



Original Article

# Nest defensibility decreases home-range size in central place foragers

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Variation in the home-range size of nesting animals is thought to be driven by nutritional requirements, food availability, and predation risk of the animals during foraging. Only few studies have considered that the risk of nest predation may also affect home-range size because nests become more difficult to defend as animals move further away. We used a theoretical model to explore the combined effects of nest defensibility, nest predation risk, and food availability on foraging distance from the nest, and hence home-range size. In our model, foragers adjust the foraging distance around the central place such that the required amount of food is collected within the available time with the lowest predation risk for the nest. We found that foraging distance decreased with food availability and the risk of nest predation during absence, but also with nest defensibility. When food was abundant, both nest predation risk and defensibility hardly influenced foraging distance. When food was scarce, animals able to deter predators foraged close-by, whereas animals less able to deter predators foraged further away. Likewise, animals that were themselves vulnerable to predation stayed closer to their nest if the nest provided safety, as is typical for central place foragers. This study is the first to assess the importance of nest defense and nest predation risk for foraging distance of central place foragers and provides a better understanding of the drivers of home-range size.

**Key words:** Central place foraging, nest predation, theoretical model, movement behavior, defensibility.

## INTRODUCTION

Many organisms are tightly associated with a nest or burrow during at least part of their life. Animals regularly leave their nest or burrow to acquire food, either for themselves, for their partner, or for their offspring. Central place foraging theory (CPF) (Orians and Pearson 1979) assumes that such foraging trips typically involve cost-benefit trade-offs, such as the costs of exposure to predators versus the potential resources gained during the trip (Ydenberg 2007). These trade-offs drive behavioral decisions of foragers, such

as the foraging distance from the nest to collect food items (Olsson et al. 2008). These behavioral decisions, in turn, determine home-range size, and hence population densities and dynamics (Adams 2001).

CPF models typically do not focus on predicting home-range size. Originally, the empirical question of interest concerned how optimal load size should vary with distance as a result of diminishing returns to adding more to a forager's load (Lima et al. 1985; Houston and McNamara 1985; Elliot 1988). More generally, central place effects include load-size dependent travel costs, distance-dependent predation risk, and resource depletion with distance (Olsson et al. 2008). In virtually all cases, sites nearer to the nest will be more valuable foraging sites than those farther away, simply

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because of reduced travel time and costs (Olsson and Bolin 2014). Therefore, food requirements, food availability, and also predation risk of the foraging animal can be important drivers of home-range size, and these aspects have been included in more recent CPF models (Olsson et al. 2008). Home-range size tends to be positively correlated with animal body mass and thus food requirement (Swihart et al. 1988; Ottaviani et al. 2006), and increasing food availability has in some cases been found to decrease home-range size (Hixon 1980; Boitani and Fuller 2000; Adams 2001), but not always (Adams 2001). Furthermore, increasing predation risk while foraging can drive contraction of home-range size (Blumstein 1998; Candolin and Voigt 2001).

Most studies of CPF that consider predation risk assume that only the forager is subject to predation risk while away from the safety of the nest or burrow (Olsson et al. 2008; Olsson and Bolin 2014). However, the nest itself may contain precious items that are crucial to the animal's long-term fitness, such as nestlings or food supplies for the winter, which are prone to predation or pilfering. While away, the forager leaves the nest undefended, which may compromise the safety of the nest (Martindale 1982). When present, foragers may be able to defend their nests by attacking or distracting the predator, especially if the forager is relatively large (Montgomerie and Weatherhead 1988). This nest defensibility may decrease as the forager moves farther away from the nest (Hakkalainen et al. 2002). Martindale (1982) provided a graphical model for how nest predation risk should alter foraging decisions, but no further modeling has been done since. Given the importance of nests to many organisms and their need to protect it, nest predation risk should be an important driver of foraging distance, in addition to food availability and predation risk to the forager itself. When predicting home-range sizes for species that need to defend a nest, it will be necessary to extend the CPF theory to include nest predation risk and nest defensibility, and how these interact with food requirements and food availability.

In this paper, we investigate how foraging distance, a proxy for home-range size, is affected by nest predation risk, the forager's ability to defend the nest, and food availability in the environment. We develop a theoretical model and investigate differences in scenarios of nest predation risk, food availability, and contrasting characteristics of the forager and the nest. Specifically, we aim to answer 2 questions: 1) what is the relative importance of food availability and nest predation risk to foraging distance; 2) in determining foraging distance, how does the risk of nest predation during the forager's absence interact with the ability of the forager to defend its nest?

## METHODS

### Model description

We consider a situation where a foraging animal provisions nestlings that reside at a central location, den or nest (from here onwards the nest). To fledge the young, the forager must acquire a fixed amount of food items  $F$  during a fixed period of time (fledging period) by making repeated foraging trips. While the forager is away, the nestlings are exposed to predators. In between foraging trips, the forager remains at the nest feeding young, resting, and providing safety to the nestlings. Thus, the objective of the forager is to minimize the probability that the nest is depredated prior to harvesting  $F$  food items.

