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Modeling scan and interscan durations in antipredator vigilance

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Many prey species alternate between bouts of foraging and bouts of antipredator vigilance. Models of vigilance typically predict how much total time prey animals should allocate to vigilance but do not specify how that time should be scheduled throughout foraging. Here, we examine how the scheduling of vigilance pays off in terms of food intake and predator detection. Specifically, we study how changes in ecological factors affect the expected duration of scans to look out for predators and the duration of interscan intervals dedicated to foraging. Our framework includes factors like the risk of attack, how difficult it is to locate food and predators, and the distance to protective cover. Our individual-based model makes several predictions about scan and interscan durations, which are discussed in relation to the available empirical evidence in birds and mammals. This model of antipredator vigilance is a first step in incorporating constraints related to food gathering and the detection of predators. Adding such constraints adds a novel dimension to vigilance models and produces a variety of predictions that await empirical scrutiny.

1. Introduction

Many species interrupt foraging to scan their surroundings for predators (Beauchamp, 2015). Performance in this case depends on the amount of food collected, conditional on evading predation through vigilance. In alternating bouts of foraging and vigilance, food intake will increase or predator detection will be more efficient when more time is available to feed or to scan for predators, respectively. Given that time is limited, the best balance between foraging and vigilance will likely be a function of how exactly investment in time pays off in terms of food intake or predator detection. However, earlier antipredator vigilance models, which have been used to predict how much time should be allocated to foraging and to vigilance, have made simplifying, and sometimes restrictive assumptions about how investment in time is related to both food intake and predator detection.

In the first explicit model of antipredator vigilance, animals alternated between foraging and scanning bouts. Food intake was not modeled, however, and scan duration was assumed to be small and constant (Pulliam, 1973). Predator detection occurred during the duration of a scan but (given that scan duration is short) the model implied that the probability of predator detection was independent of scan duration and that longer scans would be wasteful. A further refinement of this model took a time-budget approach, trying to predict how much time should be allocated to both foraging and scanning (Pulliam et al., 1982). In this model, animals still alternated between foraging and scanning bouts, and scanning was still assumed to last a small and fixed amount of time. Foragers required a fixed total feeding time and this feeding time was directly

proportional to the amount of time spent foraging, thus assuming indirectly that food intake increases linearly with foraging bout duration. Another influential model of vigilance also used a time-budget approach, but how animals partition time into bouts of foraging and bouts of scanning was not specified (McNamara and Houston, 1992). In an elaboration of their basic model, McNamara and Houston considered that longer scans would increase the probability of predator detection but with diminishing returns. However, they did not relate this particular function to any known mechanism and did not consider the possibility that a change in scan duration could also have an impact on foraging. Some studies introduced a scale-free parameter to model the effectiveness of vigilance to detect predators, but this was not directly related to scan duration (Ale and Brown, 2007; Brown, 1999). Finally, a more recent model assumed that detection occurs instantaneously during a scan (Scannell et al., 2001).

It has long been thought that the quality and quantity of information obtained during a scan should vary with scan duration (Desportes et al., 1991), but this has generally been ignored in models that explore both food gathering and antipredator vigilance. Empirically, it is clear that scan duration is not always short and that scans are often variable in duration (Cowlishaw et al., 2004; Creel et al., 2008; McVean and Haddlesey, 1980). In addition, in a recent review of the literature in birds, scan duration was shown to vary with group size in many species (Beauchamp, 2008). It seems likely that longer scans can allow individuals to view a larger portion of their surroundings (Fernández-Juricic, 2012), thus allowing a greater chance of detecting an approaching predator. Interestingly, scan duration and frequency can vary depending on how food

intake changes with time spent foraging, or with the difficulty of the foraging task (Lawrence, 1985; Lendrem, 1983; Popp, 1988). For instance, scan duration may be curtailed if the rate of food intake is slower.

In terms of foraging, the relationship between food intake and bout duration is probably more complicated than assumed previously. Food intake may not always increase linearly in an essentially deterministic way with the length of a continuous block of time spent foraging. This may be a reasonable approximation for a forager feeding on small, abundant food items that are not hidden from the forager; an example of this might be filter feeding. However many foragers are searching for discrete prey that are hard to detect and scattered across the environment, requiring considerable concentration to detect. In this case, prey capture becomes a more stochastic process over timescales relevant to individual intervals between antipredator vigilance scans (Carrascal and Moreno, 1992; Fritz et al., 2002).

