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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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Abstract

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, making its impact on risk perception complex and context – dependent, and from the choice of the proxy used to measure cover in the field, which leads 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 cat *Felis catus* predation on Kerguelen archipelago. We assess how cover shapes risk perception in prey and develop an easily implementable and inexpensive field method to index proximity to cover. In contrast to protocols considering the "distance to the closest cover item", we focus on the overall "surface to the cover items". We show that rabbit' fine – scale habitat use is clearly related to our measure, in accordance with our hypothesis of cover being a source of risk in this predator – prey – habitat system. In contrast, classical measures of proximity to cover are not retained in the final predictive models of habitat use. 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.

Introduction

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

First, cover is a (visual/physical) barrier for the focal individual prey but also for its predator(s). Hence, the ratio between its contrasting obstructive (i.e., prevents the prey to see or escape from the predator) and protective (i.e., prevents the predator to see or attack the prey) properties (Lazarus and Symonds 1992, Mysterud and Østbye 1999) (i.e., the overall risk perception), is highly specific to a predator(s) – prey system. Obviously, this obstructive/protective ratio depends on the intrinsic physical properties of the cover itself (its dimensions, opacity etc.), in relation to, among others, the physical characteristics (body size, visual acuity etc.) and escape/hunting tactics of the focal prey and its predator(s) (e.g., Lima 1990, Murray et al. 1995, Newberry and Shackleton 1997). However, intra – specific variability

is also further expected because individuals 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 in relation to a specific cover type (e.g., Götmark and Hohlfält 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.

The second reason why the role of cover for prey remains ambivalent arises from field measurements. They are probably usually too basic to provide biologically relevant proxies of risk perception. At any given time and for a given predator(s) – 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 dimension of the cover the prey faces. Although the shortest distance to cover is of importance as this gives in particular 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 small patch of trees or 10 meters away from tree line.

(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.

There is thus a need for a measure of *all* distances between the focal patch and covers in the surroundings (i.e., a 360° approach, see Metcalfe 1984 and Gómez – Serrano and López – López 2014), i.e., a need for a *surface*. We suggest that such a metric would provide a more reliable measure of the "proximity to cover" and thus, of risk perception, than the commonly used "distance to the closest cover item". In the present paper, our aims were to (1) develop such a method, from field measurements to its geometrical aspects and (2) use this metric 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.

Because of the complex nature of cover, one of the potential issues in studies relating animal behavior to cover is to infer cover property *post hoc*, i.e., from its effect on animal behavior. This might lead to circularity if this effect is seen as an adaptive response to the property of cover (Lazarus and Symonds 1992). Instead, cover properties, and thus the way it is expected to trigger risk perception in prey, should arise from the knowledge of the system (attack/escape tactics of the predator/prey, physical properties of the cover). Hence, making a prediction 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. Yet, patch choice by prey is also shaped by foraging profitability (Lima and Dill 1990). This leads to complex situations as cover may be associated with food resources (e.g., Morgantini and Hudson 1985): cover may impact food resources characteristics (e.g., plants growth and composition impacted by the amount of shade or the presence of specific plants) or cover may be food (e.g., Mysterud and Østbye 1999, Dellafiore et al. 2014). In the present paper, we took advantage of a simple predator – prey – habitat system allowing us to hypothesize that predation threat was the main driving force of habitat use by rabbits. Given the specific characteristics of the system, we predicted that rabbits should avoid patches with high proximity to cover.

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 m^2 area covered by mounds lower than 2m 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 flat topography, covered with dense swards of *Acaena magellanica*.

At the same period, we also censused active burrows in a 0.73 km^2 area including the patches used in this study. We found 51 burrows. Although we do not know the relationship between the number of active burrows and the population size in this habitat, previous published relationships led to about 22 rabbits (i.e., about 30 rabbits / km^2) (Ballinger and Morgan 2002). Fifteen more active burrows were present outside the 0.73 km^2 area, 800 m away from the study area.

Predicting the effect of proximity to cover on habitat use by rabbits

The following characteristics of our system allowed us to confidently assess the role of cover in shaping risk perception in rabbits.