Without loss of generality and for simplicity, we consider a unidirectional 1-dimensional environment. This means that the nest is at one end of the environment and the forager can choose to harvest resources at different points along the line in one direction from the nest (Figure 1a). The results can be extended to 1-dimensional and 2-dimensional environments where the nest resides centrally, and the forager can move in any direction from the nest. Such extensions do not alter the qualitative properties of the predictions.

We assume that at the start of the nesting season there is some distribution of initial food abundances,  $R_I(D)$ , that varies with distance from the nest (Figure 1b and c). For simplicity, we assume a linear relationship between initial food availability and distance:

$$R_I(D) = R_0 + mD \quad (1)$$

where  $R_0$  is the initial amount of available food at the nest ( $D = 0$ ) and  $m$  is the linear change of initial food availability with distance  $D$  away from the nest. The total amount of food initially available up to some maximum distance of foraging  $D_{tot}$  is:

$$R_{tot} = \int_0^{D_{tot}} R_I(D) dD = R_0 D_{tot} + \frac{(m D_{tot}^2)}{2} \quad (2)$$

Equation 2 for total initial food availability between the nest and  $D_{tot}$  holds for all  $m \geq 0$  and for  $m < 0$  as long as  $D_{tot} < R_0/m$ , insuring that food availability does not go negative.

In a similar fashion, we assume that the risk of a predator depredating the nest changes with the forager's distance from the nest:

$$\mu(D) = b + cD, \quad (3)$$

where  $b$  is the risk of nest predation when the forager is at the nest and  $c > 0$  describes the linear rate of increase in risk as the foraging moves away from the nest. When  $b = 0$ , the nest is perfectly safe when the forager is at the nest. Values of  $b > 0$  imply lower nest defensibility, and nest predation may occur even when the forager is at the nest. For simplicity, we assume a linear change of initial food availability with distance  $D$  away from the nest. As predation risk cannot exceed 1, this formulation requires that  $D_{tot} < (1 - b)/c$ .

We assume that the forager has a type I functional response (linear increase in intake rate with food density; Holling 1959). Its instantaneous harvest rate is given by:

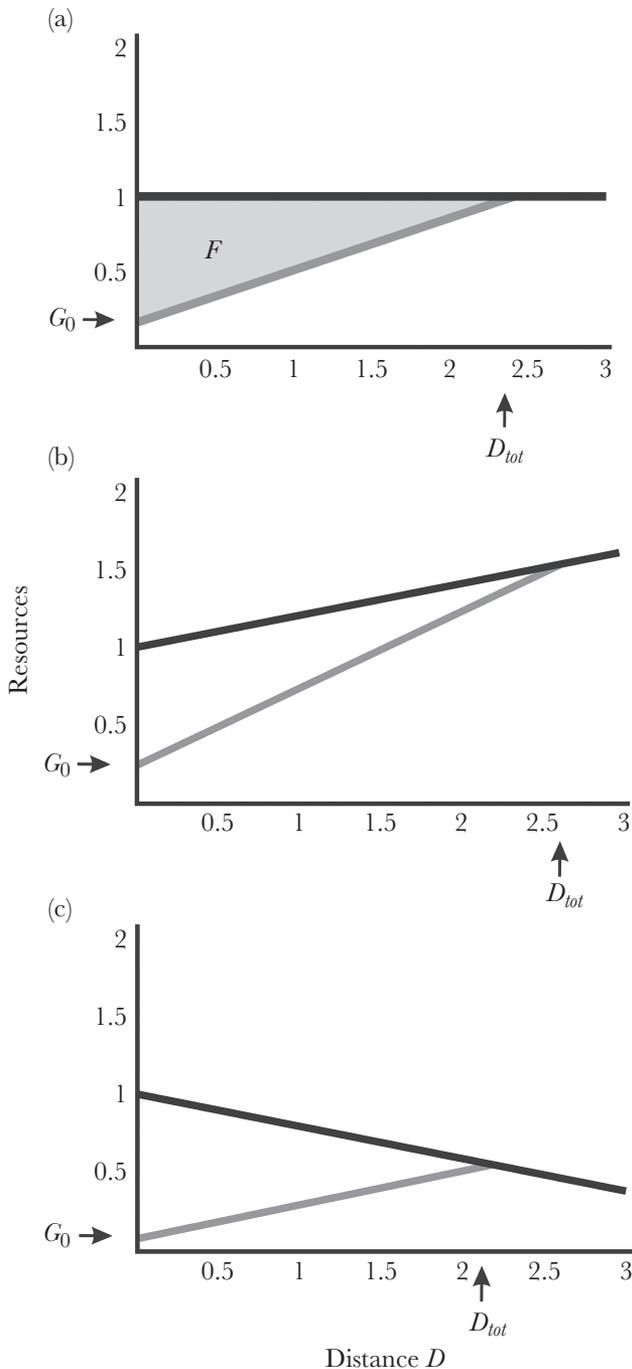
$$h(D) = aR(D) \quad (4)$$

where  $a$  is the encounter probability, and  $R(D)$  is the current food density at  $D$ . We assume that resources are not renewed during the fledging period and the forager depletes the food resources as it spends time feeding at different distances from the nest.

