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# Accounting for central place foraging constraints in habitat selection studies

Simon Benhamou  | Nicolas Courbin 

Centre d'Ecologie Fonctionnelle et  
Evolutive, CNRS, Montpellier, France

## Correspondence

Simon Benhamou

Email: [simon.benhamou@cefe.cnrs.fr](mailto:simon.benhamou@cefe.cnrs.fr)

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## Abstract

Habitat selection studies contrast actual space use with the expected use under the null hypothesis of no selection (hereafter neutral use). Neutral use is most often equated to the relative frequencies with which environmental features occur. This generates a considerable bias when studying habitat selection by foragers that perform numerous trips back and forth to a central place (CP). Indeed, the increased space use close to the CP with respect to distant places reflects a mechanical effect, rather than a true selection for the closest habitats. Yet, correctly estimating habitat selection by CP foragers is of paramount importance for a better understanding of their ecology and to properly plan conservation actions. We show that including the distance to the CP as a covariate in unconditional Resource Selection Functions, as applied in several studies, is ineffective to correct for the bias. This bias can be eliminated only by contrasting the actual use to an appropriate neutral use that considers the CP forager behavior. We also show that the need to specify an appropriate neutral use overall distribution can be bypassed by relying on a conditional approach, where the neutral use is assessed locally regardless of the distance to the CP.

## KEYWORDS

(conditional) logistic regression, biased selection ratio, resource selection function, spatial constraint

## INTRODUCTION

Since the seminal paper by Johnson (1980), the intensity with which an animal may select different types of resources and habitat features has become an important question in theoretical and applied ecological studies (Fortin et al., 2008; McLoughlin et al., 2010; Svanbäck & Bolnick, 2005). Addressing this question makes it possible to identify environmental factors that shape animal space use and to predict population distributions (Boyce

et al., 2002; Fieberg et al., 2021; Johnson et al., 2013; Manly et al., 2002), and thereby to improve conservation and management actions (Courbin et al., 2022; Thurfjell et al., 2014).

A key concept in habitat selection analyses is the selection ratio  $w_{x,y} = u_{x,y}/a_{x,y}$ , where  $u_{x,y}$  is the value, at location  $(x, y)$ , of the probability density function (PDF) of actual use, and  $a_{x,y}$  is the value, at the same location, of the PDF of the expected use under the null hypothesis ( $H_0$ ) of no selection trend for any particular

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environmental features. If the environmental feature corresponds to discrete types of the habitat (e.g., “forest” and “meadow”), the selection ratio for a given habitat type  $H$ , irrespective of the other features to which an animal may be sensitive, is  $w_H = U_H/A_H$ , with  $U_H = \iint_H u_{x,y} dx dy$  and  $A_H = \iint_H a_{x,y} dx dy$ , where  $\iint_H dx dy$  means that integration is done for all locations  $(x, y)$  occurring within habitat type  $H$ . Classically,  $a_{x,y}$  is referred to as the availability, and is often considered a synonym of relative frequency in the geographical space considered. Following Johnson (1980), Rosenberg and McKelvey (1999), and Matthiopoulos (2003) rightly considered it should rather be understood as a synonym of accessibility. Indeed, the expected use of a given resource level (continuous case) or habitat type (discrete case) under the null hypothesis of no selection corresponds to the relative frequency with which resource level or habitat type considered occurs only when all locations are equally accessible. This occurs only if one has good reasons to think that  $a_{x,y}$  is uniformly distributed or if the relative frequencies of occurrences (i.e., the proportions of the various habitat types in the discrete case) are not correlated with a spatial feature (e.g., the distance to given location) to which  $a_{x,y}$  may depend on. To avoid any ambiguity, hereafter we will refer to  $a_{x,y}$  as the “neutral use.”