Summing up, previous models of antipredator vigilance have often made restrictive assumptions about how animals acquire resources and detect predators. A different approach is needed to open up the black box of individual choices in these functional models and incorporate constraints related to food gathering and predator detection. Our model provides explicit solutions for interscan (i.e. foraging) and scan durations when incorporating such constraints. That is, we allow flexibility both in the frequency with which antipredatory scans occur and the length of those scans, and we examine the impact of the combination of both of these behavioural factors on food gathering as well as predator detection.

In essence, we aim to provide a bottom-up model of vigilance (based on individual behavioural events) to complement the top-down approach (based on overall distributions of events or mean values) used in earlier models (Fernández-Juricic et al., 2004). These top-down models tell us how much time should be allocated to foraging and scanning but do not address the precise way animals organize their foraging and scanning bouts. Some recent vigilance models have also used a more bottom-up approach (Beauchamp et al., 2012; Jackson and Ruxton, 2006; Sirot and Pays, 2011), and we adopt a similar approach to describing the organization of foraging and scanning bouts.

2. The model

We follow the ODD protocol (Overview, Design concepts, and Details) to describe the individual-based model (Grimm et al., 2006). The model was implemented in FreeBasic.

2.1 Purpose

To evaluate how constraints related to food gathering and the detection of predators can affect vigilance and foraging (Fig. 1).

2.2 State variables and scale

The unit of the model is a single individual, called a forager, searching for food and exposed to predation threats. Foragers experienced one of two mutually exclusive states: searching for food and vigilant. Foragers searched for food during an interscan interval and maintained vigilance during a scan. We leave aside the situation where vigilance can also be carried out during food search as it would require additional

assumptions about potential trade-offs between food search and vigilance. Attacks by a predator occurred at random times irrespective of the forager's state.

The model simulated the search for food as a function of time but did not include an explicit spatial component. Only distances between the predator and forager and between the forager and protective cover were explicitly specified. The predator, forager and protective cover could be imagined as lying on a straight line. Time is discretized into short time steps of equal duration. Each time step allowed the predator to get closer to the forager or increased the chances that the forager obtained food.

2.3 Process overview and scaling

At each time step, the predator could appear with a fixed probability P_{pred}. Concretely, if a random number drawn from a uniform distribution (scaled between 0 and 1) was lower than P_{pred} then the predator appeared at a fixed distance D_{pred} from the forager; otherwise, the predator remained absent. D_{pred} can be thought of as the maximum distance at which predators can be detected. This will be constrained by the physical environment, cryptic traits of the predators, and sensory and cognitive systems of the forager. After initial appearance, the predator moved S_{pred} units of distance per time step toward the forager. The predator remained in the habitat until the forager was captured or until the time the forager detected the predator, fled from it and successfully reached protective cover. Only at most one predator could be present at a time.

We consider first the case where the predator was absent. At the beginning of each time step, the forager could be vigilant or searching for food. Time was

incremented by one unit. If the forager was searching for food and the updated time was lower than the set interscan duration, the forager remained in the searching state for the next time step. If the updated time reached the set interscan duration, the forager switched to the vigilant state at the next time period. At each time step during search, the forager can obtain a food item with probability P_{food}. Concretely, if a random number drawn from a uniform distribution (scaled between 0 and 1) was lower than P_{food} then the forager obtained one food item; otherwise, no food was obtained. If P_{food} is relatively small, the cumulative number of food items collected during one interscan will follow a Poisson distribution. If the forager was vigilant instead and the updated time was lower than the set scan duration, the forager remained in the vigilant state for the next time step. If the updated time reached the set scan duration, the forager switched to the searching state in the following time step. No food was obtained during vigilance.

We turn now to the case where the predator was present and the forager was searching for food. The predator moved toward the forager by distance S_{pred} during the time step. If the updated distance between the predator and the forager was greater than zero, which means that capture was not possible, the forager remained in the same state or switched to vigilance in the following time step using the rules described above. An attack was successful if the distance between the predator and the forager was equal to zero. In this case, survival for the forager in this simulation was set to zero and a new simulation started.

