by rabbits in the Kerguelen
304 archipelago. Fewer pellets were present in patches with smaller “domains of safety”, i.e., with
305 smaller visible area from the center of a 25 m radius theoretical circle around the patch, and
306 thus closer potential danger, and with greater proximity of physical barrier, and thus
307 restrained escape possibilities.

308 The “domain of safety”

309 The consideration of the “domain of safety” **helped at understanding** the role of the proximity
310 to cover in fine-scale habitat use by rabbits. With classical approaches, i.e., with the distance
311 to the “closest cover” (i.e., closest mound and / or corner) as an explanatory variable, the
312 conclusion of an absence of (or weak) differences between the patches in the amount of
313 pellets according to the proximity of cover would have emerged (i.e., no or weak effect of
314 closest mound or closest corner distance in our analyses, respectively). Yet, our results
315 strongly suggested that cover shaped habitat use by rabbits inside this habitat. The use of a

partial measure of the proximity to cover may explain the absence of significant results in studies investigating behavioral adjustments of prey in relation to cover while other studies in the same population report such an effect, depending on which particular cover item is considered (e.g., Pays et al. 2012, 2014). Investigating the **explicative power** of our proxy in these prey-predators-habitats systems, including **large scale covers** such as tree lines, may be informative. Moreover, our method requires no particular expertise – we provide a R-script to implement the formulas used to calculate the surfaces (see Supplemental information file 2). A **rangefinder including angle displays may be expensive**, but this can be substituted by a basic model (or even by a tape measure) and a basic compass. A limit of our method is the subjectivity **inherent to the classification of a portion of the cover item as linear or no linear**. However, this subjectivity is more pronounced when the cover is far, i.e., when the rabbit also faces visual limitations.

Remote sensing technologies, such as terrestrial LiDAR (Light Detection And Ranging), can provide accurate proxies of vegetation structure (Lefsky et al. 2002), including **aerial parts**. Canopy is not concerned by our 2D method, although similar approaches might be used concomitantly to ours for prey also facing **aerial predators (or attacking from trees)** and / or escaping by flying towards the sky or aerial cover, e.g., Kopp et al. 1998 (see also alternative approaches including those based on hemispherical photography, Jennings et al. 1999). While most of the studies investigating the use of LiDAR in ecological aspects come from forestry or remote sensing literature (Vierling et al. 2008), recent results suggest interesting applications in behavioral ecology (Olsoy et al. 2015). Yet, LiDAR technologies require expensive equipment and high level of expertise (Olsoy et al. 2015). Moreover, many more studies are needed to assess to which extent this approach could reliably index the

complex, multi-scales and contrasting properties of cover from a prey, and thus from a predator, perspective.

Rabbits, cats and cover

The fact that the “domain of safety” better explained the variability in pellets quantity among patches than any of the proxies based on mound corners (number of corners, mean distance to corners and distance to the closest corner) suggests that the role of mounds as physical barriers when escaping may be an important determinant of overall risk perception by rabbits. Alternatively, this may also indicate that cats may hide at the top of the mounds and not solely behind corners, although this was never observed.

Beside the unquestionable role of predation pressure as a driver of the pattern we report, we cannot rule out the influence of non exclusive additional selective pressures. Reduced visibility may also lead to decreased opportunity to monitor conspecifics while foraging. Although this may again indirectly relate to predation risk (loss of information about conspecifics vigilance / escape behaviour and decreased “confusion effect” as other prey individuals are also less visible to an attacking predator), this is further expected to decrease foraging and social opportunities (e.g., localization of high quality patches, scrounging, gathering information about potential mates / competitors) (Beauchamp 2014 for a review, Monclús and Rödel 2008 for rabbits). Finally, high values of “domain of safety” are also expected to mechanistically lead to more foraging opportunities (i.e., an increased overall surface of edible plants) and thus to an increased attractiveness, i.e., to an increased of overall time spent foraging.

Because we selected patches with similar level of foraging pressure (grazed sward of similar height), and in a context of no other herbivore species in the study area, the difference

in pellet quantity between patches is not a consequence of a difference in exploitation level among patches. This could rather be explained by rabbits avoiding long feeding bouts in patches displaying low values of “domain of safety” (thereby decreasing dropping occurrence) in order to reduce (1) the probability of being spotted by a cat in these risky places and / or, if spotted, (2) the time available for a cat’s stalking bout. Hence, the similar grazing pressure among our focal patches would be the consequence of an increased number of shorter foraging bouts in patches displaying poor visibility / escape possibilities or of the same number of foraging bouts with an increased foraging speed (through bite rate / size) and thus a decreased exposure time in these patches (Lima and Dill 1990). Moreover, additional activities such as grooming or playing may also occur in safer places (e.g., Cowlshaw 1997, Blumstein 1998), leading to an increased in the overall amount of time spent and thus in dropping probability. Further studies could also investigate the role of additional parameters in relation to the patch “domain of safety” values such as vigilance behavior in relation to the magnitude of its foraging costs or its social component (e.g. Fortin et al. 2004a,b, Blanchard and Fritz 2007, Monclús and Rödel 2008) or foraging time budget according to variation in predation pressure level (Lima and Dill 1990).