Many habitat selection studies focus on the third selection order, that is, how an animal uses space within its home range (Johnson, 1980). In the particular case of central place (CP) foragers, the neutral use PDF should not be expected to be uniform because the numerous back and forth movements to the CP are expected to mechanically result in a neutral use PDF that peaks at the CP. Individuals of many taxa behave as CP foragers, either during the major part of their adult life, such as hymenopterans (e.g., Kacelnik et al., 1986), or during the breeding period, such as birds (e.g., Ventura et al., 2022) and wolves (e.g., Ylitalo et al., 2021). Assuming that  $a_{x,y}$  for a CP forager is uniform should therefore result in flawed habitat selection ratios (Appendix S1: Section S1), except if the resource is distributed at random with respect to the CP.

Other strong spatial constraints may affect space use, in particular the occurrence of areas that are hardly accessible. For example, for colonial pelagic birds that nest on a continental cliff and systematically avoid flying above the ground, space use cannot be expected to be evenly distributed in all directions around the nest. Similarly, in territorial species where individuals actively defend their whole home ranges, the areas belonging to conspecifics’ territories are not very accessible. Such spatial constraints are easily taken into account when designing the neutral use PDF (e.g., Courbin et al., 2022;

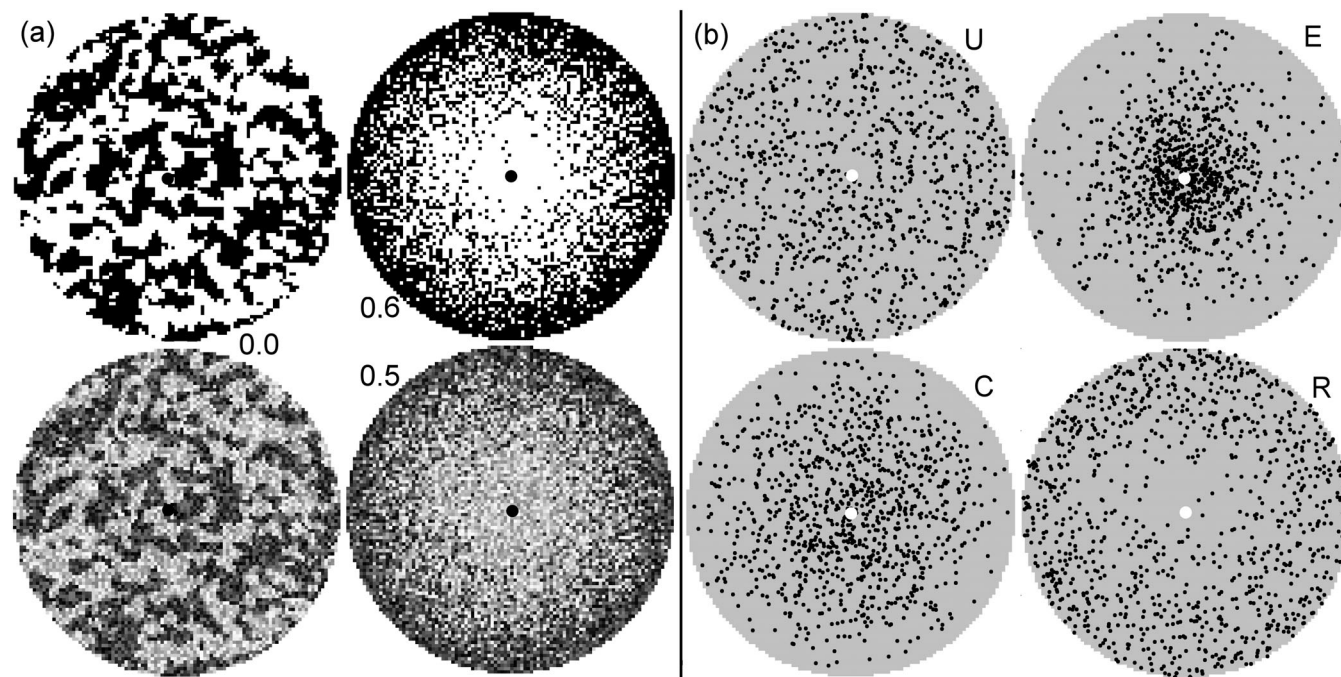
Fluhr et al., 2017; Raymond et al., 2015; Wakefield et al., 2011), because they only involve rating some areas as fully accessible/available and some other as fully inaccessible/unavailable. We focused on the non-binary constraint due to CP behavior, which is harder to account for, as distant areas are less accessible than closer ones.