If the forager was vigilant, the predator also moved toward the forager by distance S_{pred} during the time step. Unless the updated distance closed the gap between the predator and forager to zero, the forager detected the predator with probability P_{detect}, which depended on the updated distance between the predator and forager. The relationship between P_{detect} and this distance is described in the submodel section. Concretely, if a random number drawn from a uniform distribution (scaled between 0 and 1) was lower than P_{detect} then the forager detected the predator; otherwise, the predator was not detected. The probability of failing to detect the predator over successive time periods during one scan decreases in a geometric fashion so that longer scans yield a higher probability of detection but with diminishing returns. If the predator was not detected, the forager remained vigilant or switched to searching for food using the above rules. If detection occurred, the forager moved S_{prey} units of distance per time step towards cover located D_{cover} units of distance away. If the time needed by the forager to reach cover was greater than the time needed by the predator to get to the forager then the forager was captured, survival was set to 0 in this simulation, and a new simulation started. Otherwise, the forager survived and the time needed to escape was added to the current time before the next time step. The forager then resumed its foraging activities as before with no further delay.

Fitness was calculated at the end of the simulation. If no capture occurred during the simulation, the total number of food items collected was translated into fitness units with a function described in the submodel section. Fitness F ranged between 0 and 1.

2.4 Design concepts

One simulation lasted 9000 time steps or until the moment of capture. A set of 1000 simulations was performed for each possible combination of scan and interscan duration. Scan and interscan duration could each last from 1 to 20 time units, and the 400 possible combinations of the two durations were each tested in a set of 1000 simulations. Average fitness was calculated over a set of 1000 simulations, and the combination of scan and interscan duration that yielded maximum fitness was determined. This process was repeated 15 times, with a different seed for the random number generator each time, in order to get an estimate for the mean and standard deviation for maximum fitness, vigilance and searching times.

2.5 Initialization

The predator was absent at the beginning of each simulation and the forager was vigilant.

2.6 Input

No external variables were included in the model.

2.7 Submodels

The total number of food items collected during one simulation was translated into fitness units using a sigmoidal function (s-shaped, Table 1). Fitness F was the probability of future survival given the number of food items collected. Fitness first increased slowly with the number of food items collected and then more rapidly before reaching a plateau at the largest values. The sigmoidal function used to describe fitness is characterized by two parameters, namely, k and m. An increase in the value of m shifts

the distribution to higher values, which means that more items must be collected to achieve the same fitness. The parameter *k* controls the shape of the distribution with higher values flattening the s-curve. With this function, collecting more food items produces small increments in fitness if the total number of food items collected is either very small or very large. Future survival thus most strongly increased with intermediate values of collected food items, a usual assumption in foraging models (Houston et al., 1993).

For a given scan duration, the probability of detecting the predator varied in a sigmoidal fashion with the distance between the predator and forager: the probability was close to one when the predator was close and decreased rapidly thereafter before reaching a plateau at low values when the predator was further away (Fig. 2). The ability to visually detect threats decreased rapidly with distance in this manner in birds (Fernández-Juricic and Kowalski, 2011; Moore et al., 2013; Tisdale and Fernández-Juricic, 2009). A greater visual acuity would result in the detection of threats at a greater distance. The presence of visual obstacles in the local environment, like vegetation cover or rocks, can also reduce the ability to detect a threat at a given distance (Arenz and Leger, 1997; Devereux et al., 2006; Lima and Zollner, 1996).

2.8 Parameter values

The model was evaluated over a range of values changing one variable at a time (Table 1). Predator speed was set at higher values than prey escape speed to reflect the larger body size of predators. The specific ratio that we selected applies to birds of prey attacking small prey bird species (Lind et al., 2002). This would apply broadly to other

carnivore systems where predators are also expected to weigh about 10 times more than their prey (Vézina, 1985). In addition to scan and interscan duration, we also calculated scan rate (number of scans per 60 time units) and the percentage of time spent scanning, which was given by the average scan duration divided by the sum of average scan and interscan duration. We used a polynomial regression to illustrate trends between each of these dependent variables and each independent variable tested.

3. Results and discussion

3.1 Probability of predator presence

An increase in the probability of predator presence per unit time, which translates into a higher risk of attack, produced a large, non-linear decrease in fitness (Fig. 3a). As the risk of attack increased average scan duration increased in a non-linear fashion and interscan duration decreased more substantially (Fig. 3a,b). As a result, both scan rate and time spent scanning increased (Fig. 3c,d). Although these trends are consistent, there was sometimes strong variation between replicate runs, suggesting a relatively flat plateau in terms of the fitness value of solutions around the optimal.