Previous studies on habitat selection by rabbits in relation to cover reported contrasted results, echoing with the ambivalent properties of cover and with the large range of predators rabbits face in their worldwide distribution. While the protective function of cover in rabbits habitat selection patterns has been emphasized by several studies (Villafuerte and Moreno 1997, Dellafiore et al. 2014), leading to a greater use of patches farther away from cover when predation pressure is lower (Banks et al. 1999), cover may also be avoided when it impairs visual field (Moreno et al. 1996). The heterogeneity among studies may further be explained by the use of the partial “distance to cover” to index proximity to cover, widespread in this

species also (e.g., Moreno et al. 1996, Villafuerte and Moreno 1997). Moreover, the obstructive / protective ratio of a given cover for a given population may vary according to the period of the day (Moreno et al. 1996): rabbits have been reported to preferentially feed closer to cover during the day (hiding from birds of prey) than at night (avoiding stalking carnivorous mammals).

A cover item displaying total visual and physical obstructions, as occurring in our study area, is probably uncommon. Assessing the obstructive / protective ratio and thus the risk perception associated to a cover item may generally require a measure of visual and physical obstruction (see below). Moreover, rabbits faced a single type of cover item in our study area, which is probably also uncommon. The calculation of the “surface to the cover items” should thus commonly be performed by item type. Cover items can all be of the same nature (e.g., overall protective / obstructive properties ratio > 1) but still differ in their intensity of protective *versus* obstructive properties, or can be of opposite nature (e.g., some with an overall protective / obstructive properties ratio > 1 and some others with a ratio < 1): for example, a feeding patch for a mountain ungulate in the vicinity of a cliff and of several shrubs and rocks may be characterized by a “domain of safety” (overall surface to the shrubs and rocks) and a “domain of risk” (overall surface to the cliff) if the individuals face stalk-and-ambush predators unable to reach their prey in a cliff.

Further than “proximity”

Our study focused on how proximity to cover (e.g., a tree line) drives risk perception. What happens if the focal point is inside the cover (e.g., behind the tree line, inside the forest)?

(1) Where finer-scale cover items are present around the focal patch (e.g., trunks, bushes, rock and anything that may impair the prey and / or the predator ability to see and / or

move), the same questions and method we developed here may be of interest. Still, analyses could include an additional explanatory variable, i.e., “habitat type”, and investigate how risk perception is shaped by the “surface to the cover items”, in relation to “habitat type” (with “closed” as a modality of the factor “habitat type” in our example - “habitat type” might also be computed as a covariate, see below). In this approach, “habitat type” may carry important large-scale information for the prey, that are not considered *per se* in our “surfaces to the cover items” approach, such as the probability of presence of whatever predator, which is a different aspect than the probability of “detection” of this predator.

(2) Where the focal point is surrounded by diffuse vegetation, such as thin and soft trunks in young forest, no cover items (i.e., individually impairing the prey and / or the predator ability to see and / or move) can be identified, so that no distance can be measured. In this case neither our method nor the classic “distance to the closest cover item” can be directly performed. In this context, studies typically quantified “visual obstruction”, using several methods based on pole (Robel 1970) or cover board (Nudd 1977) approaches (Limb et al. 2007). Nevertheless, where a focal point is surrounded by sectors of diffuse vegetation of different visual obstruction levels as assessed by classical methods, a theoretical circle can still be defined and the corresponding area can still be computed following formulas given in Fig. 1B(1), leading to a more detailed picture of the “visual obstruction” in the surroundings of a focal point. Yet, while this approach would provide an interesting way for a more in-depth quantification of vegetation structure in such habitats, this would give a quite incomplete proxy of “cover” in a landscape of fear context. Risk perception is shaped by many different visual components of cover, so that a measure of an overall “visual obstruction” of a given habitat, even with the refinement of a measure performed at the height of the prey, would be insufficient. The visual component of a cover in a predator(s) – prey