- Food resources. We selected patches of a single preferred plant species, *Poa annua* (Chapuis et al. 1994). This is a highly nutritive alien grass which represents most of rabbit diet in our study area (over 90% of the plant fragments found in pellets at the time of the year our study took place, Boussès et al. 1988). As the study area is relatively restricted, meteorological and

152 edaphic conditions are probably very similar. Moreover, *Poa annua* was heavily grazed (1 – 2
153 cm high) throughout the study area. Hence, because patches were likely to be similar in food
154 quality and quantity, the effect of cover was not confounded by foraging profitability. Finally,
155 rabbits face no interspecific competition for feeding resources in this habitat (in particular,
156 reindeer *Rangifer tarandus* have not been observed in the study area).
157 - Predators. Predation by subantarctic skua (*Catharacta skua lönnbergi*) on rabbits occurs
158 on the Kerguelen archipelago, but mostly on small islands (Chapuis et al. 1994) and on
159 young/sick rabbits (myxomatosis virus introduced in 1950's to control populations). Given that
160 our study site was on the mainland and in a closed area (i.e., see below and Supplemental
161 information file 1), that no skuas nested around, that no rabbits were observed or killed (as part
162 of other protocols) with apparent signs of myxomatosis, that our study took place before the birth
163 period, that cats were observed daily in our study area and finally that rabbits are the primary
164 prey of cats in Kerguelen archipelago (Pontier et al. 2002), we believe that predation pressure
165 experienced by rabbits in this habitat is mostly due to cats. This contrasts with other studies on
166 rabbits, and probably on other prey species, where predators are often diverse. Our field
167 observations of cats hunting bouts revealed that cats are stalk – and – ambush predators
168 (although they also visit burrows). A foraging rabbit is clearly at risk if surprised by a cat, while
169 an early visual detection of the cat allows escape, especially in open areas (i.e., with no physical
170 barriers).
171 - Cover types. We focused on a habitat with a single type of cover: earth mounds (i.e.,
172 visually opaque and physically impenetrable, see Supplemental information file 1) and
173 considered as "cover item" any mound higher than 20 cm (i.e., hiding an ambushed cat to a
174 rabbit even in an upright posture; and hiding a rabbit, except in an upright posture, for a cat).

Yet, most of the mounds were taller than 1 m high. Cats may attack straight from a mound's corner, but also from behind the mound (for smaller ones) or possibly from their top (for bigger ones).

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 intrinsic refuge property – once potential burrows (see below) are statistically accounted for) than protective (rabbits hidden from cats by the cover). Accordingly, the overall "surface to the cover items", i.e., the (visually and physically) unobstructed area, was referred to as a "domain of safety" (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".

"Patch" characterization and data collection

We defined a "patch" as a circular area with a 2m diameter, covered exclusively with *Poa annua*, whose center was distant by at least 20 m from the center of another patch. The studied area was fully searched for patches, which numbered 32.

In every patch, we made a one – time collection of all the faecal pellets, thereby assuming that the disappearance time of pellets was not related to the variables we considered. We also kept the pellet collection time very short (2 days) to reduce extra droppings occurrences over the study period. Pellets were subsequently dried for 4 days at 40°C – i.e., until their weight stopped decreasing – and weighed. Pellet count is a reliable method to assess rabbit abundance at the scale of the habitat (Palomares and Delibes 1997, Palomares 2001, Cabrera-Rodriguez 2006). At a finer scale, pellet counts have been shown to index rabbits visitation level (Bakker et al. 2005).

We thus expected more pellets (i.e., higher values of total dry weight) for patches displaying larger "domains of safety", i.e., a larger surface without visual/physical barriers.

