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Interference from adults forces young red knots to forage for longer and in dangerous places

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In birds and mammals, juvenile and adult foragers are often found apart from each other. In this study, we found this is also true for red knots, *Calidris canutus canutus*, wintering on the intertidal flats of Banc d'Arguin, Mauritania. Not only did juveniles feed separately from adults, they also fed at places where they were more vulnerable to predation by large falcons. That the dangerous areas used by juveniles were no better feeding areas led us to reject the food—safety trade-off that explained age-related distribution differences in many earlier studies. Instead, juveniles were displaced by adults in dyadic interactions which suggests that they suffered from interference from adults. Juveniles retreated to feeding areas that were more dangerous and yielded lower intake rates, and coped by extending foraging time by using higher, nearshore intertidal areas that were exposed for longer. When disturbed by predators in these nearshore areas, juveniles continued feeding whereas adults left. Thus, rather than compensating for increased predation danger by higher intake rates, on the Banc d'Arguin red knot juveniles foraged for longer.

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Foraging animals must choose between locations that differ in many aspects, but food conditions and safety usually explain a lot of the variation found (van Gils, Edelaar, Escudero, & Piersma, 2004; Piersma, 2012). It is theoretically plausible (Houston & McNamara, 1999; Houston, McNamara, & Hutchinson, 1993) and has been empirically demonstrated (reviews by Brown, 1999; Brown & Kotler, 2007; Cresswell, 2008; Lima, 1998) that individuals are capable of responding in adaptive ways to trade-offs between energy gain and safety from predators, trade-offs that may be mediated by the energy state of the animal (Barnett, Bateson, & Rowe, 2007; Kotler, Brown, Mukherjee, Berger-Tal, & Bouskila, 2010; Real & Caraco, 1986). According to the ideal free distribution model, foragers should aggregate at patches where their food is most abundant. If patches also differ in safety, prey tend to aggregate in safer patches, even when these patches are relatively poor in resources (Heithaus, 2001; Hugie & Dill, 1994). Ultimately, owing to the balanced effects of interference, safety in numbers and habitat choice by their own predators, foragers are generally considered to trade rich and dangerous feeding opportunities against poor and safe options (Bednekoff, 2007; Hugie & Dill, 1994; Moody, Houston, & McNamara, 1996).

However, individuals differ in their position on the food—safety continuum (Houston & McNamara, 1999; Stephens & Krebs, 1986). For instance, foraging animals that balance energy intake and expenditure are expected to choose to forage in areas that are safest from predators even when these areas are less rewarding (Brown, 1988; van Gils et al., 2004; Houston & McNamara, 1999). Other individuals may forage in more danger-prone ways, for instance because hunger forces them to exploit the rewards of dangerous areas (see studies reviewed in Lima & Dill, 1990), or because inferior competitive abilities and inexperience prevent them from satisfying their daily requirements in the presence of dominants (Cresswell, 1994; Parker & Sutherland, 1986). Models of adaptive behaviour then predict that greater danger is compensated for by higher energy intake rates (Houston & McNamara, 1999). Indeed, this is corroborated by field observations in a wide range of species (reviewed in Lima & Dill, 1990). For example, in a Scottish estuary in winter, adult and juvenile redshanks, *Tringa totanus*, segregated into two areas, a mussel bed and a saltmarsh (Cresswell, 1994). Juveniles were excluded from the mussel bed by adults. Predation danger at the saltmarsh was much higher than at the mussel bed, but food abundance was higher as well so that juvenile redshanks in the saltmarsh achieved the highest intake rates.

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The present study at Banc d'Arguin, Mauritania, can in the first place be regarded as a verification of the age-related differences in foraging distributions shown by Cresswell (1994), albeit in a tropical setting and for a different shorebird species, the red knot, *Calidris canutus canutus*. It can also be regarded as another test of the general idea that predation danger and intake rates may be traded off in class-specific distributional decisions. We investigated age-related foraging patterns in the context of food and predator abundance and tested whether the previous finding that juveniles accept danger in return for better food is more generally observed.

METHODS

Study System

Up to 256 000 red knots (over 75% of the flyway population of this subspecies; Piersma, 2007) have been estimated to winter at Banc d'Arguin (Davidson & Piersma, 2009; Hagemeijer et al., 2004). Adults arrive from late August onwards, followed by juveniles a month later (Davidson & Piersma, 2009). Most birds leave Banc d'Arguin in late April and early May to breed in north-central Siberia (Dick, Piersma, & Prokosch, 1987; Piersma et al., 1990), returning in August–September, but they generally do not go north before their third calendar year (Piersma, van Gils, & Wiersma, 1996).

