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Struggle for safety

van den Hout, Pieter Johannes

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Evaluating patch use decisions by extending Brown's patch use model with a parameter for interference

Piet J. van den Hout, Joel Brown, Sjoerd Duijns and Mary Ngozi Molokwu

One way of trying to understand why some birds forage in locations that are not only more dangerous but in which the danger is not compensated by higher food abundance, is by evaluating patch use decisions in the face of predation. We include the influence of stronger competitors by expanding the patch use model in Brown and Kotler (2004) with a parameter for competitive foraging. The patch use model is based on the patch departure rule, meaning that a forager should leave a patch at the point where energy gain no longer outweighs foraging costs (Brown, 1988). For our wintering Red Knots we assume that they attempt to maximize the probability of surviving over the non-breeding season with the requirement of maintaining a certain energy state. We therefore apply the following fitness formulation (Brown, 1988):

$$\text{Max } p \text{ subject to } F \geq k \quad (1)$$

where p is the probability of surviving predation over a finite time interval. F is the survivor's fitness, and k is the individual's energy state.

For this fitness formulation Brown derived the optimal patch use strategy, stating that a patch should be left when the benefits of the reward rate H no longer exceeds the sum of metabolic costs C , predation costs P , and missed opportunity costs MOC of foraging. The MOC , which like the other costs may have units of energy per unit time, items per unit times, or units of resource per unit time, places a value on alternative fitness enhancing activities (Brown and Kotler, 2004). $H = C + P + MOC$, as derived by Brown for optimal patch strategy (Brown, 1992), can be recognized in the following formula:

$$H = C + \frac{\mu\mathcal{P}}{\varphi_F(\delta_F/\delta_e)} + \frac{\varphi_t}{\varphi_F(\delta_F/\delta_e)} \quad (2)$$

Here μ is predation danger; it is converted into the currency of H by multiplying the predation danger by the marginal rate of substitution of energy for safety. δ_F/δ_e is the marginal value of energy. φ_t is the marginal fitness value of time if the time constraints were relaxed by providing more time, and φ_F is the marginal survivorship value of favourably adjusting the energetic-state constraint (Brown and Kotler, 2004, Olsson *et al.*, 2008).

We now extend equation 2 with the interference effects exerted by dominants, in this case adults N_a , and affecting the foraging costs experienced by subordinate juvenile birds. The dominants may influence the foraging costs of subordinates in several ways. First, we assume dominants to increase the metabolic cost of foraging C such that

$$C = c + \frac{a_m N_a}{X_m + N_a} \quad (3)$$

Here c denotes baseline metabolic foraging costs, a_m is the maximum adult effect, and X_m is the half-saturation constant.

Second, we assume that, within a patch, adults increase predation danger for juveniles, e.g. by chasing them towards intrinsically more dangerous foraging locations, such as the periphery of the group. We again assume a saturating effect, such that

$$\mu_j = m + \frac{a_p N_a}{X_p + N_a} \quad (4)$$

Here m is the baseline predation danger, a_p is the maximum adult effect, and X_p is the half-saturation constant.

Third, we assume adults to directly affect the feeding rate H such that the feeding rate becomes

$$H = f_j e^{-a_f N_a} \quad (5)$$

Here, f_j is the maximum feeding rate of a juvenile, which is slowed down by the presence of adults according to $e^{-a_f N_a}$, where a_f is a constant. Bringing these parts together and substituting in equation 2 gives:

$$f_j = c e^{-a_f N_a} + \frac{a_m N_a e^{a_f N_a}}{X_m + N_a} + p e^{-a_f N_a} \left(m + \frac{a_p N_a}{X_p + N_a} \right) + \frac{\varphi_t e^{a_f N_a}}{\varphi_f(\delta_F/\delta_e)} \quad (6)$$

The more additional foraging costs adults inflict upon a juvenile j , the fewer adults the latter should tolerate in its presence. In fact, the number of adults tolerated before the bird should leave the patch is determined by a foraging cost plateau set by the juveniles (Fig. IV.1). We evaluate the effects of predation on the number of adults tolerated by juveniles, by imposing three levels of predation costs related to

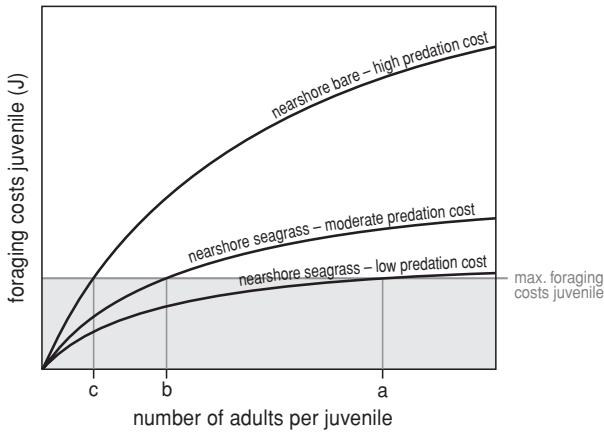


Figure IV.1 This graph shows the foraging costs as a function of the number of adults (dominants) relative to juveniles (subordinates) for three levels of predation costs, corresponding to far-shore seagrass (low cost), nearshore seagrass (moderate cost) and nearshore bare habitat (high cost). If foraging in a far-shore seagrass habitat, juveniles should leave when the foraging costs inflicted by adults cross the foraging cost plateau set by the juveniles and are forced to forage in a patch that incurs higher predation costs (from a to b). When incoming tide forces more adults to forage in nearshore seagrass they again drive juveniles towards a cost plateau forcing them to leave to near-shore bare habitat (from b to c).

habitat (near-shore bare, near-shore seagrass, and far-shore seagrass respectively; Fig. IV.1). Far-shore seagrass beds are safest as predators rarely hunt here (encounter probability of $0.03 \text{ raptors h}^{-1}$) and due to the openness of the landscape detection chances are high, so lethality of attack must be low. Seagrass beds at moderate distance to shore are more dangerous (encounter probability of $0.28 \text{ raptors h}^{-1}$); while the dune-bordered bare habitat are most dangerous for not only the encounter probability is relatively high ($0.17 \text{ raptors h}^{-1}$), but as birds forage approximately 0-40 m from obstructive cover created by vegetated dunes, lethality of attack must be very high (Dekker and Ydenberg, 2004, van den Hout *et al.*, 2008, Cresswell *et al.*, 2010). Thus, we assign far-shore seagrass beds as 'safe', near-shore seagrass beds as of 'moderately dangerous', and near-shore bare habitat as 'very dangerous'.

We predict that in a scenario where predation danger is not compensated by food abundance: (a) foraging decisions of subordinate birds must be governed by the foraging costs that dominant birds inflict on them, (b) in order to avoid starvation juveniles put a maximum on the foraging costs they accept, and (c) foraging cost levels increase as a function of danger, decreasing the threshold level of dominants that renders a patch unprofitable for a juvenile; the proportion of juveniles in a flock should therefore decrease with increasing numbers of adults at incoming and outgoing tides (Fig. IV.1, from a to b to c).

Although we have indications that such mechanisms actually occur (Chapter 5), we need more data on age-related foraging patterns, particularly in far-shore seagrass, to prove our point.