The challenge to the forager is to select the total amount of resources to harvest at each distance,  $H(D)$  such that:

$$F = \int_0^{D_{tot}} H(D) dD \quad (5)$$

This harvest results in a giving-up density (GUD), Brown et al. 1988 the amount of resources left behind at each distance,  $G(D) = R_I(D) - H(D)$ . Based on work by Gilliam and Fraser (1987) and Brown (1992), foragers will harvest at a certain distance  $D$  until the benefits of harvesting at this distance no longer outweigh the costs (in predation risk). For our model, this conforms to the  $\mu/h$  rule where the forager should harvest each distance so that at its GUD  $\mu(D)/h(D) = k$  is equalized across all distances. To minimize the



**Figure 1** Predictions of our foraging-distance model under basic parameters. (a) The local initial food availability  $R_l$  (horizontal line) and the GUD (gray line) at each location with constant predation risk ( $c = 0$ ) and constant food availability ( $m = 0$ ) over distance  $D$  from the nest. The minimum GUD  $G_0$  can be found at the nest ( $D = 0$ ). The forager eats from the resources until  $D = D_{tot}$ . The light gray area in between the black and gray lines represents the amount of food units needed  $F$ . (b and c) Model predictions of food availability  $R_l$  at each location (black line) and giving-up density (GUD, gray line) as function of the distance  $D$  from the nest for 2 patterns of local food availability: (b) increasing with distance from the nest ( $m = -0.2$ , equation 1) and (c) decreasing with distance from the nest ( $m = 0.2$ ). Parameter values:  $a = 0.2$ ,  $b = 0.1$ ,  $F = 1$ ,  $R_0 = 1$ ,  $c = 0.2$ .

probability of the nest suffering predation, the predator selects the smallest value of  $k$  such that equation (5) is satisfied and the total resources harvested meets the requirement  $F$ , to fledge the nestlings. As  $h(D) = aG(D)$  and  $H(D) = R_l(D) - G(D)$ , we can write the optimization problem as:

$$\min(k) \text{ subject to } F = \int_0^{D_{tot}} (R_l(D) - \frac{\mu(D)}{ak}) dD. \tag{6}$$

The forager must select  $k$  such that the total harvest matches the needs of the nest  $F$ . Hence,  $k(F)$  is an increasing function of  $F$ . When  $\mu(D)/aR_l(D) > k$ , the initial food density at that distance is too low to justify the risk. If  $\mu(D)/aR_l(D)$  increases with  $D$ , as is likely the case for most natural circumstances, then  $D_{tot}$  satisfies  $\mu(D_{tot})/aR_l(D_{tot}) = k$ , and this will define the maximum foraging distance of the forager.

For the model presented here we can substitute equations (1) and (3) for  $R_l(D)$  and  $\mu(D)$ , respectively, into equation (6) to give an explicit form to the optimization problem:

$$\begin{aligned} \min k \text{ subject to } F &= \int_0^{D_{tot}} \left( R_0 + mD - \frac{b + cD}{ak} \right) dD \\ &= D_{tot} \left[ \left( m - \frac{c}{ak} \right) \left( \frac{D_{tot}}{2} \right) + \left( R_0 - \frac{b}{ak} \right) \right] \end{aligned} \tag{7}$$

Where:

$$D_{tot} = \frac{akR_0 - b}{c - akm}, \text{ when this expression is } > 0. \tag{8}$$

When equation (8) returns a negative value; then the home-range size goes to infinite, and the forager simply harvests an infinitesimal amount of food from each distance. Because of the feedback of these parameters on  $k$ , the only realistic means for the forager to want an infinite range size is if  $c = 0$  or  $R_0 = 0$ . This happens because in this model we are considering travel times and costs to be negligible relative to the cost of preventing nest predation. A travel cost or load size cost would once again result in a finite home-range size. For what follows, we assume that equation (8) returns a positive value.

Equation (7) can be solved to derive explicit results for how the various parameters relating to predation risk of both the nest and the forager, initial food abundances, and feeding needs of the nestlings (Table 1) influence  $k$ , the maximum foraging distance  $D_{tot}$ , and GUDs at the nest  $G_0$  and at different distances,  $G(D)$ .

## RESULTS

### Basic model

We start with the simple case of the model (Figure 1a) where initial food abundances are constant as the forager moves away from the nest. Thus,  $m = 0$  and  $R_l = R_0$  across all distances. This basic model investigates the role of increasing risk to the nest of foraging farther and farther from the nest. Setting  $m = 0$  in equations (7) and (8) and substituting (7) into (8) for  $D_{tot}$  returns an equation that is quadratic in  $k$  with the following solution:

$$k = \frac{abR_0 + aFc + \sqrt{a^2Fc(2bR_0 + Fc)}}{a^2R_0^2} \tag{9}$$

**Table 1**  
Variables in the model for foraging distance of a central place forager under the risk of nest predation

Variable	Description	Range
$F$	Total amount of food required	$0-\infty$
$h$	Harvest rate	equation 4
$\mu$	Nest predation risk	equation 3
$D$	Distance from the nest	$0-\min(R_0/m, (1-b)/c)$
$R_l$	Local food availability	equation 1
$a$	Foraging efficiency	$0-1$
$b$	Nest defensibility	$0-\infty$
$c$	Nest predation risk	$0-\infty$
$m$	Change in local food availability with distance from the nest	$-\infty-\infty$
$R_0$	Local food availability at nest	$0-\infty$
<i>Responses</i>		
$k$	Ratio between nest predation risk and harvest rate	equation 6
$D_{tot}$	Maximum foraging distance away from the nest	$0-\infty$
$H$	Total amount of resources to harvest at each distance	$0-\infty$
$G$	Distance-specific giving-up density	$R_f(D) - H(D)$

Thus, we can model foraging activity along the gradient away from the nest (Figure 1a). The GUD increases with distance from the nest, even though food availability is initially constant along this gradient. The ratio  $k$  increases with the risk of nest predation  $c$  over distance (Figure 2). Higher values for  $k$  mean that the forager is more constrained by predation risk (higher values of  $c$ ), which leads to a decrease in both  $D_{tot}$  (equation 8) and the GUD at the nest  $G_0$ .

To study the effect of food availability and nest predation on the maximum foraging distance  $D_{tot}$  we solved the model for  $D_{tot}$  with (1) increasing or decreasing food availability  $R_0$  around the nest while exploring cases where initial food abundance either increases,  $m > 0$ , or decreases,  $m < 0$ , with distance from the nest, (2) increasing the rate at which nest predation risk increases with the forager's distance from the nest,  $c$ , and (3) decreasing nest defensibility  $b$  while the forager is at the nest (Table 1), while keeping other parameters constant. Unless stated otherwise, we used parameter values:  $m = 0$ ,  $a = 0.2$ ,  $b = 0.1$ ,  $F = 1$ ,  $R_0 = 1$ ,  $c = 0.2$ . For the following results, equations (8) and (7) when combined produce an equation (cubic with respect to  $k$ ) that is not easily solved analytically. But, it is straightforward to derive numerical solutions.

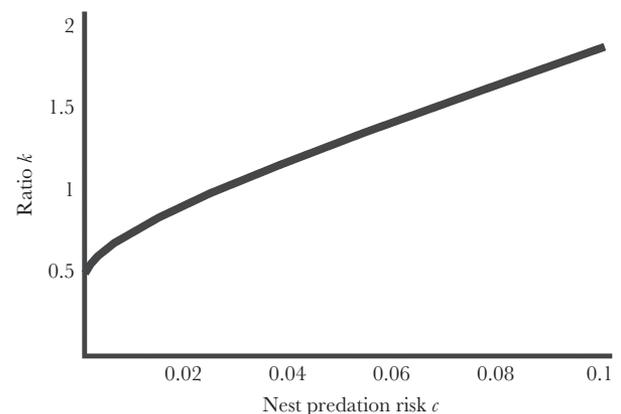
### Differences in Food Availability

Given a constant predation risk ( $b$ ,  $c$ ), foraging efficiency ( $a$ ), food availability at the nest ( $R_0$ ), and requirement ( $F$ ), we found that the maximum distance of the forager  $D_{tot}$  is shorter when the local food availability  $R$  decreases away from the nest ( $m < 0$ ) than when  $R$  increases away from the nest ( $m > 0$ ) (Figures 1b and c and 3a). This result is not surprising. By way of additional predictions, if  $m > 0$  then patch use is less thorough with higher GUDs and lower  $k$ , and vice-versa when  $m < 0$ .

An increase in the food availability at the nest  $R_0$  (which also increases the overall quality of the environment) leads to a decrease in  $D_{tot}$  which is further increased when local food availability increases away from the nest ( $m > 0$ ) (Figure 3b). Improved food availability, via  $R_0$  or  $m$ , leads to higher GUDs and lower  $k$ . When in response to feeding opportunities, a smaller home range will be associated with a higher  $k$  and higher GUDs. Similarly, reducing the amount of energy required to fledge the nest,  $F$ , has the same effect as raising overall food abundances.