Lower fitness when the risk of attack is higher ensues because of the direct loss of life during a predation event. Indirect effects include the lower rate of food intake due to higher vigilance and the time lost in seeking cover if the attacker is detected before it is too late. The response to the rate of attack included an increase in scan duration but also a decrease in interscan duration. Since the decrease in interscan duration was larger than the increase in scan duration, scan rate increased with attack

rate. Therefore, it appears that the best response to an increase in the rate of attack is to increase the quality of a scan and the frequency of scanning at the expanse of foraging. Increasing the quality of a scan allows individuals to detect predators sooner, which increases the chances of seeking cover safely. Increasing the rate of scanning reduces the amount of time spent unable to detect predators.

Predator presence is a well-known factor leading to longer scans in birds and mammals (Dacier et al., 2005; Devereux et al., 2006; Glück, 1987; Li et al., 2009; Mathot et al., 2009) although there are exceptions (Jones et al., 2007; Lima, 1992). Scan duration is also known to increase when animals are disturbed by people (Dyck and Baydack, 2004). However, our model is concerned with proactive vigilance (before the predator is in sight) rather than vigilance after detecting a threat. As predicted by the model, scan duration increased in kudus (*Tragelaphus strepsiceros*) when the immediate risk of attack by African lions (*Panthera leo*) was higher although no such responses occurred in two other less preferred prey species (Périquet et al., 2012). A similar increase in scan duration was detected in a shorebird foraging in a habitat with a higher risk of attack (Barbosa, 1997) and in a small passerine bird foraging in more exposed parts of their habitat (Carrascal and Moreno, 1992).

3.2 Detection in relation to distance

Predator detection is expected to be high when the distance between the predator and forager is small and lower otherwise. When the mid-point of the sigmoidal function for detection is larger, the probability of detecting the predator remains higher longer (Fig.

2) implying that detection is more likely when the predator is further away. An increase in the mid-point values should thus lead to greater safety.

An increase in predator detection ability, caused by this shift in the mid-point value of the sigmoidal function, led to an increase in fitness (Fig. 4a) and a decrease in interscan duration (Fig. 4b). Scan duration first increased and then decreased with increasing detection ability (Fig. 4a). As a result, scan rate increased slowly at first and then faster with detection ability and time spent scanning generally increased (Fig. 4c, d).

Foragers reduced scan duration when predators were easier to detect at least over a certain range of detectability. Since shorter scans provide less information about predator presence, foragers compensated by decreasing interscan duration to increase scan rate. This strategy of using more frequent but less informative scans works well when predators are likely to be detected further away. In the situation where predators are more difficult to detect, foragers also switched to a strategy of shorter scans, suggesting that scans can be short when their utility is low. In the extreme case where detection can only occur at very short distances, scans would become even shorter because scanning might often be insufficient to allow successful escape. We believe this is what explains why scan duration first increases and then decreases with detection ability.

In three small passerine birds, which often forage together in mixed-species flocks, the species with the highest visual acuity (thus able to detect threats from further away) moved the head the least during vigilance (Moore et al., 2013), but the

relationship between scan duration and head movement rate was not investigated.

House sparrows (*Passer domesticus*) have a lower visual acuity than European starlings (*Sturnus vulgaris*) and so can detect predation threats at a given distance less accurately (Tisdale and Fernández-Juricic, 2009). Yet, house sparrows adopted a vigilance strategy including shorter but more frequent scans than starlings, which is the opposite of that predicted here. The difficulty with interspecific studies is that different species can vary in a number of traits besides visual acuity. For instance, house sparrows are smaller than starlings and have a smaller blind area, which might select for an increase in scan frequency at the expense of scan duration. Intraspecific studies are needed to examine the effect of predator detection distance on vigilance strategies, perhaps altering the physical environment between treatments to control ease of detection at different distances.