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

- The GPS coordinates. This allows us to subsequently statistically investigate the existence of a spatial structure in our dependent variable, the pellet total dry weight.
- The total number of burrows within a 20m diameter circle around the center of the patch. There was no fresh burrow (i.e., typically, with fresh pellets and/or clear evidence of passage) in the study area. Yet, we recorded these old burrows as they represent escape possibilities for the rabbit, as sometimes observed. The hypothesis that fresh burrows outside our study site (whose localization was known as they were part of another protocol) may have impacted our results (namely, more rabbits closer to their inhabited burrows) was 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, in the way a rabbit would escape) to the closest burrow (as defined above).
- The number of "contact points" with *Poa annua* around the focal patch. Contact points referred to position on the ground at 1, 3 and 5 m every 45° from the center of the focal patch (i.e., n=24 in total for each patch). A proxy of the isolation of the focal patch of *Poa annua* was then 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 positively related to how it was isolated from other *Poa annua* spots or conversely, that patches surrounded by a high overall *Poa annua/Acaena* ratio could have

been more attractive for rabbits. Moreover, this measure allowed us to investigate the hypothesis that risk perception would be increased in case of abundant *Acaena* around the focal patch if this impaired a rabbit's visual field when feeding head down.

- The distances (m) from the center of the patch to the closest mound and to the closest mound's 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 predictive 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 rectilinear mound (i.e., forming a straight line) started and stopped, the distance from the center of the patch and the corresponding angle were recorded. When a mound did not appear rectilinear, the measurements were recorded for each of its rectilinear segment. This gave us a set of triangles with an angle and the length of the two adjacent sides, 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 (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 behavior by cats. Because the longest cat course towards a feeding rabbit we observed was about 25 m, we first considered this distance. Then, in order to identify the radius of the theoretical circle with the highest predictive 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 with radiuses ranging from 1 to 150 m.

Depending on whether the mound fell entirely inside the circle, entirely outside the circle or was secant 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 used 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", ranging from 25.3 to 1646.1 m^2.

Statistical analyses

Since the pellet total dry weight exhibited significant positive autocorrelation (Moran's I = 0.111, $p < 0.001$, Fig. 2), we used generalized least squares (GLS) models to account for spatial autocorrelation in model residuals (Selmi and Boulinier 2001). Different models of spatial structure (assuming spherical, exponential and Gaussian structures) were fitted and the best

fitting model (exponential in all the cases) was defined using the Akaike information criterion (Selmi and Boulinier 2001, Diniz-Filho et al. 2003).

We log transformed the pellet total dry weight to meet the assumptions of residuals constant variance and normality. To avoid collinearity issues, we only considered models including explanatory variables that were not significantly correlated (i.e., all $p > 0.14$). We did not include interactions among explanatory variables given the small sample size. For patches with no surrounding burrows (n=7), the variable "distance to closest burrow" was missing. Hence, we first tested the effect of this variable on a sub – sample and then re –ran the models without "closest burrow" to avoid artificially reducing sample size when testing the other explanatory variables. We proceeded in the same way for "distance to closest corner" (n = 2 patches with no corner inside the "domain of safety") and for "mean distance to corners" (same 2 patches). We selected the final model by fitting the complete model and removing each term successively. The significance of each term was determined by assessing the change in deviance (i.e., Likelihood ratio Test – LRT) against a Chi^2 distribution with the appropriate degrees of freedom. For non significant variables considered in several models, we present the maximum LR value and the corresponding minimum p-value and estimates. Estimates were all computed on standardized variables (mean = 0, S.D. = 1) to allow comparisons of effect 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 (number 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 ± 0.20 S.E., slope = 0.51 ± 0.16 S.E.; Fig. 3): when the "domain of safety" increased from 500 to 1000 m^2, the predicted pellet total dry weight increased from 3.38 to 7.02 g.

The mean distance to mound 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 ± 0.23 S.E., slope = 0.39 ± 0.17 S.E. and df = 1, LR = 3.776, p = 0.052; estimates: intercept = 1.39 ± 0.24 S.E., slope = 0.35 ± [illegible] 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 ± 0.27 S.E., slope = - 0.37 ± 0.16 S.E.).