### Differences in predation risk

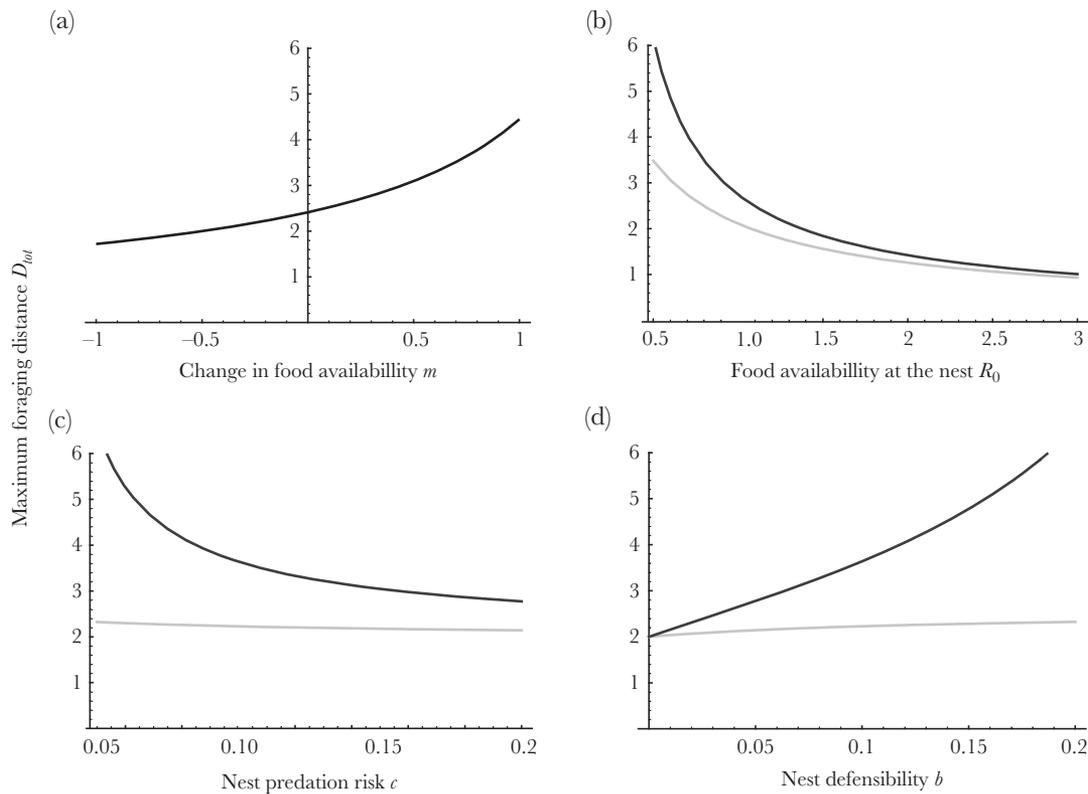
Given a constant foraging efficiency ( $a$ ), food requirement ( $F$ ) and availability at the nest ( $R_0 = 1$ ), we found that the maximum foraging



**Figure 2**

The ratio between predation risk and harvest rate  $k$  (equation 9) as a function of increase in nest predation risk along the distance away from the nest  $r$  (larger values for  $r$  imply that predation risk increases more steeply away from the nest). Parameter values:  $m = 0$ ,  $a = 0.2$ ,  $b = 0.1$ ,  $F = 1$ ,  $R_0 = 1$ ,  $c = 0.2$  (only for panel a).

distance  $D_{tot}$  decreased with change in nest predation with distance,  $c$  (Figure 3c), and declined with nest defensibility  $b$  (higher values of  $b$  infer lower nest defensibility; Figure 3d), but only when the local food availability increased with distance from the nest ( $m = 0.3$ ). When food availability was high close to the nest ( $m = -0.3$ ), both nest defensibility ( $b$ ) and predation risk ( $c$ ) had little effect on  $D_{tot}$ . Increasing the overall environmental predation risk,  $b$ , or the rate at which predation risk increases with the forager's distance from the nest,  $c$ , causes a large increase in  $k$  (Figure 2), but more subtle and smaller effects on GUDs. GUDs will always increase with distance from the nest reflecting the increased risk to the nest from the forager's absence,  $c > 0$ , and this increase will increase as  $c$  increases. In fact, as  $c$  increases GUDs will decline near the nest and increase away from the nest. Increasing overall risk to the nest independent of distance,  $b$ , strongly raises  $k$ . It too redistributes GUDs, but with the effect of increasing GUDs near the nest, decreasing them farther from the nest, and overall decreasing the increase in GUDs with distance. Hence, with CPF under the risk of nest predation, a higher steepness of the increase in GUDs with distance from the nest indicates either a higher  $c$ , lower  $b$ , higher environmental quality in terms of increases in  $R_0$  or  $m$ , or a lower provisioning requirement for the nestlings,  $F$ .



**Figure 3**

Model predictions of the maximum foraging distance  $D_{tot}$  as function of (a) the change of food availability away from the nest,  $m$  (for  $m < 0$ , local food availability decreases with distance from the nest and, for  $m > 0$ , it increases, equation 5); (b)  $R_0$ , the food available at the nest; (c)  $c$ , nest predation risk; (d)  $b$ , nest defensibility. Other parameter values were kept constant at:  $a = 0.2$ ,  $b = 0.1$ ,  $F = 1$ ,  $R_0 = 1$ ,  $c = 0.2$ . In panels b, c, and d, gray lines give values for  $m = -0.3$  and black lines for  $m = 0.3$  (note that the x axis does not start at 0 in panels b and c).