Detection ability can be related to visual obstructions. In a more visually-cluttered habitat, visual detection of a threat at a given distance is probably more difficult. Several studies have related scan and interscan duration to the degree of visual obstructions in the habitat. Alpine marmots (*Marmota marmota*) increased scan frequency but not scan duration in more visually-obstructed habitats (Ferrari et al., 2009). European starlings foraging in more visually-cluttered habitats reduced scan duration and interscan duration to increase scan rate (Devereux et al., 2006). Starlings increased their scanning when barriers blocked their lateral view but this scanning was mostly aimed at conspecifics rather than predators (Fernández-Juricic et al., 2005). Two species of ducks that adopted a foraging mode restricting peripheral vision reduced

both scan and interscan duration to achieve a higher scan frequency (Guillemain et al., 2001). By contrast, Eurasian teals (*Anas crecca*) that foraged for longer periods underwater, during which time predators cannot be detected, increased scan duration (Pöysä, 1987). Chaffinches (*Fringilla coelebs*) foraging in a field with longer swards (more limited visibility) increased scan duration but not scan rate (Whittingham et al., 2004). Dark-eyed juncos (*Junco hyemalis*) increased scan duration and scan rate when peripheral vision was obstructed with small walls (Lima and Bednekoff, 1999). American pronghorns (*Antilocapra americana*) adopted the same vigilance strategy in habitats with more limited visibility (Goldsmith, 1990). When foraging on tree trunks that can block their ability to detect predators, downy woodpeckers (*Picoides pubescens*) did not alter scan duration with the size of the trunk (Lima, 1992).

The above evidence is mostly contradictory and as such the support for the model predictions is mixed. It appears that two strategies are available when predator detection is impaired: one strategy is to increase scan rate, which is typically achieved by reducing scan duration, and the other is to decrease scan rate by increasing scan duration. There are some costs in achieving a higher scan rate. In particular, the time spent raising and lowering the head must increase with scan rate (Studd et al., 1983), and it might be the case that these costs are more prominent for some species; which would explain why different species adopt different vigilance strategies. We did not include the cost of switching between activities in the model, but future implementations could investigate what happens when such costs are considered.

3.3 Food availability

Longer interscan duration might be needed to find food items that are difficult to locate. For instance, cryptic food might be more difficult to detect against the background resulting in a longer interval being required between scans to find food items. This is also true if prey are not especially cryptic but are scattered at low density in the environment.

As expected, fitness increased when the probability of finding food increased (Fig. 5a). Fitness reached a plateau at higher values of the probability of finding food, which probably reflects the saturating sigmoidal function that we used to model changes in fitness with the number of food items collected. When the probability of finding food is large, the expected number of food items collected is also large but fitness increments associated with these large values become shallower, reflecting factors such as satiation. With a higher probability of finding food, foragers increased scan duration and invested less time in food search (Fig. 5a, b). Scan rate was poorly related to the probability of finding food but time spent scanning increased substantially (Fig. 5c, d).

The increase in fitness associated with food availability can be caused directly by a decrease in mortality resulting from an increase in vigilance and indirectly by the increase in future fitness resulting from a higher intake rate. Interestingly, when very long interscan intervals are needed (food is more difficult to get), individuals responded by a decrease in scan duration. This decrease in scan duration allows individuals to resume food searches more quickly but at an increased risk of predation. In these

circumstances, the boost to fitness from longer times spent foraging trumps concerns about safety. When finding food is easier, by contrast, individuals allocated more time to vigilance.

Vigilance has been related to food availability in many studies, but all involved groups of foragers, which makes it difficult to distinguish between social and antipredator vigilance (Beauchamp, 2015). In one particular study, for instance, vigilance increased with food density (Johnson et al., 2001), but so did aggression and presumably the need to monitor neighbours more closely.

Some studies with individual foragers reported no effect of food availability on scan duration (Baker et al., 2011; Fritz et al., 2002). One possibility to explain these findings is that the amount of time needed to locate food was not affected by food availability at the levels of food densities used in these experiments. When searching for cryptic food, nutmeg mannikins (*Lonchura punctulata*) reduced scan rate but did not alter scan duration (Courant and Giraldeau, 2008). Interscan duration increased but only in the presence of a conspecific, perhaps because an increase in interscan duration was easier to achieve when a companion could be used to decrease predation risk. It was not possible to assess whether vigilance was aimed at competitors or predators when a companion was present. In a further experiment with groups of mannikins, time spent vigilant decreased when searching for cryptic seeds but the effect was not statistically significant with the small sample size (Barrette and Giraldeau, 2006). These results thus provide only partial support for the model's predictions.

State-dependent models of vigilance predict a shift to lower vigilance when the rate of food intake increases (McNamara and Houston, 1992). This is because greater exposure to risk can pay off if it allows foragers to accumulate more reserves. Accumulation of reserves is not part of the present model. Therefore, the prediction that vigilance should increase when finding food is easier probably applies best to foragers that are not in urgent need of accumulating resources to avoid future risk of starvation.