Over the past decades, habitat selection has been mainly studied with Resource Selection Functions (RSFs, Boyce et al., 2002; Fieberg et al., 2021; Johnson et al., 2013; Manly et al., 2002). Rosenberg and McKelvey (1999) claimed that, for a CP forager, the selection trends could be correctly assessed within the classical (unconditional) RSF framework by comparing the actual use with a uniform neutral use while including the distance from the CP as a covariate. Although this approach was used in a number of habitat selection studies (e.g., Bond et al., 2009; Chudzińska et al., 2015), we doubted that it could provide reliable selection ratio estimates, because the actual distribution of distances to the CP may be poorly related to the appropriate neutral use PDF. Using simple examples, we investigated the extent to which a misspecification of the neutral use can be corrected, by including CP distance-based covariates in unconditional RSF models when applied to CP foragers. Alternatively, selection trends can be estimated locally in a matched design (local actual use being paired with local resource availability in a conditional RSF design: Compton et al., 2002; Duchesne et al., 2010; McDonald et al., 2006; Prima et al., 2017; or in Step Selection Function: Avgar et al., 2016; Forester et al., 2009; Fortin et al., 2005). As these conditional models should relax the spatial constraint due to the CP, some authors (e.g., Carlson et al., 2021; Carrete & Donazar, 2005) assumed that these models should provide estimates of selection trends unbiased by CP behavior. However, this was not demonstrated. A robust statistical design to study habitat selection by CP foragers is still lacking. Here, we investigate how to properly apply unconditional RSF to CP foragers. Further, using computer simulations, we checked whether the CP constraint could be efficiently relaxed by a conditional approach. Finally, we proposed guidelines to improve studies of animal habitat selection under severe spatial constraints.

## METHODS

### Landscape configurations

We considered a forager exploiting a circular home range from a place located at the center of its home range. We first modeled the landscape within the home range as made of two equally abundant habitat types. They were



**FIGURE 1** Landscape configurations and use distributions. (a) Two landscape configurations with two types of habitat (top; 1 in white and 2 in black) and continuous version (bottom; where types 1 and 2 are replaced by a resource level uniformly distributed between 0 and 0.5, and 0.5 and 1, respectively and shown as gray levels); In the CP-independent landscape (left), the resource level is independent of the distance to the CP. In the CP-dependent landscape (right), the proportion of type 2 or the resource level is proportional to the squared distance. The value written close to each circle is the correlation between the type or resource level and the squared distance. (b) Four types of bivariate PDF were considered: U, uniform; E, exponential; C, conical and R, reverse conical. For clarity, only 1000 locations (small black dots) are shown in addition to the CP (central white dot), whereas the results were obtained by drawing 100,000 locations.

mixed according to two landscape configurations. In the CP-independent configuration (Figure 1a, top-left), the local proportions of cells of types 1 and 2 did not depend on the distance to the CP. In the CP-dependent configuration (Figure 1a, top-right), the local proportion of cells of habitat type 2 ranged from 0 to 1 proportionally to the squared distance to the CP. Thus, the proportion of cells of any of the two habitat types was overall the same as in the CP-independent configuration but the proportion of type 2 cells was proportional to the squared distance to the CP. With the CP-independent configuration, we aimed only to check whether, when the CP cannot bias the selection ratios for the two habitat types, correct results are obtained by an unconditional RSF model where the neutral use simply reflects the relative abundance of the two types. With the CP-dependent configuration, we aimed to determine the bias induced by this wrong specification of the neutral use PDF in an unconditional RSF model for different actual use PDF, and whether this bias could be corrected by introducing the distance to the CP in the model. We also applied this unconditional RSF approach to a resource whose level varies continuously rather than being assigned to discrete habitat types. To keep the same two kinds of landscape

configuration (CP-independent, Figure 1a, bottom-left, and CP-dependent, Figure 1a, bottom-right), the resource level attributed to a given cell was drawn at random from a uniform distribution either between 0 and 0.5 or between 0.5 and 1, depending on whether this cell was initially assigned to type 1 or type 2, respectively. The resource was therefore characterized by a level that, overall, followed a uniform distribution between 0 and 1, and by a spatial level-weighted distribution that did or did not depend on the distance to the CP, according to the landscape configuration. Finally, based on the discrete version of the CP-dependent landscape, we simulated the movement of a CP-forager that prefers habitat type 2  $k$  times more than type 1, and checked whether the relative selection estimated by a conditional RSF model correctly matches the relative preferences set in the movement model.