### Relative importance of parameters

Food availability at the nest  $R_0$  affected the maximum foraging distance  $D_{tot}$  slightly more than the change in food availability  $m$  did (Figure 4a), whereas  $m$  had a stronger effect on  $D_{tot}$  than did nest predation risk (Figure 4b). The provisioning requirements of the nest,  $F$ , and nest defensibility  $b$  had similar effects on the maximum distance  $D_{tot}$  foraged: both an increase in  $F$  and an increase in  $b$  resulted in a larger  $D_{tot}$ , but an increase in  $b$  had a stronger effect (Figure 4c). The predation parameters  $c$  and  $b$  had contrasting effects, but an increase in  $b$  has a stronger effect on  $D_{tot}$  than a decrease of  $c$  (Figure 4d). This implies that overall nest defensibility has the strongest effects on foraging distance, more so than food requirements  $F$  or rate of increase in predation risk with distance  $c$ .

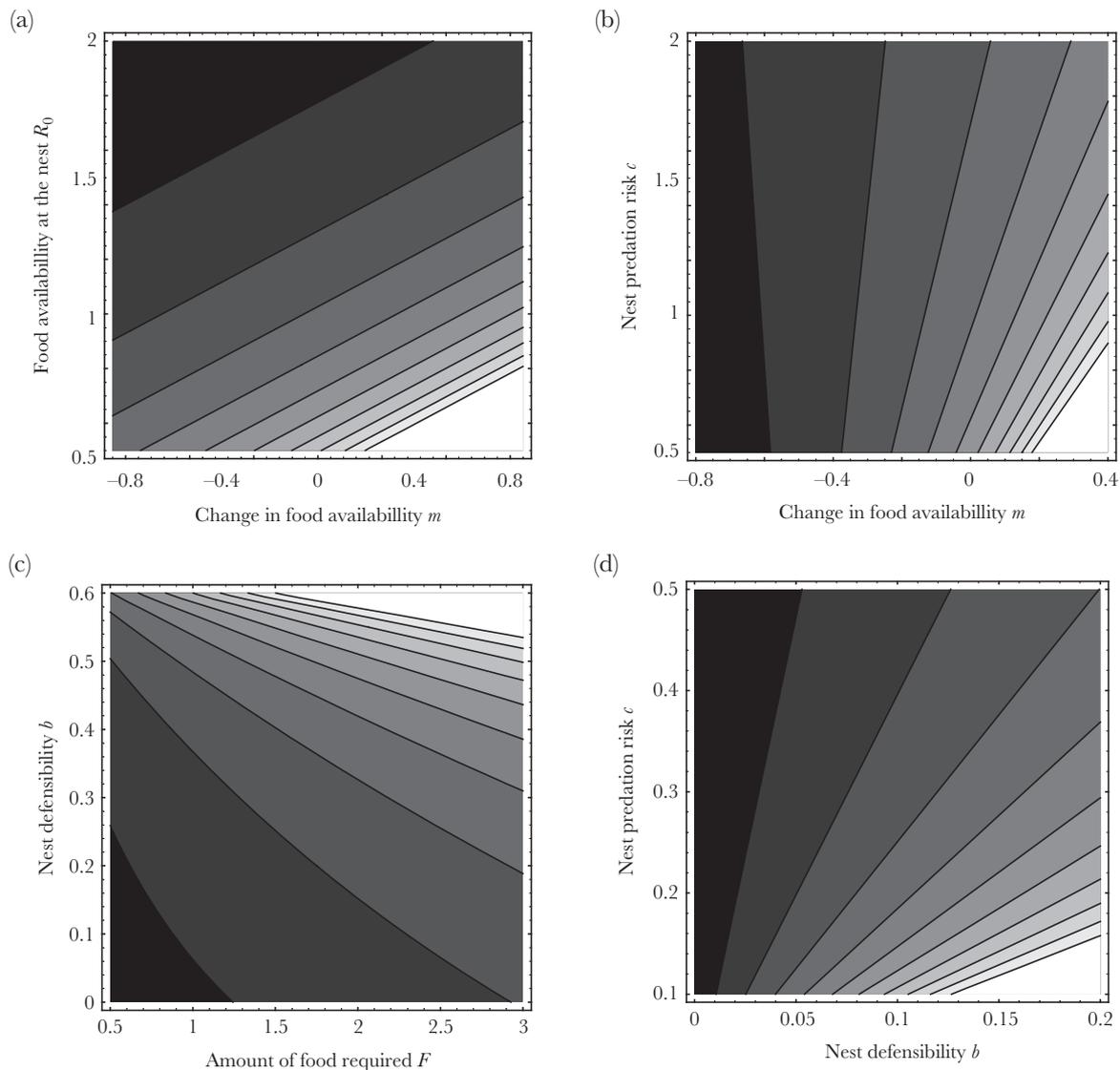
### Relaxing assumptions

We analyzed the model where the forager experiences a unidirectional, 1-dimensional environment. The nest is then at one side of a line that stretches away from the nest. Making the environment 1-dimensional and bidirectional (nest at the center of a line that stretches out in opposite directions), multiplies food availabilities with distance by 2 (except for right at the nest). If all parameters remain the same, then the qualitative predictions remain the same, but now the forager does not need to forage as far, and will have a steeper increase in GUDs with distance. The forager harvests  $F/2$  from each direction of its environment. The quantitative predictions of the uni versus bidirectional 1-dimensional environments

become equivalent by simply doubling  $F$  and halving  $b$  and  $m$  for the unidirectional environment.