context also depends on the height of the predator(s) involved (e.g., a mouse may be preyed upon by predators of the height of a snake or a heron: the relevance of cover items as visual barriers for a given prey depends on the relative abundance of the predators involved in the system). Furthermore, “visual obstruction” also refers to the predator side (i.e., the visual protective property of cover from the prey perspective), so that the measure should also be performed for the size of the relevant predator(s), given the size of the prey, directed towards the focal patch. Only few studies have tried to decouple visual protective *versus* obstructive properties (i.e., concealment *versus* visibility) of cover (e.g., Camp et al. 2012). Finally, beside visual aspects, the obstructive properties of cover in a landscape of fear context also encompass physical obstruction (Schooley et al. 1996). Visual and physical obstructions are not necessary related (e.g., a dense patch of tall grasses and a patch of cactus of the same dimensions may have the same visual obstruction but contrasted physical obstructions). A metric of physical obstruction of a cover in respect to a particular predators-prey system is a clear technical challenge.

Acknowledgments

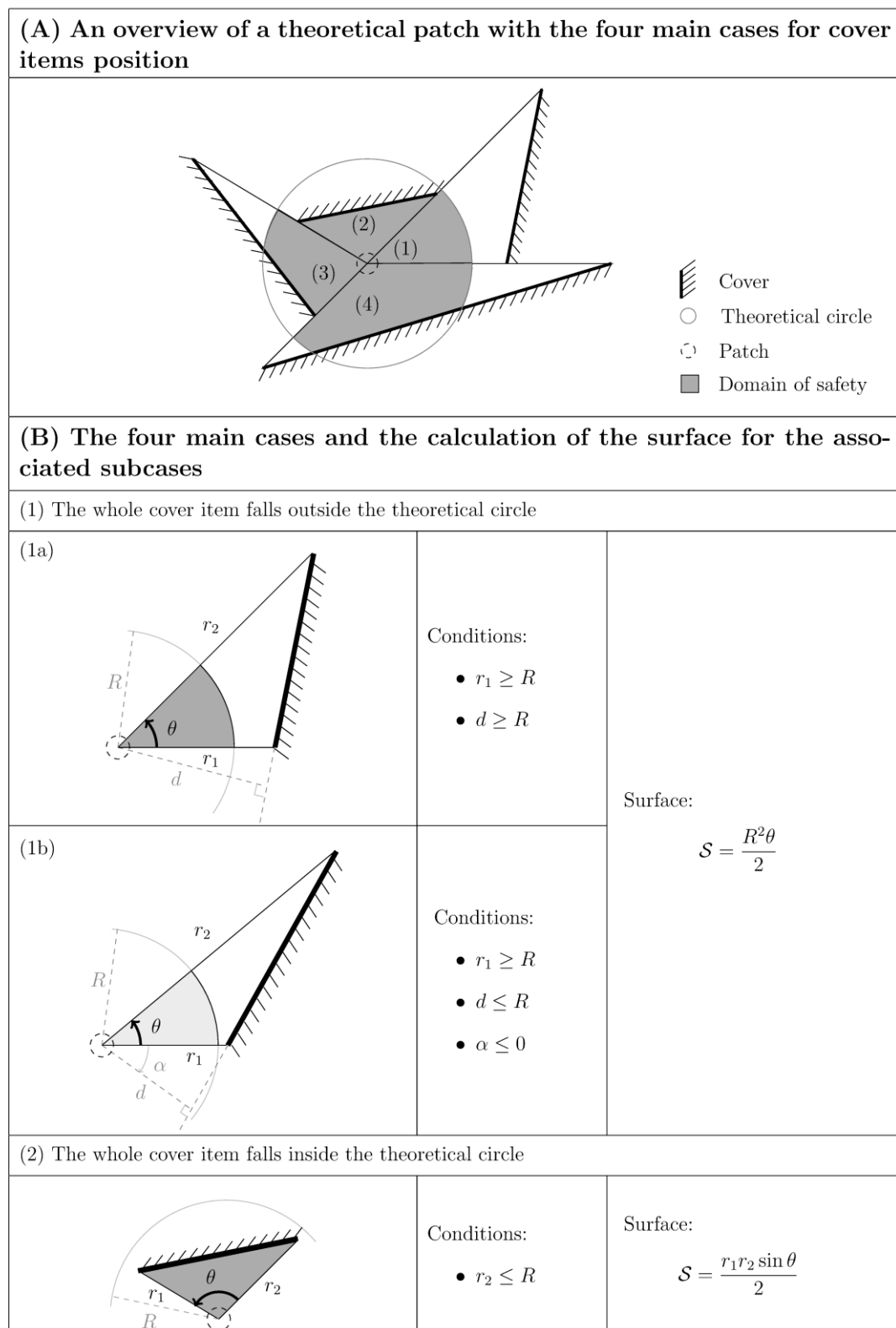
We thank Fabien Egal, Johan Chervaux and Adrien Tavernier for field assistance and Gaël Grenouillet for help with spatial analyses.