## Unconditional RSF framework

To determine whether, in the unconditional approach, including the distance to the CP as a covariate makes it possible to correct the results obtained when the neutral use PDF is wrongly assumed to be uniform, we



contrasted two RSF models. One focused only on the resource  $R$ , whereas the other included both the resource  $R$  and the distance  $D$  to the CP. These two RSF models were expressed as  $\hat{w}_R = \exp(\beta_0 + \beta_1 R)$  and  $\hat{w}_{R,D} = \exp(\beta_0 + \beta_1 R + \beta_2 D + \beta_3 D^2)$ , respectively, with  $R$  corresponding to either a categorical (with two types) or a continuous level variable. The various regression coefficients  $\beta$  (often called selection coefficients in the RSF context) are estimated through likelihood maximization. Although  $D$  was expected to affect the selection ratio in a monotonic way, we considered a quadratic form to allow a more flexible fit.

When the resource  $R$  is categorical, one of the types has to be taken as reference because there is a unit-sum constraint on the (actual and neutral) use of the different habitat types ( $\sum_H U_H = \sum_H A_H = 1$ ). The variable  $R$  is then reduced to an indicator function (often called a dummy variable in a statistics context). Thus, with type 1 taken as the reference, one gets  $R = 0$  if location  $(x, y)$  lies in habitat type 1, or  $R = 1$  if it lies in habitat type 2. The value of the selection coefficient associated to  $R$ ,  $\beta_1$ , then expresses the logarithm of the ratio of selection ratios (i.e.,  $\ln(\hat{w}_2/\hat{w}_1)$ ), so that  $\exp(\beta_1)$  represents the selection of habitat type 2 relative to habitat type 1. It is worth noting that the selection ratios for the different types have a limited meaning by themselves, because they depend on the set of types that are considered relevant for the analysis (Johnson, 1980). However, as they are affected in the same way by the arbitrary set composition, the selection coefficient for a given type is independent of this composition and therefore constitutes a reliable metric of the selection of this type relatively to another one taken as reference. This can be generalized to RSF involving continuous resource variables, where the value of  $\exp(\beta_1)$  is referred to as the relative selection strength, that is, the relative selection for each increase of one unit (Avgar et al., 2017). The relative selection for a continuous resource level  $R$  with respect to a given value,  $v$ , taken as reference is given by  $\exp(\beta_1(R - v))$ .

We contrasted two kinds of neutral use PDF for  $D \leq r$ , where  $r$  is the home range radius (Figure 1b). One is the classical, but misspecified for a CP forager, bivariate uniform PDF ( $a_{x,y} = (\pi r^2)^{-1}$ ). The other is the bivariate exponential PDF ( $a_{x,y} = 1.5/(\pi \sigma^2) \exp(-\sqrt{3}D/\sigma)$ , with  $\sigma^2 = E(D^2)/2 = 0.75 E^2(D)$ ), which is the expected PDF for a non-selective forager relying on a CP-biased correlated random walk process (Benhamou, 1989, 1994). We truncated this distribution at the 0.95 cumulative isopleth ( $D = 2.74\sigma$ ) and divided the  $a_{x,y}$  values by 0.95 to obtain a cumulative distribution that sums to 1 within  $r$  of the CP. We also contrasted three kinds of actual use PDF for  $D \leq r$  (Figure 1b): bivariate uniform ( $u_{x,y} = (\pi r^2)^{-1}$ ), conical ( $u_{x,y} = 3(1 - D/r)/(\pi r^2)$ ), or reverse conical ( $u_{x,y} = 1.5(D/r)/(\pi r^2)$ ), reflecting typical space use behaviors.