In going to the 2-dimensional world, unless one adjusts initial food densities to fall sharply with distance, the farther one goes the more total food will be available. Relative to the 1-dimensional world, the total fraction of  $F$  harvested with distance will increase with distance in a 2-dimensional relative to 1-dimensional world. But, in the 2-dimensional environment there will be a sharper increase in GUDs with distance, all else equal. All qualitative predictions remain the same.

In developing the model, we assumed that there was sufficient time for the forager to achieve  $F$  and that there were no additional energetic or mortality costs to the forager of foraging or travelling to and from the nest. Hence, the number of visits to the nest, and the actual tactics for achieving the optimal GUDs with distance were not considered. The actual time required to harvest a patch from its initial abundance to the GUD is  $t = \{\ln[R_0(D)/G(D)]\}/a$ . Integrating over the entire harvest gives the amount of time the forager spends away from the nest. If this entails additional needs for food consumption by the forager then its total harvest must be  $F$  plus the needs of the forager. The model is still tractable numerically but not analytically by adding the time to harvest resources, travel times back and forth to the nest, and consideration of load size. Regardless, such considerations will simply increase the total amount of resources harvested, raise the quitting  $\mu/h = k$ , and result in lower GUDs overall, a larger home-range size, and a less steep increase of GUD with distance. Qualitative results will all remain the same.



**Figure 4**

Heat maps of the predicted maximum distance  $D_{tot}$  that the forager moves away from the nest as a function of (a) change in food availability  $m$  and food availability at the nest  $R_0$ ; (b) change in food availability  $m$  and nest predation risk  $c$ ; (c) the amount of food required  $F$  and the nest defensibility  $b$ ; and (d) nest defensibility  $b$  and nest predation risk  $c$ . Lighter gray represents high values of  $D_{tot}$ . For panels a and b, other parameter values were kept constant at:  $a = 0.2$ ,  $b = 0.1$ ,  $F = 1$ ,  $R_0 = 1$ ,  $c = 0.2$  (panels a and b) or at:  $a = 0.2$ ,  $R_0 = 1$ ,  $m = 0.2$ ,  $c = 0.3$  (panels c and d).

## DISCUSSION

We modeled and investigated how nest predation risk and defensibility affect the foraging distance, and thus home-range size, of central place foragers. We found that 1) foraging distance declined with food availability (see also Olsson and Bolin 2014), 2) foraging distance declined when the risk of predation to the nest increases with the forager's distance from its nest, such foragers stay closer to the nest, while 3) foraging distance decreased with nest defensibility, that is, foragers unable to defend their nest moved farther away, and 4) when food was abundant, the predation risk to the nest had little effect on foraging distance when food was abundant. This means that the effect of the ability of the forager to defend the nest ( $b$ ) and increase in nest predation risk with distance ( $c$ ) on foraging distance and home-range size can be significant, especially when food availability is low. Including these effects in models of central place foraging may improve predictions.

Our work connects with previous CPF models by our finding that nesting foragers in landscapes with high food availability will adopt smaller home ranges, as found in the habitat selection model of Olsson and Bolin (2014). Also, when predation risk of the nest or forager ( $c$ ) increases with distance from the nest, organisms will attain smaller home ranges, as previously suggested by Olsson et al. (2008) based on higher GUDs and smaller load sizes at more distant foraging patches. Smaller territories under increased predation risk are indeed found for sticklebacks when cover from predators was experimentally removed (Candolin and Voigt 2001). Appending to existing knowledge, we find foraging distance to be most sensitive to nest predation risk ( $c$ ) when food availability at the nest location ( $R_0$ ) is low and increases with distance from the nest ( $m > 0$ ). Foragers must range far from the nest to collect food, and will range substantially less as risk to the nest increases. In landscapes where food is abundant, foragers that nest on a spot with high food availability ( $m < 0$ ) can stay close to their

nest and change their ranging patterns little in response to changes in predation risk.

Assuming that a larger foraging distance translates into a larger home range, our findings agree with several empirical examples. In Eurasian oystercatchers *Haematopus ostralegus* (Ens et al. 1992), territories with high egg survival were located adjacent to the feeding area ( $m < 0$ ), whereas territories with low egg survival had the nesting area separated from the feeding area ( $m > 0$ ). Birds in the latter territories had lower egg survival (van de Pol 2006), probably because parents spend more time away from the nest. Higher predation pressure under low food availability was also found in Seychelles warbler *Acrocephalus sechellensis*, which faced a trade-off between nest guarding and foraging, resulting in higher egg predation rates in territories with low food availability (Komdeur and Kats 1999). In our model, the relative importance of nest predation risk is greater than food availability, but it depends on the landscape, as foraging distance is more strongly influenced by nest defensibility (foraging distance increases with  $b$ ) than by the total demand for food units ( $F$ ), only in landscapes with low food availability.