The other explanatory variables, including the distance to the closest mound, 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 ± 0.27 S.E., slope = 0.25 ± 0.17 S.E.; total number of burrows: df = 1, LR = 0.247, p = 0.619; estimates: intercept = 1.40 ± 0.19 S.E., slope = - 0.08 ± 0.14 S.E.; distance to the closest burrow: df = 1, LR = 1.847, p = 0.174; estimates: intercept = 1.27 ± 0.51 S.E., slope = - 0.27 ± 0.18 S.E. ; isolation: df = 1, LR = 1.014, p = 0.314; estimates: intercept = 1.41 ± 0.31 S.E., slope = - 0.15 ± 0.15 S.E.).

Finally, the biologically relevant distance for the radius of the theoretical circle ranged between 19 and 29 m, in line with our field observations of cat hunting behaviors (Fig. 4).

Discussion

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

The "domain of safety"

The consideration of the "domain of safety" helped to understand the role of the proximity to cover in fine – scale habitat use by rabbits. With classical approaches, i.e., with the distance to the "closest cover" (i.e., closest mound or corner and thus shortest time lag before being predated and shortest distance before being blocked/able to escape) as an explanatory variable, the conclusion of an absence of (or weak) differences between the patches in the amount of pellets according to the proximity of cover would have emerged (i.e., no or weak effect of closest mound or closest corner distance in our analyses, respectively). Yet, our results 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 predictive 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). Although a rangefinder including angle displays may be expensive, 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 of the classification of a portion of the cover item as rectilinear or not. However, this subjectivity is more pronounced when the cover is far, i.e., when the rabbit also faces visual limitations.

Rabbits, cats and cover

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 behavior 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 grazed sward was of similar height all over the study area, patches probably faced a similar level of foraging pressure by rabbits (although we cannot rule out the possibility of fine – scale edaphic variations, leading for example to higher productivity in some patches,

and thus to higher foraging pressures despite similar height). Accordingly, in a context of no other herbivore species in the study area, the difference in pellet quantity between patches could 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., Cowlishaw 1997, Blumstein 1998), leading to an increase 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 (Courchamp et al. 2003). 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.

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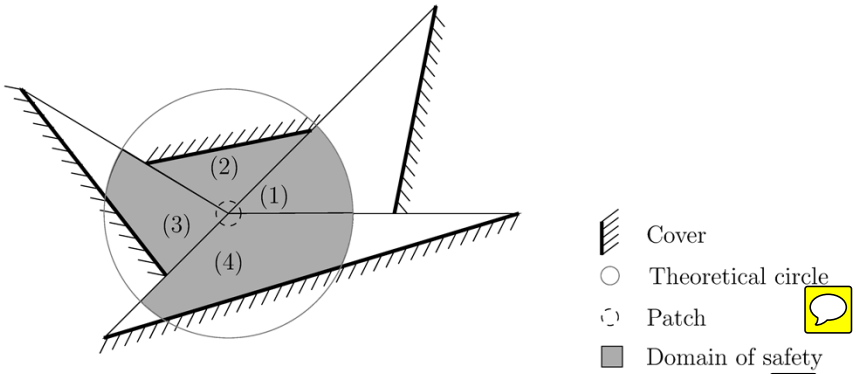
Fig.1

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

460 Fig.1 (continued)

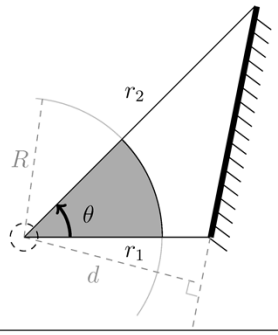
(A) An overview of a theoretical patch with the four main cases for cover items position



(B) The four main cases and the calculation of the surface for the associated subcases

(1) The whole cover item falls outside the theoretical circle

(1a)



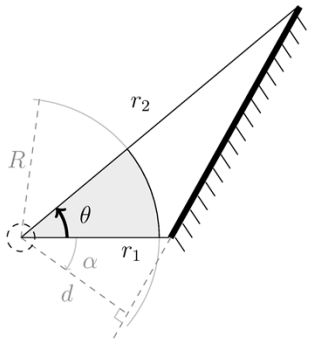
Conditions:

- $r_1 \geq R$
- $d \geq R$

Surface:

$$\mathcal{S} = \frac{R^2\theta}{2}$$

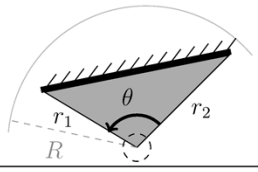
(1b)



Conditions:

- $r_1 \geq R$
- $d \leq R$
- $\alpha \leq 0$

(2) The whole cover item falls inside the theoretical circle



Conditions:

- $r_2 \leq R$

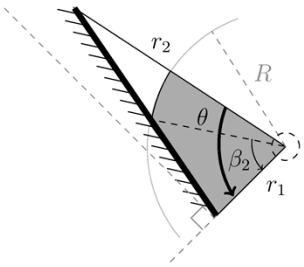
Surface:

$$\mathcal{S} = \frac{r_1 r_2 \sin\theta}{2}$$

462 Fig.1 (continued)

(3) The cover item intersects the theoretical circle in one point

(3a)



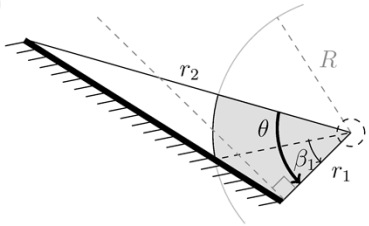
Conditions:

- $r_1 \leq R$
- $r_2 \geq R$
- $r_2 \cos\theta \leq r_1$

Surface:

$$\mathcal{S} = \frac{R^2(\theta - \beta_2)}{2} + \frac{Rr_1 \sin\beta_2}{2}$$

(3b)



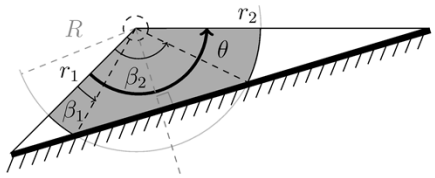
Conditions:

- $r_1 \leq R$
- $r_2 \geq R$
- $r_2 \cos\theta \geq r_1$

Surface:

$$\mathcal{S} = \frac{R^2(\theta - \beta_1)}{2} + \frac{Rr_1 \sin\beta_1}{2}$$

(4) The cover item intersects the theoretical circle in two points



Conditions:

- $r_1 \geq R$
- $d \leq R$
- $\alpha \geq \theta$

Surface:

$$\mathcal{S} = \frac{R^2(\theta - \beta_2 + \beta_1)}{2} + \frac{R^2 \sin(\beta_2 - \beta_1)}{2}$$

(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:

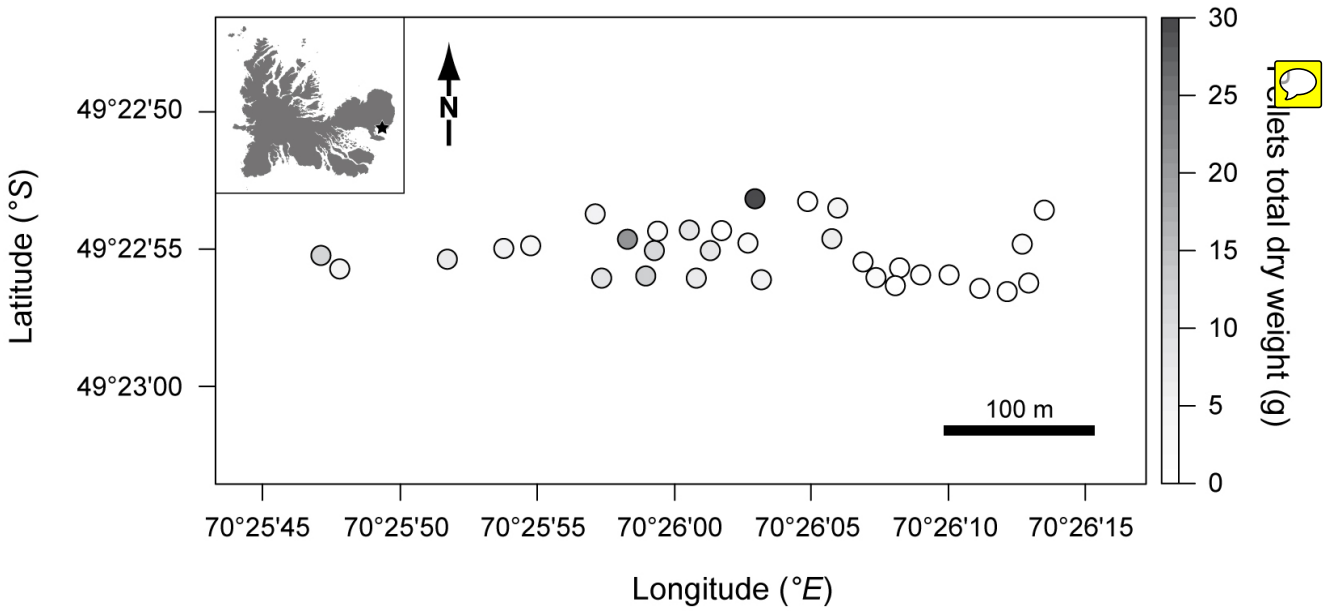
$$\beta_1 = \arccos\frac{r_1 r_2^2 \sin^2\theta + \sqrt{(R^2(r_1^2 + r_2^2 - 2r_1 r_2\cos\theta) - r_1^2 r_2^2 \sin^2\theta)(r_2\cos\theta - r_1)^2}}{R(r_1^2 + r_2^2 - 2r_1 r_2\cos\theta)}$$