451 Fig.1

452 The different potential cases for **cover items position** in relation to the theoretical circle
 453 around the patch and the corresponding formulas for the calculation of the surfaces (S in (B))
 454 between the center of the patch and the item or the theoretical circle. The “domain of safety”
 455 is calculated by summing all these surfaces (see also Supplemental information file 2). Cases
 456 number (1) to (4) in (A) refer to the **same cases number** in (B). Dark grey for surfaces
 457 represented in (B) is for sub-cases already represented in (A), light grey for other sub-cases of
 458 the four main cases. Inequalities in (B) are not strict: for limiting cases, the different
 459 corresponding formulas can be used and lead to the same results. All the angles are counter
 460 clockwise. R is the radius of the theoretical circle. D, α , β_1 and β_2 are defined in (C). We set
 461 $r_1 \leq r_2$. The only **requested** field measurements are r_1 , r_2 and θ .

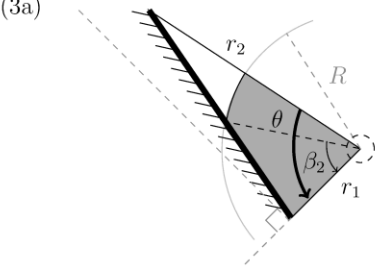
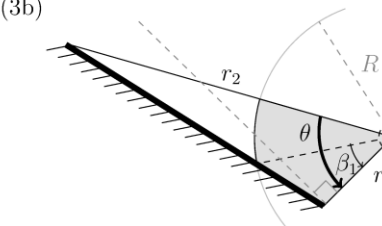
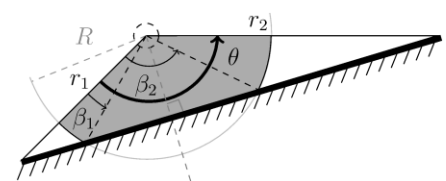
462

463 Fig.1 (continued)



464

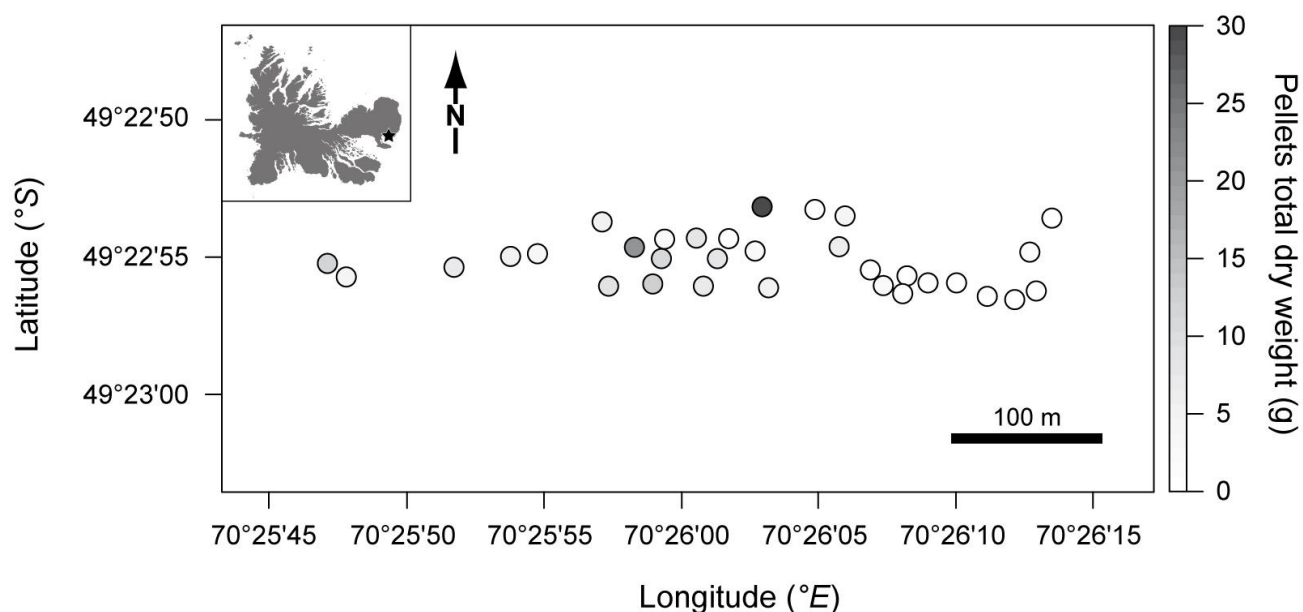
465 Fig.1 (continued)