3.4 Foraging payoffs

The fitness accrued by individuals that have escaped predation depends on how food collected during a bout translates into future survival. This was modeled using a sigmoidal increasing function of the amount of food collected. Shifting the mid-point of the foraging payoff function to higher values means that more food must be collected to achieve the same fitness. This could be the case for hungry foragers or for those with low reserves. For these foragers, only the collection of a large number of food items can lead to a substantial gain in fitness.

As expected, fitness decreased when the mid-point values for the foraging payoffs function increased (Fig. 6a). Concomitantly, scan duration decreased but interscan duration only varied slightly (Fig. 6a, b). Scan rate did not vary much with foraging payoffs but time spent scanning decreased substantially (Fig. 6c, d). The decrease in scan duration allows individuals to increase time spent foraging when the fitness gains from foraging are lower but this comes as the expense of predator detection. The large decrease in scan duration makes foraging bouts more frequent.

Hungry animals put more value on foraging, a finding that can be used to examine the prediction that hungrier foragers should reduce vigilance. More hungry ruddy turnstones (*Arenaria interpres*) increased interscan duration, which was interpreted as a decrease in vigilance (Beale and Monaghan, 2004). Indirect evidence comes from the following observations. Dark-eyed juncos rejoining their groups after a period of food deprivation showed decreased vigilance (Lima, 1995). Female Eastern grey kangaroos (*Macropus giganteus*) in poor body condition preferred a vigilant posture that interfered less with foraging (Edwards et al., 2013). Hungrier female Belding's ground squirrels (*Urocitellus beldingi*) invested less in vigilance (Nunes et al., 2000) and were also less likely to interrupt feeding to become vigilant following an alarm call (Bachman, 1993).

3.5 Distance to cover

Again as expected, an increase in the distance to protective cover led to a reduction in fitness (Fig. 7a). Both scan and interscan duration first increased, then decreased and eventually reached a plateau as distance to cover increased (Fig. 7a, b). Both scan rate and time spent vigilant decreased at a decreasing rate with distance to cover (Fig. 7c, d). Distance from protective cover thus influenced vigilance and foraging the most when foragers were closer to cover.

Two opposite strategies are possible to deal with an increase in distance to protective cover. Individuals could adopt a high-vigilance strategy such that animals remain longer in more distant food patches and accumulate food at a lower rate. Alternatively, individuals could reduce their vigilance, and thus increase foraging payoffs

at the risk of higher predation. Consistent with this alternative tactic, foragers in the model adopted short scans further away from cover and typically reduced overall vigilance. Shorter scans prevailed both very close and far away from protective cover. Short scans might allow predators to creep closer during their approach but this is less of an issue when foragers can reach cover rapidly. By contrast, if foragers are too far away from cover, early detection of predators becomes pointless given that the predators can catch up with fleeing foragers before they reach cover. If foragers can feed elsewhere rather than very far from cover, this strategy of reducing scan duration may not be documented.

Another option that is not available in the model is to feed faster to retreat to a safe place sooner. In the model, individuals are forced to remain in a food patch the full length of the time horizon and cannot curtail exposure to predators by foraging faster. In this situation, it might be possible to see foragers reduce vigilance to bring down the amount of time spent exposed to predators (Beauchamp and Ruxton, 2007; Favreau et al., 2009). This could be added in a future model by making time in the patch an outcome of the model rather than a fixed value.

Dark-eyed juncos increased scan duration when foraging further away from a refuge (Lima et al., 1999). Eurasian siskins (*Carduelis spinus*) foraging further away from protective cover reduced interscan duration but did not change scan duration, resulting in an increase in scan rate (Pascual and Senar, 2013), the opposite of what the model predicted. Blue tits (*Parus caeruleus*) foraging closer to the ground, and thus further away from protective cover, increased scan rate by decreasing interscan duration but

not scan duration (Lendrem, 1983). Red-necked pademelon (*Thylogale thetis*), a solitary marsupial species, decreased interscan duration but not scan duration when foraging further away from cover (Pays et al., 2009). By contrast, black-billed magpies (*Pica pica*) increased scan duration when away from cover (Diaz and Asensio, 1991). In Eurasian teal, scan duration first decreased with distance to cover and then increased further away, a finding thought to reflect greater conspicuousness to predators when away from protective cover (Pöysä, 1994). Conspicuousness to predators as a function of distance to cover was not considered in the model but could explain some of the conflicting results reported thus far.