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

464 Fig. 2

465 Pellet total dry weight (indexed by grey levels as mentioned on the right y axis) measured in the
466 studied patches (dots) according to their spatial position (left y axis and x axis). The hypothesis
467 that the proximity to fresh burrows partly explains the spatial pattern reported here might be
468 relevant as fresh burrows were localized at about 100 meters north – west from the boarder of the
469 study area, i.e., on the side of the patches with higher values in pellet total dry weight.

470



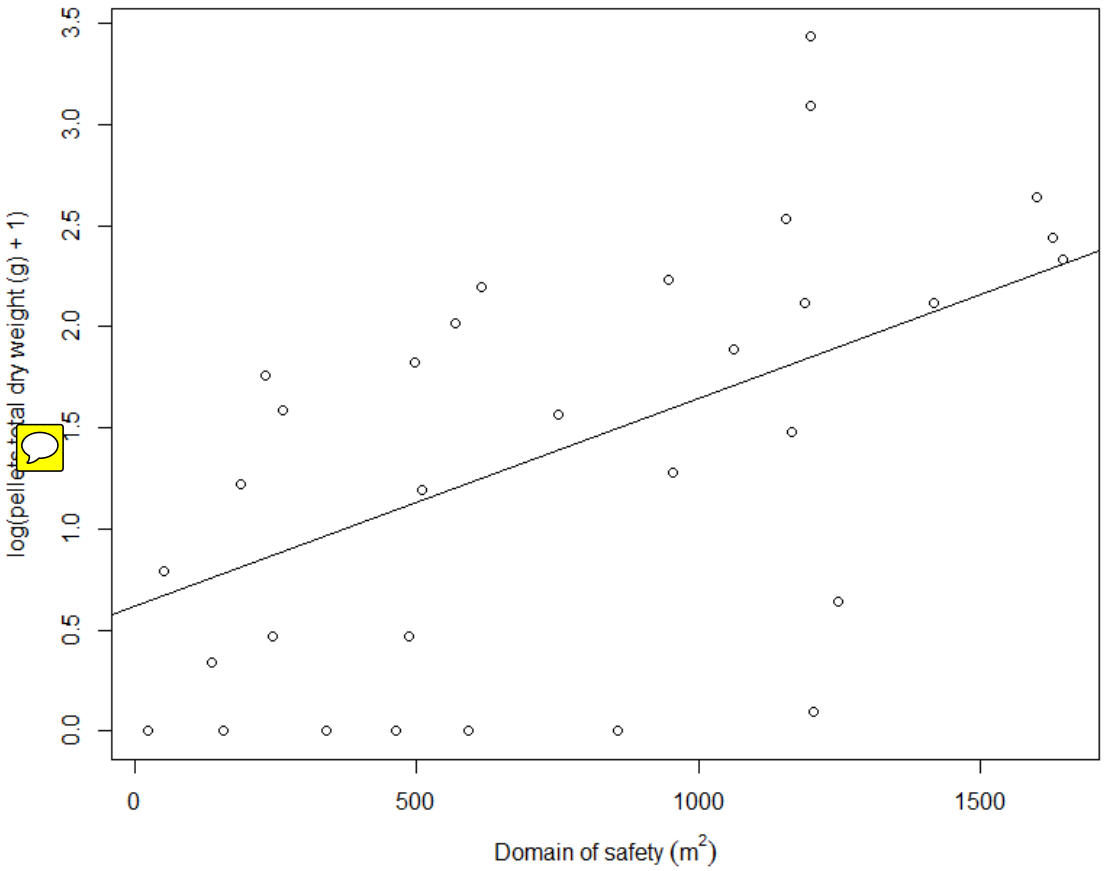
471

472 Fig. 3