(3) The cover item intersects the theoretical circle in one point		
(3a) 	Conditions: • $r_1 \leq R$ • $r_2 \geq R$ • $r_2 \cos \theta \leq r_1$	Surface: $S = \frac{R^2(\theta - \beta_2)}{2} + \frac{Rr_1 \sin \beta_2}{2}$
(3b) 	Conditions: • $r_1 \leq R$ • $r_2 \geq R$ • $r_2 \cos \theta \geq r_1$	Surface: $S = \frac{R^2(\theta - \beta_1)}{2} + \frac{Rr_1 \sin \beta_1}{2}$
(4) The cover item intersects the theoretical circle in two points		
	Conditions: • $r_1 \geq R$ • $d \leq R$ • $\alpha \geq 0$	Surface: $S = \frac{R^2(\theta - \beta_2 + \beta_1)}{2} + \frac{R^2 \sin(\beta_2 - \beta_1)}{2}$
(C) Notations and formulas		
• Minimal distance (altitude length) between the center of the patch and the cover item: $d = r_1 r_2 \frac{ \sin \theta }{\sqrt{r_1^2 + r_2^2 - 2r_1 r_2 \cos \theta}}$ • 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 item and the theoretical circle: $\beta_1 = \arccos \frac{r_1 r_2^2 \sin^2 \theta + \sqrt{(R^2(r_1^2 + r_2^2 - 2r_1 r_2 \cos \theta) - r_1^2 r_2^2 \sin^2 \theta)(r_2 \cos \theta - r_1)^2}}{R(r_1^2 + r_2^2 - 2r_1 r_2 \cos \theta)}$ $\beta_2 = \arccos \frac{r_1 r_2^2 \sin^2 \theta - \sqrt{(R^2(r_1^2 + r_2^2 - 2r_1 r_2 \cos \theta) - r_1^2 r_2^2 \sin^2 \theta)(r_2 \cos \theta - r_1)^2}}{R(r_1^2 + r_2^2 - 2r_1 r_2 \cos \theta)}$		

466

Fig. 2

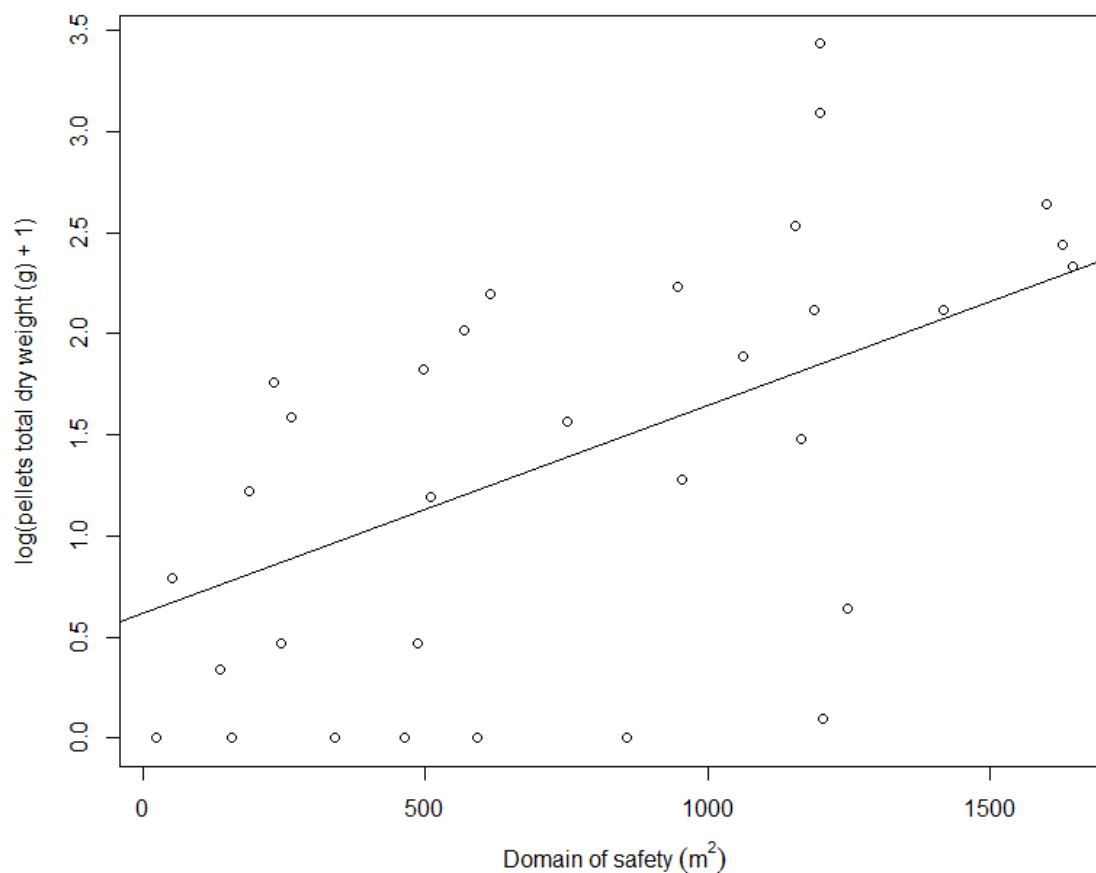
Pellet total dry weight measured in the studied patches according to their spatial position. The hypothesis that the proximity to fresh burrows partly explains the spatial pattern reported here might be relevant as fresh burrows were localized at about 100 meters north-west from the boarder of the study area, i.e., on the side of the patches with higher values in pellet total dry weight.