The conical PDF roughly matches the well-specified (i.e., exponential) neutral use PDF for a CP forager, but with a reduced contrast between the highly used nearby areas and the marginally used faraway areas for the conical PDF compared to the exponential PDF. The reverse conical PDF mimics what happens with some colonial seabirds that avoid exploiting the area close to the colony (continental shelf) and preferentially exploit distant productive areas (e.g., continental slope, oceanic fronts) by commuting between the CP and these distant areas. Finally, the uniform PDF corresponds to an intermediate situation where the forager tends to compensate the mechanical overuse of areas close to the CP (which may be observed if, for example, the forager tends to move more slowly the farther it is from the CP).

We drew  $n = 100,000$  “actual” locations from bivariate uniform, conical, or reverse conical PDFs within the  $r$ -radius circle, and  $m = 100,000$  “neutral” locations (usually called pseudo-absences, available points, or background points) from a bivariate exponential and uniform PDFs within the same circle. We generated these PDFs, as well as the two landscape configurations, with the R software (R core Team, v3.6.2, 2019) packages NLMR (Sciaini et al., 2018), raster (Hijmans, 2021), and *sp* (Bivand et al., 2013). The selection coefficient  $\beta_1$  was estimated using an unconditional logistic regression (Keating & Cherry, 2004; Manly et al., 2002; McDonald, 2013). It is based on the expression  $\text{logit}(P_{R,(D)}) = \ln(\hat{w}_{R,(D)} n/m)$ , where  $P_{R,(D)}$  is the probability that a location characterized by a given habitat type (discrete case) or resource level (continuous case), and possibly (in the resource-distance model) lying at a given distance  $D$  from the CP, belongs to the whole set of actual rather than neutral locations. The correct selection trends are those obtained with the resource-only model based on a neutral use distributed according to a bivariate exponential PDF, which is the appropriate neutral use PDF for a forager relying on a CP-biased correlated random walk process. The resource-only model based on a bivariate uniform neutral use PDF, that is, which simply reflects the relative frequencies with which the resource occurs, should result in biased selection trend estimates only in the CP-dependent landscape. The resource-distance model based on a uniform neutral use PDF allowed us to determine to which extent including the distance to the CP could correct for considering a uniform neutral use PDF, which does not correspond to the use PDF expected for a non-selective CP forager.

## Conditional RSF framework

We determined whether, in a landscape made of two habitat types, the relative preference of a CP forager for

habitat type 2 over type 1 could be suitably reflected by the selection coefficient estimated using a conditional RSF model. We simulated a CP-biased correlated random walk made of 100,000 steps with a length equal to the cell size in the discrete CP-dependent landscape previously used in the unconditional analysis (Figure 1a, top-right). A walker with no particular preferences was assumed to move a step per unit time. A preference for habitat type 2 cells  $k$  times larger than for type 1 cells was simulated by designing a walker that stayed  $k-1$  unit times without moving each time it reached a type 2 cell. As the results obtained with the unconditional RSF model for the discrete and continuous cases are similar (see below), we only considered the discrete case (which is easier to simulate and interpret) in our conditional RSF approach. We estimated the selection coefficient  $\beta_1 = \ln(\hat{w}_2/\hat{w}_1)$  with a conditional logistic regression (R package *survival*, Therneau, 2021) that paired the habitat type of the cell actually used at any given unit time with the habitat types of the eight non-chosen cells out of the  $3 \times 3$  cells surrounding the animal's location at the previous unit time. We also simply computed the relative selection as the ratio of the mean local selection ratios, with the local actual use being equal to 0 or 1 depending on whether the animal reached a cell of the type considered or of the other type, and the local neutral use based on the relative abundances of the two types (when both present) in the  $3 \times 3$  cells surrounding the previous location.