473 The positive relationship between the log(pellet total dry weight (g) + 1) and the "domain of

474 safety" (in m^2) computed for a theoretical circle with a 25 m radius.

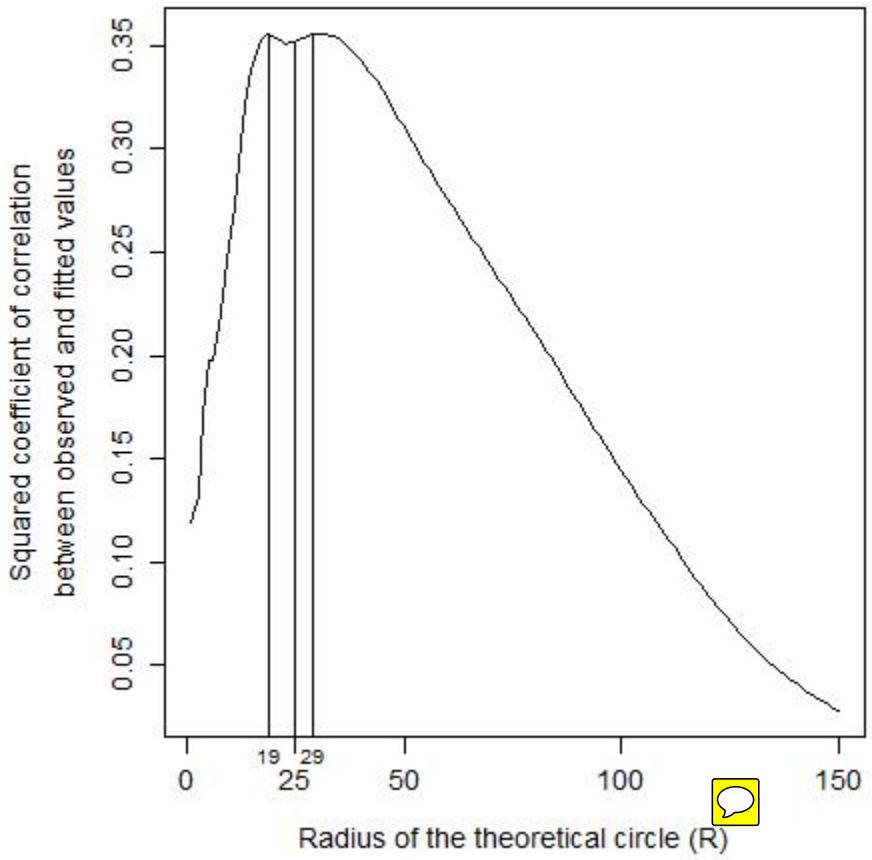
475



476

Fig. 4

Squared coefficients of correlation between the observed and the fitted values for models built with values of "domain of safety" calculated for theoretical circles of radiuses (R in Fig. 1, in m) ranging from 1 to 150 m and plotted on x axis. The biologically relevant distance ranges between 19 and 29 m, in line with our field observations of cats hunting bouts.



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