One difficulty here is that the model predicts non-linear changes in vigilance where both increases and decreases are conceivable depending on the distance to protective cover. In addition, testing the model requires a large range of distances to cover, but it is clear that animals may refuse to feed too far from cover. We note that many of the above studies investigated vigilance and distance to cover using artificial sources of food, which might have altered the state of the foragers.

Indirect evidence comes from a study in which the wing loading of zebra finches (*Taenopygia guttata*) was artificially altered to increase flight costs. With an increase in wing loadings, individuals would be expected to take longer to reach cover following an attack. Faced with such an increase in predation risk, individuals increased scan duration (Mathot and Giraldeau, 2008). A more direct way of modeling this issue would be to vary prey speed to reach cover.

4. General discussion

One of the more general findings from the model is that there are many ways to combine scan and interscan duration to produce the same changes in scan rate or time spent vigilant. In some cases, scan and interscan duration are expected to vary in the same direction leading to a much lower effect for time spent vigilant. In other cases, scan and interscan duration varied in opposite direction leading to a lower effect for scan rate. Prey animals control the durations of both scan and interscan intervals and it is these options that should be investigated rather than scan rate and time spent vigilant, which are just epiphenomena sometimes poorly correlated to scan or interscan duration, or both.

4.1 How to test the model

Before testing the model, it is essential to determine whether foragers are exposed to the prescribed contingencies for a sufficient amount of time, sufficient enough that foraging can lead to changes in future survival. For instance, if foragers leave patches with low foraging payoffs rapidly or spend little time very far from cover, it would be difficult to test the predictions of the model because foragers are expected to stay under these conditions the whole duration of the time period. This is more an issue for observational studies where foragers may have access to a broad range of foraging patches.

The qualitative predictions of the model can be tested as a first step. Once these predictions are verified, it is possible to envisage testing quantitative predictions. The model should be tested in solitary foragers, but it is possible to test the model in social

species as long as group size remains constant across the various conditions examined.

A caveat here is that it is not known whether the predicted effects are similar in

magnitude in groups of different sizes. A further difficulty is that individuals in a group

are not necessarily at the same distance from the predator. This would be less

problematic when the spatial spread of the group is small relative to attack distance. It

would also be worthwhile examining the various assumptions made in this model. We

used various sigmoidal functions to model both foraging payoffs and predator

detection; significant departures from such shapes would invalidate the model.

While we focused on general trends in scan and interscan duration with changes

in ecological factors, we also noted a wide variation in the tactics specified by the model

from run to run (witness wide standard deviation bars in many of the figures). Given

that fitness was always very similar from run to run, we conclude that different

combinations of scan and interscan duration can provide the same fitness. This suggests

that the fitness peaks in relation to scan and interscan duration can be relatively flat.

Whether this is always the case remains to be investigated in a fuller analysis, but the

practical consequence is that a large sample size might be required to test the trends

that we reported.

4.2 Future directions

We investigated the effect of one variable at a time in the model. However, it is

conceivable that some of the variables that we considered interact together in the field.

For instance, the effect of distance to cover might be more pronounced when the risk of

attack is higher. Our main goal here was to develop a framework to incorporate

constraints. Future work could examine interactive effects to extend the range of predictions.

Other variables can also be tested in the current framework, including the speed at which both predator and prey move. The model was developed for solitary foragers in mind, and an obvious next step would be to examine what happens to the predictions in groups. It is conceivable that some of the trends reported here interact with group size. For instance, scan duration could increase with the risk of attack but to a lesser extent in larger groups because individuals in groups benefit from a reduction in predation risk through several mechanisms like the many-eyes effect and risk dilution (Beauchamp, 2015).

The model of antipredator vigilance that we developed should be viewed as a first step in incorporating constraints in food gathering and in predator detection. Analytical solutions for (even simplified versions of) the model would be most welcomed to establish convergence on the optimal solutions. Additional information about constraints will help tailor predictions to particular species. Adding such constraints adds a novel (but generally applicable and biologically grounded) dimension to vigilance models and produces a variety of predictions that await empirical scrutiny.