Our study indicates that foraging distance can be strongly affected by perceived nest predation risk, but that foraging distance also depends on characteristics of the forager. Let us imagine a goose (*Anseriformes*) incubating eggs on a nest, a period during which bird species typically act as central place foragers, alternating long incubation bouts on the nest with short foraging visits in the close surroundings (Shojit et al. 2011). The goose is incubating on a nest on an island without mammalian predators, but has to leave the nest to forage in order to survive the incubation period. Eggs in the nest can be robbed by gulls (*Larus* sp.) when the goose is absent from the nest ( $c > 0$ ), but not when it is present ( $b = 0$ ; B  ty et al. 2002; de Fouw et al. 2016). Our model predicts that this goose will stay close to the nest during foraging, to prevent the gulls from robbing eggs. This prediction matches the incubation strategy of the Emperor goose *Chen canagica* (Thompson and Raveling 1987), a relatively large goose species that faces a high risk of nest predation by avian predators such as gulls when it is away from the nest (high  $c$ ), but this goose is effective in repelling these predators while at the nest (low  $b$ ). As predicted, this species has a higher nest attendance than smaller goose species, and forages close to the nest. According to our predictions, such an incubation strategy is only possible when food availability close to the nest is sufficient (de Fouw et al. 2016). If we replace the gulls in our model by foxes, which can attack the goose even while on the nest ( $c = 0$ ,  $b > 0$ ), then even this large species is predicted to forage farther away from the nest. The situation becomes more complex when both predators are present ( $c > 0$ ,  $b > 0$ ), but increasing risk of predation by foxes (higher  $b$ ) should have a larger effect on foraging distance than increasing risk of predation by gulls (higher  $c$ ). This is especially true for geese, as they are long-lived species that will put their own survival over the survival of their nests.

Our model can also be used to explore how the maximum foraging distance is affected by predation risk to the forager itself, when the nest or burrow does not require protection. Rodents such as rabbits or marmots are usually safe when at or inside their burrow ( $b = 0$ ), but face an increasing risk of predation as they forage farther away from the burrow ( $c > 0$ ). These rodents will tend to stay close to the burrow, as found in many burrow residing rodents (Blumstein 1998; Thorson et al. 1998) and hyraxes (Druce et al. 2006). When food availability is high, the effect of predation on maximum foraging distance becomes less important, as shown

experimentally for rabbits, which spend a longer time on patches where food quality is increased regardless of increased predation risk (Bakker et al. 2005). Interestingly, the foraging distance of these animals is expected to increase when their burrow becomes less safe, for example, when predators such as snakes are able to penetrate the burrow (Figure 3d).

It is important to note that the specific predictions of our model depend on the model's assumptions. For example, we do not consider time for traveling between the nest and foraging sites. Patches at larger distance will require a longer travelling time, which can decrease their profitability (Lima et al. 1985; Olsson et al. 2008; Olsson and Bolin 2014). Also, we assume that food gets depleted, yet food may also be renewable, for example, for foragers that feed their young over a prolonged period. In addition, we assume a fixed requirement  $F$ , yet foragers may be able to reduce their foraging effort  $F$  when perceiving high predation risk, for example, by raising fewer or lower-quality offspring (Eggers et al. 2006). Modifying these assumptions would result in a smaller predicted foraging distances and a steeper increase in GUDs with distance. Finally, the linear response in nest predation risk  $c$ , as has been chosen for simplicity, may not be entirely realistic as this means that nest predation risk runs up to 100% at a certain distance from the nest. This may indeed not reflect reality, and a saturating function may be more realistic.

We also did not consider a potential increase in detection probability by predators when foragers spend longer periods of time, or make repeated visits to the nest (Roper and Goldstein 1997; Wheelwright & Dorsey 1991). When foragers stay closer to their nests, this may also increase the detection chance and simultaneously increase nest predation risk. In this view, it becomes relevant to what extent foragers are able to defend their nest, as nest detection by predators may be less problematic for foragers that can defend their nest. Finally, our results do not apply to foragers that take turns in guarding the nest, for example, in incubating shorebirds (Bulla et al. 2016). Taken together, the results of our model may not apply to all cases of CPF, as in some cases other aspects may be more important determinants of foraging distance than predation risk.

In conclusion, we find that nest predation risk and the ability of the forager to defend the nest can be important determinants of foraging distance and ultimately home-range size, especially in landscapes where food availability is low. Although the importance of supplemental feeding has been studied extensively in experimental studies, with significant effects on home-range size (reviewed by Boutin 1990), the effect of nest predation risk is still largely unknown. It is, however, relatively easy to manipulate perceived nest predation risk for nesting animals, by placing (stuffed) predators in close proximity to their nests (Hakkarainen et al. 2002; Desrochers et al. 2002). Different types of perceived predation risk and thus differences in nest defensibility can be achieved by using a range of predators (Templeton et al. 2005), either dangerous for both the forager and the nest or for only the forager. Especially, given the recent availability of increasingly small and affordable electronic tracking devices, it has also become easier to measure home range remotely in many animals (Kays et al. 2015). We, therefore, encourage experimental studies to further explore the importance of nest predation risk and defensibility. Our study contributes to developing theory for central place foraging and provides predictions for future empirical studies on home-range sizes.

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