Struggle for safety

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Box V

Escape decisions: trade-offs between energy and safety prospects

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Introduction

Birds typically respond to attack by escape flight. Predators often use obstructive landscape structures to decrease detection opportunities by prey as much as possible. Yet, detection is not always followed by immediate escape. Apart from the option to stay put, which may be a good way of avoiding attack by Peregrine *Falco peregrinus*, which may be reluctant to take prey from the ground (Cresswell 1993), birds may just delay escape flight for some reason. This implies that differences in time delay between flight responses – or alarm calls for that matter – in response to attack may not be taken as evidence for differences in attentiveness (Ydenberg & Dill 1986).

Fleeing entails costs, such as the relatively high costs of short flight (Hambly *et al.* 2004) and loss of feeding opportunity, which birds should trade-off against the cost of remaining in place, which may involve the chance of getting killed. The latter may depend on, for instance, escape destination. Passerines that escape into vegetation may be more inclined to forage longer before deciding to flee when they are closer to that bush, their escape destination. Alternatively, birds that lack such an escape destination, such as many shorebird species that forage on exposed mudflats, may use other escape tactics such as socially-coordinated escape. For such species the proximity of recruits for coordinated escape flight may guide their escape decision (Chapter 9 in this thesis). In any case, the extra feeding time gained by not fleeing should compensate for the increased risk of capture, and thus we expect this to depend on the state of the animal. This should equally apply to the resumption of feeding after attack.

Field observations

In their wintering area, on the Banc d'Arguin, Mauritania, while tallying age-proportions in flock of Red Knots foraging at incoming tide on near-shore seagrass beds (see Chapter 5), from time to time such flocks were disturbed by raptors attacks. In 21 of such occasions I had just finished such a flock composition assessment, which gave me the chance to compare this to the flock size and composition of birds that foraged on the site immediately after the disturbance (I use disturbance, not attack, as I could not determine which of the remaining individuals had actually been targeted or just disturbed).

Results

Obviously, flock size shortly after disturbance was much smaller, as most birds had left the area either to return after a couple of minutes or longer, or to leave to another foraging patch, or else for the roost and stay there until receding tide. More strikingly, shortly after the disturbance the relative abundance of juveniles nearshore was much higher than before, indicating that juveniles have a higher propensity to stay or at least resume feeding shortly after disturbance (Figure V.1).

Discussion

I will speculate as to possible explanations for the fact that juveniles have a lower tendency to flee from predators. First, individual difference in the prospects of successful escape might explain the observation. If juveniles would be less skilful in coordinated flockwise escape flights, the prospects for safety by fleeing would be less favorable for them than for adult conspecifics, so costs of fleeing are high (F_{high} in Fig. V.2). This would make them less inclined to flee (dependent of the cost of

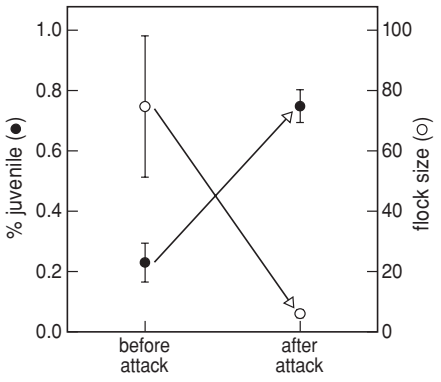

Figure V.1 Flight propensity after disturbance by a raptor, showing that juveniles are less inclined to flee and/or have higher propensity to resume feeding immediately after disturbance than adults.

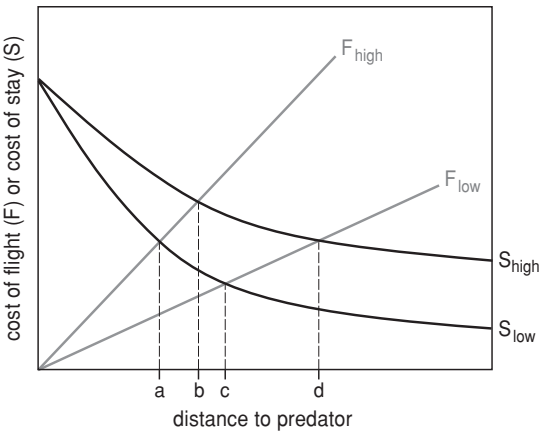

Figure V.2 Graphic illustration of the costs of fleeing (F) and staying (S) for poor foraging juveniles and good foraging adults. See text for explanation. (Adapted after (Ydenberg and Dill, 1986).

staying – see further on – the option for juveniles would be (a) or (b)). The propensity to stay put could even be the result of juveniles foraging at the edge of a flock, which would make them less able to quickly merge with conspecifics in socially-coordinated escape flight.

An alternative explanation, though not incompatible with the former, would be that these juveniles are poor foragers, which due to a low energy state, are less willing to give up feeding opportunity for escape (an interpretation that would correspond with the results as presented in Chapter 5). Thus, juveniles would have lower cost of staying (S_{low}) which corresponds to a lower tendency to flee with an approaching raptor (dependent of the costs of fleeing, this would yield options (a) or (c)). Of course, both mechanisms could work together, and this would yield (a) as the appropriate option for juveniles in case both cost of staying were low and cost of fleeing were high.

In conclusion, an immediate escape upon detection of a predator does not have to be the optimal response. The optimal escape decision may be subject to individual abilities in foraging and sociality. Finally, as detection does not necessarily lead to an immediate escape response, a delay in response cannot per definition be regarded as a delay in detection. In other words, the recognition or detection phase must be separated from the pursuit or escape phase (Caro 2005; Vermeij 1982). This has to be taken into account when interpreting results of vigilance studies that link for example response time to flock size and corresponding detection potential (Ydenberg & Dill 1986).