475 Fig. 3

476 The positive relationship between the $\log(\text{pellet total dry weight (g)} + 1)$ and the “domain of
477 safety” (in m^2) computed for a theoretical circle with a 25 m radius.

478

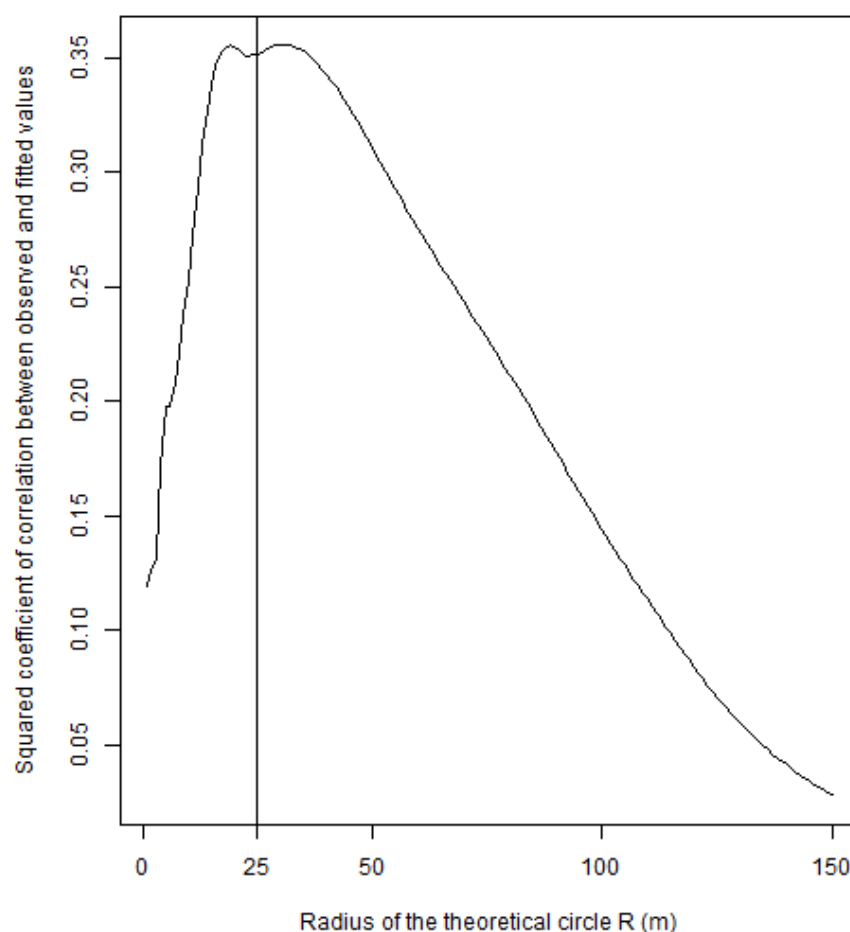


479

480 Fig. 4

481 Squared coefficients of correlation between the observed and the fitted values for models built
 482 with values of “domain of safety” calculated for theoretical circles of radiuses (R in Fig. 1, in
 483 m) ranging from 1  50 m and plotted on x axis. The biologically relevant distance ranges
 484 between 19 and 29 m, in line with our field observations of cats hunting bouts.