## RESULTS

### Unconditional RSF framework

The results we obtained for a resource considered in terms of either habitat types or continuous level were fully consistent. In the CP-independent landscape, the value of the selection coefficient for the resource  $\beta_1$  should be equal to 0 (no selection trend for a particular habitat type or resource level) and was correctly estimated as so by all unconditional RSF models (Appendix S1: Table S1). This held true for all actual use PDFs (uniform, conical or reverse conical), even if the neutral use PDF was wrongly assumed to be uniform. In contrast, when the relative proportions of the two habitat types (discrete case) or the resource level (continuous case) depended on the distance to the CP, the resource-only model based on the appropriate (i.e., exponential) neutral use PDF showed that the type of cell that was the most frequent at large distance (type 2 in the discrete case, cell with a resource level higher than 0.5 in the continuous case) was clearly over-selected, for any of the three kinds of actual use considered (Figure 2, Appendix S1: Table S2).

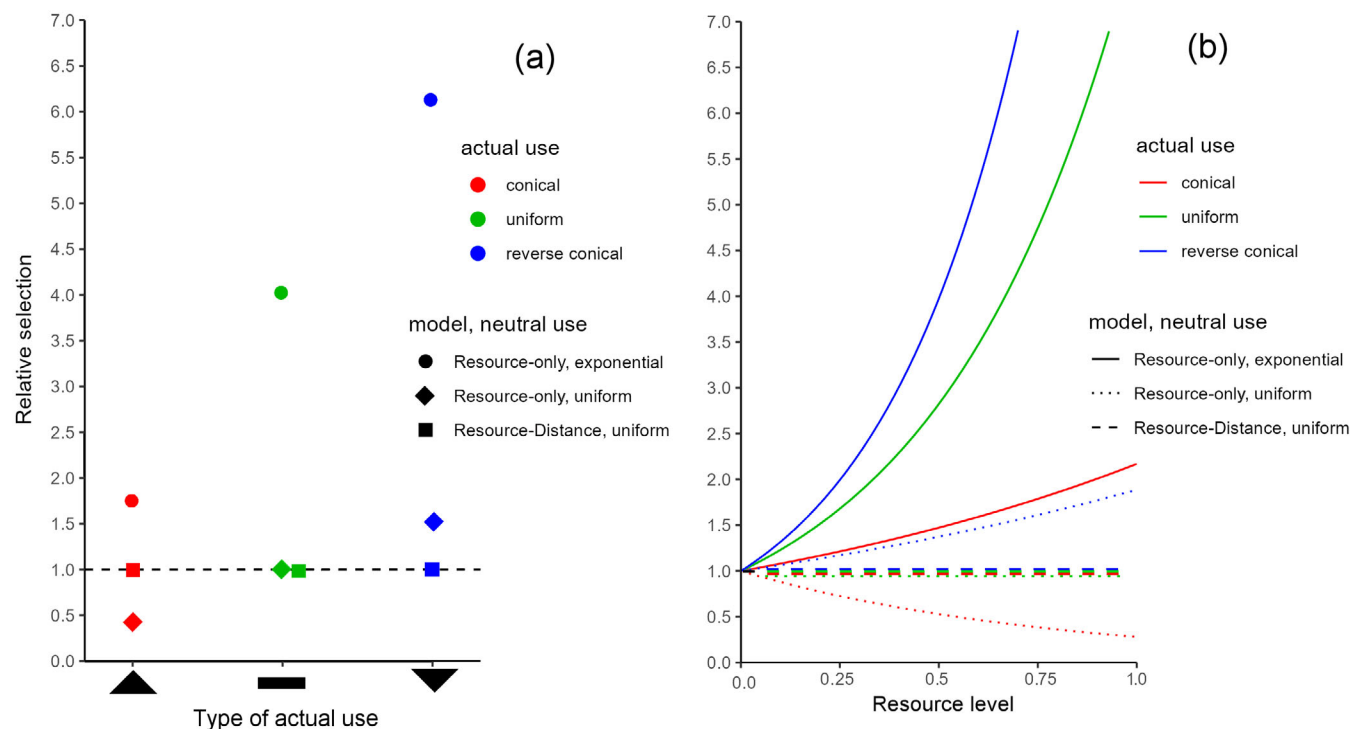
With an inappropriate (uniform) neutral use PDF in CP-dependent landscape, the relative selection estimated with a resource-only model were far lower than the correct values for the three actual use PDF considered (for a conical actual use, the relative selection estimated was even reversed, with the most frequent type of cell at large distance then estimated as being under-selected, Figure 2, Appendix S1: Table S2). Incorporating the distance to the CP in the unconditional RSF erased the selection trend. Thus, the bias was only partly corrected when the actual use PDF was conical, not corrected when the actual use PDF was uniform, and even increased when the actual use PDF was reverse conical (Figure 2, Appendix S1: Table S2). Overall, incorporating the distance to the CP into the unconditional RSF model in an attempt to correct for the bias due to an inappropriate specification of the neutral use is therefore hazardous. Moreover, specifying the actual and neutral use PDFs in polar rather than Cartesian terms (Appendix S1: Section S3) and/or including an interaction term between habitat types and distance  $D$  to the CP (as Rosenberg & McKelvey, 1999 did; Appendix S1: Section S4) did not lead to improvements.