We assumed that the red knots we studied in the nonbreeding season followed a satisficing strategy, that is, they balanced energy intake and expenditure, at least until they started preparing for migration to the breeding areas (van Gils, Battley, Piersma, & Drent, 2005). This means that they chose the safest foraging areas as long as these allowed them to balance gross energy intake rate and energy expenditure (Nonacs & Dill, 1993). At the Banc d'Arguin this would mean that they should avoid nearshore areas, where the presence of raptor-concealing cover makes them vulnerable to surprise attack by large falcons (Dekker & Ydenberg, 2004; van den Hout, Spaans, & Piersma, 2008; Rogers, Battley, Piersma, van Gils, & Rogers, 2006). Despite this prediction we observed that most red knots caught by falcons were in fact juvenile (van den Hout et al., 2008). In the present study, we were able to assess the roles of conspecific density and interference (Sutherland, 1996; Vahl, van der Meer, Weissing, van Dullemen, & Piersma, 2005) because before and immediately after high tide shorebirds are forced to forage together, a feature of tidal systems exploited before in studies of oystercatchers, *Haematopus ostralegus* (Ens & Goss-Custard, 1984; Goss-Custard & Durell, 1987; Sutherland & Koene, 1982; Zwarts, Ens, Goss-Custard, Hulscher, & Durell, 1996).

Following Lank and Ydenberg (2003), we define 'danger' and 'risk' as follows. 'Danger' depends on predator abundance and habitat structure and thus is essentially an attribute of the environment. 'Risk' is the probability of a bird being caught, which is a function of both danger and the antipredator measures taken by prey through behaviour (Caro, 2005; Cresswell, 2008; Lima & Dill, 1990) or body composition (van den Hout, Mathot, Maas, & Piersma, 2010; van den Hout, Piersma, Dekinga, Lubbe, & Visser, 2006; Lima, 1986).

Study Area

The Parc National du Banc d'Arguin is an area of shallow water, intertidal sand- and mudflats and islands along the northern Atlantic coast of Mauritania, bordering the Sahara desert from about 20°50′N, 16°45′W to 19°20′N, 16°28′W (Isenmann, 2006; Wolff, 2005; Wolff & Smit, 1990). It covers an area of 12 000 km², 500 km² of which is intertidal. Much of the Banc d'Arguin is covered by vast sea grass beds on the intertidal flats mainly consisting of *Zostera noltii* (Altenburg, Engelmoer, Mes, & Piersma, 1982; van Gils et al., 2012; Isenmann, 2006; Wolff & Smit, 1990).

We studied red knots on the Iwik Peninsula (19°53′N, 16°17′W) during the winters of 2002/2003 to 2008/2009, and in 2010/2011. The central part of the peninsula consists of low barren hills (not higher than 15 m), as well as the central part of site 7 (Fig. 1a), which were favoured resting and perching sites of large falcons (lanner, *Falco biarmicus*, barbary, *Falco pelegrinoides*, and peregrine falcon, *Falco peregrinus*), and also functioned as points of departure for their attack flights. Low dunes border the mudflats in areas 1 and 2 (Fig. 1a). These are used by large falcons as cover for surprise attacks on shorebirds. Some sea grass beds (sites 8 and 9; Fig. 1a) are separated from the peninsula by an approximately 1–1.5 km wide channel. Other sites, including 6, 7, 10 and 11 (Fig. 1a), are separated from the peninsula by narrow channels of 150–250 m.

Age Distribution

Observations with a telescope (20–60× magnification) allowed us to distinguish juveniles from adults by plumage. Juveniles were characterized by their whitish underparts with a pink-buff wash and greyish brown upperparts; the coverts had pale fringes and dark subterminal lines (Prater, Marchant, & Vuorinen, 1977). Although these characteristics gradually faded in the course of winter, some inner grey-brown coverts with subterminal bars remained. Even when these bars had been lost, the brownish coverts were distinctive.

We examined flock sizes and age compositions at low tide (from 3 h before until 3 h after low tide). We made sure that all habitat types in as large an area as possible were covered (Fig. 1). Birds and flocks were assigned to habitat type and site (see Fig. 1a); for 421 of the 696 flocks exact GPS positions were recorded (Fig. 1b). All field observations on flock sizes and age distribution were done by P.J.v.d.H. The overall contribution of juveniles to the local population was estimated by dividing the total number of juveniles observed across all areas by the total number of birds sampled. Owing to limited access to offshore sea grass beds in the early years, we were not able to establish separate year-to-year estimates and used an overall estimate of the juvenile percentage in the population.

Predation Danger

During 1239 h of observations divided over 320 sessions which lasted on average 4.0 h (range 0.5–12 h) a total of 26 different observers recorded the presence of predators. Predators included mainly falcons and harriers (mainly marsh harrier, *Circus aeruginosus*, and an occasional Montagu's harrier, *Circus pygargus*). Kestrels, *Falco tinnunculus*, although commonly encountered, were not considered to be dangerous to shorebirds, and were therefore not included in analyses. Several other raptor species (black kite, *Milvus migrans*, Bonelli's eagle, *Hieraaetus fasciatus*, and golden eagle, *Aquila chrysaetos*) were observed only once. Jackals, *Canis aureus*, were occasionally seen, but during daylight hours hardly seemed to disturb shorebirds. As hunting predators tended to move over much larger areas than foraging shorebirds, each predator observation was assigned to one of the subsites in which we divided up the study site (see Fig. 1; van den Hout et al., 2008).

Responses to Predation Danger

We measured responsiveness to predation danger through behaviour and body state. As raptors as a rule rely on opportunities to catch their prey during surprise attacks, habitat structures that conceal attacks, such as dunes, significantly contribute to predation danger by increasing the lethality of attack (Cresswell, Lind, &