485



486

487 **References**

- 488 Bakker, E. S. et al. 2005. Experimental manipulation of predation risk and food quality: effect
489 on grazing behaviour in a central-place foraging herbivore. – *Oecologia* 146: 157–167.
- 490 Banks, P. B. et al. 1999. Behavioural, morphological and dietary response of rabbits to
491 predation risk from foxes. – *Oikos* 85: 247–256.
- 492 Beauchamp, G. 2014. *Social Predation*. – Elsevier.
- 493 Blanchard, P. and Fritz, H. 2007. Induced or routine vigilance while foraging. – *Oikos* 116:
494 1603–1608.
- 495 Blumstein, D. T. 1998. Quantifying predation risk for refuging animals: a case study with
496 golden marmots. – *Ethology* 104: 501–516.
- 497 Bowyer, R. T. et al. 1999. Birth-site selection by Alaskan moose: maternal strategies for
498 coping with a risky environment. – *J. Mammal.* 80: 1070–1083.
- 499 Boussès, P. et al. 1988. Rôle du facteur trophique sur la biologie des populations de lapins
500 (*Oryctolagus cuniculus* L.) des Iles Kerguelen. – *Terre Vie – Rev. Ecol. A* 43: 329–
501 343.
- 502 Burger, J. et al. 2000. Factors affecting vigilance in springbok: importance of vegetative
503 cover, location in herd, and herd size. – *Acta Ethol.* 2: 97–104.
- 504 Cabrera-Rodriguez, F. 2006. Microhabitat selection of the European rabbit on La Palma,
505 Canary Islands, Spain. – *Acta Theriol.* 51:435–442.
- 506 Camp, M. J. et al. 2012. When to run and when to hide: the influence of concealment,
507 visibility, and proximity to refugia on perceptions of risk. – *Ethology* 118: 1010–1017.
- 508 Caro, T. 2005. *Antipredator defenses in birds and mammals*. – University of Chicago Press.
- 509 Chapuis, J. L. et al. 1994. Alien mammals, impact and management in the French subantarctic
510 islands. – *Biol. Conserv.* 67: 97–104.

511 Courchamp, F. et al. 2003. Mammal invaders on islands: impact, control and control impact. –
 512 Biol. Rev. 78: 347–383.

513 Cowlshaw, G. 1997. Refuge use and predation risk in a desert baboon population. Anim.
 514 Behav. 54: 241–253.

515 Dellafiore, C. M. et al. 2014. Seasonal habitat use by the European rabbit (*Oryctolagus*
 516 *cuniculus*) in a coastal dune system in SW Spain. – Anim. Biodiv. Conserv. 37: 233–
 517 242.

518 Diniz-Filho, J. A. F. et al. 2003. Spatial autocorrelation and red herrings in geographical
 519 ecology. – Global Ecol. Biogeogr. 12: 53–64.

520 Fortin, D. et al. 2004a. Foraging costs of vigilance in large mammalian herbivores. Oikos
 521 107:172 –180.

522 Fortin, D. et al. 2004b. Multi-tasking by mammalian herbivores: overlapping processes during
 523 foraging. Ecology 85:2312–2322.

524 Gelman, A. and Hill, J. 2007. Data analysis using regression and multilevel/hierarchical
 525 models. Cambridge University Press.

526 Götmark, F. and Hohlfält, A. 1995. Bright male plumage and predation risk in passerine birds:
 527 are males easier to detect than females? – Oikos 74: 475–484.

528 Kopp, S. D. et al. 1998. Habitat selection modeling for northern bobwhites on subtropical
 529 rangeland. J. Wildlife Manage. 63: 884–895.

530 Krause, J. and Ruxton, G. D. 2002. Living in groups. – Oxford University Press.

531 Lazarus, J. and Symonds, M. 1992. Contrasting effects of protective and obstructive cover on
 532 avian vigilance. – Anim. Behav. 43: 519–521.

533 Laundré, J. W. et al. 2010. The landscape of fear: ecological implications of being afraid.
 534 Open Ecol. J. 3: 1–7.