With an environment made of two habitat types, and a simulated process by which type 2 was preferred  $k$  times over type 1, the relative selection value obtained in the CP-dependent landscape using a conditional logistic regression suitably reflected the preference ratio used in the simulation:  $\hat{w}_2/\hat{w}_1 = 0.98$  for  $k = 1$ ,  $\hat{w}_2/\hat{w}_1 = 1.97$  for  $k = 2$ , and  $\hat{w}_2/\hat{w}_1 = 2.97$  for  $k = 3$ . Interestingly, we obtained the same results simply by computing the relative selection as the ratio of the mean local selection ratios.

## DISCUSSION

We showed that a strong spatial constraint on animal movements, such as the need to come back frequently to a CP, may dramatically bias habitat selection trends if not properly considered. In the unconditional habitat selection approach, spatial constraints have to be integrated as such when designing neutral use (i.e., when generating the set of neutral locations). Contrary to the claims of Rosenberg and McKelvey (1999), including this constraint as an additional covariate while designing the neutral use simply as reflecting the relative frequencies with which environmental features occur is unlikely to provide unbiased estimates. In contrast, a conditional approach, by which the neutral expectation is estimated based on the local distribution of resource, makes it possible to correctly determine the selection trends.

A major difficulty for the unconditional RSF approach is to design a suitable neutral use PDF. Fortunately, the simple uniform PDF is a suitable choice



**FIGURE 2** Relative selection for different PDFs of actual use and neutral use in the CP-dependent landscape. The correct values are those obtained with an exponential neutral use PDF, which is the expected PDF for a non-selective forager relying on a CP-biased correlated random walk process. The values are not important by themselves. What matters is, for each actual use PDF, the differences occurring between the different combination of models and neutral use PDFs. (a) Landscape made of two discrete habitats types; the relative selection of habitat type 2 over type 1 corresponds to  $\exp(\beta_1) = \hat{w}_2/\hat{w}_1$ . (b) Landscape characterized by a continuous resource variable that uniformly ranges between 0 and 1; the relative selection, with the resource level  $R = 0$  taken as reference, corresponds to  $\exp(\beta_1 R)$ . In both discrete and continuous cases, a value of relative selection  $s$  means that the selection ratio for the resource considered (habitat type or resource level) is equal to  $s$  times the value of selection ratio for the reference.

when the resource type (discrete case) or level (continuous case) is independent of the distance to the CP. The user should therefore always check this assumption beforehand at the population level (for non-colonial CP foragers, the independence may arise at the population level even if there are strong but reversed correlations at the individual level, which thus may compensate each other). In the general case where independence cannot be granted, the suitable choice of the neutral use PDF strongly depends on what we know about the way the animal tends to move. Some authors assumed, without sound justification, that the neutral use may decrease linearly with distance to the CP (Matthiopoulos, 2003; Wakefield et al., 2011). Here we assumed that, in the absence of any selection trend, the animal performs search loops (from and to the CP) by performing a CP-biased correlated random walk with a constant bias strength, which results in a bivariate exponential neutral use PDF (see Monsarrat et al., 2013 for an application example).