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Fig. 1. Flowchart of the major simulation steps. At each time period, the predator can be present or absent in the habitat. The forager can be in one of two states, foraging or vigilant. Each of these states lasts for a fixed amount of time. When foraging, the forager can collect one food item per time period with a fixed probability. When vigilant, the forager cannot collect food but can detect an approaching predator. After updating time, the scan (vigilance) or interscan (foraging) interval can reach the end upon which the forager adopts the alternative state. If the predator is present, the forager in foraging mode cannot detect the approaching predator. The simulation ends if the predator can reach a critical distance before the end of the foraging bout; otherwise time is updated. The vigilant forager can detect the approaching predator. If the predator is detected the forager initiates escape to reach cover. The simulation ends if the predator can reach a critical distance before the end of the vigilance bout or catches up with the fleeing forager; otherwise time is updated. At the end of the scan or interscan interval, the forager adopts the alternative state.

Fig. 2. The probability of detecting a predator decreases in a sigmoidal fashion with the distance between the predator and prey. As the curve is shifted to the right, the utility of vigilance increases, which means that the probability of detection is higher for the same distance. The following parameters were used for the sigmoidal function: k= -0.5; solid line: m=10, short-dashed line: m=15, long-dashed line: m=20.

Fig. 3. How the probability of predator presence, which translates into the risk of attack, influences vigilance and foraging. An increase in predator presence produced a decrease in fitness (broken line, right y-axis, panel A). In addition, scan duration increased (A), interscan duration decreased (B) resulting in an increase in both scan rate (C) and time spent scanning (D). Shown are the means and standard deviations (N = 15).

Fig. 4. How vigilance and foraging change when predators can be detected at a greater distance. The increase in predator detectability resulted from an increase in the mid-point of the sigmoidal function relating the probability of detection and the distance between the predator and forager. Increased detectability resulted in an increase in fitness (broken line, right y-axis, panel A). In addition, scan duration first increased and then decreased (A), interscan duration increased (B) resulting in an increase in both scan rate (C) and time spent scanning (D). Shown are the means and standard deviations (N = 15).

Fig. 5. How the probability of finding food per unit time spent foraging influences foraging and vigilance. An increase in this probability resulted in an increase in fitness (broken line, right y-axis, panel A). In addition, scan duration increased (A), interscan duration decreased (B) resulting in a general increase in scan rate (C) and an increase in time spent scanning (D). Shown are the means and standard deviations (N = 15).

Fig. 6. How foraging fitness payoffs affect vigilance and foraging. Food accumulated through foraging is translated into future fitness. When the mid-point of the sigmoidal function relating foraging payoffs to the amount of food collected is shifted to higher values, foragers require more food to achieve the same payoffs. Fitness decreases when the foraging payoffs are slighter (broken line, right y-axis, panel A). In addition, scan duration decreased (A) but there was little effect on interscan duration (B) and scan rate (C) while time spent scanning decreased (D). Shown are the means and standard deviations (N = 15).

Fig. 7. How the distance to protective cover influences foraging and vigilance. An increase in the distance to protective cover reduced fitness (broken line, right y-axis panel A) as foragers take longer to travel to a safe site when attacked. In addition, both scan and interscan duration first increased and then decreased (A, B). Scan rate (C) and time spent scanning (D) generally decreased. Shown are the means and standard deviations (N = 15).

Table 1

Definition and range of values for the model parameters

Parameter	Definition	Range of values
T	Number of time steps per simulation	9000
P_{pred}	Probability of predator arrival per time step	0.000025-0.0002
S_{pred}	Distance covered by the predator per time step	2
S_{prey}	Distance covered by fleeing forager per time step	0.5
D_{cover}	Distance to protective cover	4-10
D_{pred}	Initial distance between predator and forager	30
P_{food}	Probability of obtaining one food item per time step	0.01-0.1
P_{detect}	Probability of detection based on the distance between the predator and forager based on 1-$SIG(k,m,x)$	k=-0.5, m=7.5-17, x=distance
F	Fitness based on $SIG(k,m,x)$	k=-0.04, m=100-300, x=number of food items collected
$SIG(k,m,x)$	Sigmoidal function for a given independent variable x with parameter values k and m[1]	

[1] The generic sigmoidal function has the following form: $SIG(k,m,x)=1/(1+\exp(k(x-m))$

Highlights

- The model predicts the duration of scan and interscan intervals during antipredator vigilance
- The model includes factors such as the risk of attack, the ability to find food and detect predators
- The model uses a bottom-up approach to determine the temporal organization of vigilance

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