- 535 Limb, R. F. et al. 2007. Digital photography: reduced investigator variation in visual
- 536 obstruction measurements for southern tallgrass prairie. – *Rangeland Ecol. Manage.*
- 537 60: 548–552.
- 538 Jaksic, F. M. and Soriguer, R. C. 1981. Predation upon the European rabbit (*Oryctolagus*
- 539 *cuniculus*) in Mediterranean habitats of Chile and Spain: a comparative analysis. – *J.*
- 540 *Anim. Ecol.* 50: 269–281.
- 541 Jennings, S. B. et al. 1999. Assessing forest canopies and understory illumination: canopy
- 542 closure, canopy cover and other measures. – *Forestry* 72: 59–74.
- 543 Lefsky, M. A. et al. 2002. Lidar Remote Sensing for Ecosystem Studies. – *BioScience* 52: 19–
- 544 30.
- 545 Lima, S. L. 1990. Protective cover and the use of space: different strategies in finches. –
- 546 *Oikos* 58: 151–158.
- 547 Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a
- 548 review and prospectus. – *Can. J. Zool.* 68: 619–640.
- 549 Lombardi, L. et al. 2003. Habitat-related differences in rabbit (*Oryctolagus cuniculus*)
- 550 abundance, distribution, and activity. – *J. Mammal.* 84: 26–36.
- 551 Monclús, R. and Rödel, H. G. 2008. Different forms of vigilance in response to the presence
- 552 of predators and conspecifics in a group living mammal, the European Rabbit. –
- 553 *Ethology* 114: 287–297.
- 554 Moreno, S. et al. 1996. Cover is safe during the day but dangerous at night: the use of
- 555 vegetation by European wild rabbits. – *Can. J. Zool.* 74: 1656–1660.
- 556 Morgantini, L. E. and Hudson, R. J. 1985. Changes in diets of wapiti during a hunting season.
- 557 – *J. Range Manage.* 38: 77–79.
- 558 Murray, D. L. et al. 1995. Hunting behaviour of a sympatric felid and canid in relation to
- 559 vegetative cover. – *Anim. Behav.* 50: 1203–1210.

- 560 Mysterud, A. and Østbye, E. 1999. Cover as a habitat element for temperate ungulates: effects
561 on habitat selection and demography. – Wildlife Soc. B 27: 385–394.
- 562 Newberry, R. C. and Shackleton, D. M. 1997. Use of visual cover by domestic fowl: a
563 Venetian blind effect? Anim. Behav. 54: 387–395.
- 564 Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. – Wildlife Soc. B 5:
565 113–117.
- 566 Olsoy, P. J. et al. 2015. Fearscape: mapping functional properties of cover for prey with
567 terrestrial LiDAR. – BioScience 65: 74–80.
- 568 Palomares, F. and Delibes, M. 1997. Predation upon European rabbits and their use of open
569 and closed patches in Mediterranean habitats. – Oikos 80: 407–410.
- 570 Palomares, F. 2001. Comparison of 3 methods to estimate rabbit abundance in a
571 Mediterranean environment. – Wildlife Soc. B 29: 578–585.
- 572 Pays, O. et al. 2012. Detecting predators and locating competitors while foraging: an
573 experimental study of a medium-sized herbivore in an African savanna. – Oecologia
574 169: 419–430.
- 575 Pays, O. et al. 2014. On the advantages of mixed-species groups: impalas adjust their
576 vigilance when associated with larger prey herbivores. – Ethology 120: 1207–1216.
- 577 Pontier, D. et al. 2002. The diet of feral cats (*Felis catus* L.) at five sites on the Grande Terre,
578 Kerguelen archipelago. – Polar Biol. 25: 833–837.
- 579 R Core Team. 2014. R: A language and environment for statistical computing. R foundation
580 for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- 581 Robel, R. J. et al. 1970. Relationships between visual obstruction measurements and weight of
582 grassland vegetation. – J. Range Manage. 23: 295–297.
- 583 Schooley, R. L. et al. 1996. Can shrub cover increase predation risk for a desert rodent? –
584 Can. J. Zool. 74: 157–163.

- 585 Selmi, S. and Boulinier, T. 2001. Ecological biogeography of Southern Ocean Islands: the
586 importance of considering spatial issues. – *Am. Nat.* 158: 426–437.
- 587 Stratmann, A. and Taborsky, B. 2014. Antipredator defences of young are independently
588 determined by genetic inheritance, maternal effects and own early experience in
589 mouthbrooding cichlids. – *Funct. Ecol.* 28: 944–953.
- 590 Tchabovsky, A. V. et al. 2001. The effect of vegetation cover on vigilance and foraging
591 tactics in the fat sand rat *Psammomys obesus*. – *J. Ethol.* 19: 105–113.
- 592 Vierling, K. T. et al. 2008. Lidar: shedding new light on habitat characterization and
593 modeling. – *Front. Ecol. Environ.* 6: 90–98.
- 594 Villafuerte, R. and Moreno, S. 1997. Predation risk, cover type, and group size in European
595 rabbits in Doñana (SW Spain). – *Acta Theriol.* 42: 225–230.