However, other movement patterns may occur for a non-selective CP forager. In some species, such as

*Cataglyphis* ants (Wehner & Wehner, 1990), individuals search for resources during the outward journey and come back to their nest along a straight line once they had caught a prey item. One can guess that such animals rely on a simple (unbiased) Correlated Random Walk, that is, a purely diffusive movement, during the outward journey, with a diffusion coefficient that depends on the habitat type. In this case, the analysis of habitat selection may focus on the space use distribution during the outward journey with a neutral use PDF corresponding to a bivariate Gaussian distribution centered on the CP and a variance reflecting the mean diffusion coefficient (see Codling et al., 2008). More generally, a neutral use PDF can be obtained by simulating movements starting from and ending at the CP independently of the habitat features (Aarts et al., 2008; Courbin et al., 2018, 2022; Hazen et al., 2016; Raymond et al., 2015). For animals that commute between their nest and a distant area (e.g., as occurs with breeding pelagic seabirds that exploit oceanic fronts, e.g., Courbin et al., 2018; Kappes et al., 2015; Wakefield et al., 2011), one may rely on a uniform neutral use PDF after having removed the commuting

part (i.e., the path between the CP and the feeding area), which strongly reflects the CP spatial constraint.

Interestingly, a conditional RSF approach (Compton et al., 2002; Duchesne et al., 2010; McDonald et al., 2006; Prima et al., 2017) applied to a CP forager results in suitable estimates of selection trends. Indeed, a conditional approach (even in its basic form based on the simple averaging of the local choices) bypasses the need to explicitly specify the whole neutral use PDF, the neutral use being assessed locally from the local resource distribution. Therefore, when applied to a CP forager, conditional approaches (e.g., Carlson et al., 2021; Carrete & Donazar, 2005) make it possible to relax the spatial constraint due to the need to frequently return to a CP. Obviously, actual movements and resource choices are much more complex than those we simulated. They can be accounted for by much more sophisticated forms of conditional approach such as Step Selection Function models (Avgar et al., 2016; Forester et al., 2009; Fortin et al., 2005; Signer et al., 2017; Thurfjell et al., 2014), considering constraints of mobility and spatial autocorrelation on accessibility (Matthiopoulos et al., 2020). A conditional approach may sometimes be problematic because it rests on the assumption that the process of habitat selection depends only on the local conditions and can thus lead to divergent conclusions from unconditional RSFs (Michelot et al., 2017; Signer et al., 2017). However, in the present context, and more generally when strong spatial constraints occur (Matthiopoulos et al., 2020), ignoring the larger scale movement processes is clearly an advantage.

A related question is whether distance to the CP should be included as a covariate in a habitat selection analysis. When the resource distribution is not related to this distance, unbiased results about selection trends can be obtained with a uniform neutral PDF. There is a priori no objection with including the distance to the CP in this case. Otherwise, this may be problematic. With an unconditional RSF model, it is preferable to not include the distance in the model because its effect is assumed to be already accounted for by the neutral use PDF (assumed to be appropriate but usually without guarantees). This issue can be avoided by relying on the conditional approach, but this will not necessarily result in additional insight. For example, in our study, including the distance in an unconditional RSF model was useless (the relative selection for the resource remained unchanged and the selection coefficients associated to the distance were almost null). Furthermore, in both unconditional and conditional approaches, including the distance to the CP when the resource distribution is related to this distance means that these two factors become mutually confounding

and therefore requires that the results obtained be interpreted with caution.

Overall, we demonstrated the importance of properly specify the neutral use PDF in unconditional habitat selection analyses, or to shortcut this specification by relying on a conditional approach. This should be a primary consideration when evaluating habitat selection of CP forager because of the strong potential negative consequences for the understanding of species ecology and the efficiency of conservation actions.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The landscape matrices (used in both the unconditional and conditional approaches) and the code for movement simulation (used only in the conditional approach) are available in Benhamou and Courbin (2023) on Figshare at <https://doi.org/10.6084/m9.figshare.22665535.v4>.

## ORCID

Simon Benhamou  <https://orcid.org/0000-0003-0803-8559>

Nicolas Courbin  <https://orcid.org/0000-0002-6428-5012>

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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