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Original Article

Individual shifts toward safety explain age-related foraging distribution in a gregarious shorebird

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Although age-related spatial segregation is ubiquitous, the underlying mechanisms are poorly understood. Here, we aim to elucidate the processes behind a previously established age-related foraging distribution of red knots (*Calidris canutus canutus*) in their main wintering area in West Africa (Banc d'Arguin, Mauritania). Based on 10 years of observations of 1232 uniquely color-ringed individuals of 1 to 18+ years old, we examined whether the observed age-related foraging distribution resulted from 1) spatial differences in mortality or 2) age-related shifts in habitat use. Using multistate capture–recapture modeling, we showed that with age foraging red knots moved away from the shoreline, that is, to areas with fewer surprise attacks by raptors. Considering uncertainties in the subjective gradient in predation danger with increasing distance from shore (as assessed from correlations between vigilance and distance from shore in foraging birds), we applied 2 different danger zone boundaries, at 40 m and 500 m from shore. Between years, red knots had a much higher chance to move from the dangerous nearshore area to the “safe” area beyond (71–78% and 26% for 40-m and 500-m danger zone boundary, respectively), than vice versa (4% and 14%). For neither danger zone boundary value did we find differences in annual mortality for individuals using either dangerous or safe zone, so the move away from the shore with age is attributed to individual careers rather than differential mortality. We argue that longitudinal studies like ours will reveal that ontogenetic shifts in habitat use are more common than so far acknowledged.

Key words: age, foraging proficiency, habitat use, safety, survival.

Many animal species show differential habitat choice with age. This may be caused by age classes avoiding overlap in resource use, either because of dietary requirements (Werner and Gilliam 1984; Lim et al. 2016), or because of competition from older dominants (Cresswell 1994; Ficetola et al. 2013). As a result, young animals may differ from older ones in how they trade-off food rewards and safety from predators, which may result in an ontogenetic niche shift (Werner and Gilliam 1984; Cresswell 1994; Ficetola et al. 2013). However, if young animals—due to dietary constraints or competition—are forced to use areas where mortality risks are higher, instead of or in addition to an ontogenetic shift in habitat use (e.g., Werner and Gilliam 1984), age-related distributions

may be driven by spatial differences in survival (Wunderle 1991). After all, juveniles often forage in places where predator attacks are particularly frequent and/or lethal (Sih 1982; Hirsch and Morrell 2011). Distinguishing between an ontogenetic shift in habitat use and a spatial difference in survival as mechanisms underlying age-specific foraging distributions requires longitudinal studies with many individuals involved. So far, these have been limited (see, for a study on foraging oystercatchers *Haematopus ostralegus*, Caldow et al. [1999] and, for a study on bull sharks *Carcharhinus leucas*, Matich and Heithaus [2015]).

On the intertidal mudflats of the Banc d'Arguin, Mauritania, age-specific foraging distributions were observed in a wintering shorebird, the red knot *Calidris canutus canutus* (van den Hout et al. 2014). By mapping low tide distributions and by quantifying the proportions of adults and juveniles in flocks and the encounter

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rates with predators, it was shown that adults mainly foraged in large flocks on the eelgrass-covered mudflats far from shorelines, areas rarely visited by falcons, the main local predators of shorebirds (van den Hout et al. 2014). When forced by the incoming or outgoing tides, most adults visited nearshore zones briefly, but then they invariably appeared in high densities (van den Hout et al. 2008). Most juveniles foraged in smaller flocks and were separated from adults by foraging in nearshore areas (van den Hout et al. 2014). Surprise attacks by falcons concealed by shoreline cover make these nearshore zones more dangerous than offshore area (van den Hout et al. 2014). The increase in the time spent vigilant by these nearshore foragers was not compensated by higher intake rates, yet longer exposure times of nearshore foraging areas allowed them to compensate the time losses (van den Hout et al. 2014). On the basis of individually color-marked individuals, we here examine the mechanisms underpinning this age-segregated distribution. Using an information-theoretic approach, we will evaluate the support for 2 possibilities to explain the age-related distribution. Both mechanisms start from the idea that young birds are forced to feed in nearshore zones avoided by adults. This could be due to interference with older dominants (van den Hout et al. 2014) and/or a physiological inability of juveniles to cope with toxic bivalves (*Loripes lucinalis*; van Gils et al. 2013; Oudman et al. 2014), which are most abundant on the eelgrass beds offshore (Honkoop et al. 2008; van den Hout et al. 2014). On the Banc d'Arguin, juveniles were observed to have lower intake rates and to receive more aggression than adults (van den Hout et al. 2014). This suggests that they have lower competitive and foraging abilities. Because of their lower status and a lower ability to cope with toxic prey compared to adults, juveniles encounter difficulties to access the safest foraging areas. If offshore areas are used more by the older foragers, the nearshore areas must be vacated with age. Mechanisms and predictions for both explanations—differential mortality or an ontogenetic niche shift—are as follows.

First, in view of the fact that more juveniles than adults forage in nearshore area (van den Hout et al. 2014), the pattern could be caused by higher mortality of foragers in nearshore zones (henceforth denoted as “differential survival”). Despite antipredation measures such as vigilance (van den Hout et al. 2014), birds in nearshore areas may have a higher chance of being killed by a raptor (van den Hout et al. 2008, 2014). At the same time, the site-faithful adults (Leyrer et al. 2006, 2012) that keep avoiding nearshore zones would show higher survival (van den Hout et al. 2014). In this scenario, the observed age-related spatial segregation among foragers simply emerges from a spatial pattern in survival. This explanation leads to Prediction 1 that survival chances will be higher in safe (offshore) foraging areas than in dangerous (nearshore) foraging areas. During the years of study, virtually all mortality occurred in the winter quarters (Leyrer et al. 2013) and, therefore, annual survival closely resembles overwinter survival.

Second, the observed age segregation could be the result of gradual individual shifts to foraging farther from shore with age (henceforth briefly denoted as “directional movement”). This could work through a modification of the “ideal free distribution” (Fretwell and Lucas 1969) for foragers that distribute according to unequal competitive abilities (Fretwell 1972; Parker and Sutherland 1986), or through the first-come-first-serve principle of an ideal pre-emptive distribution (Pulliam and Danielson 1991). This leads to Prediction 2 that the probability to move from the dangerous nearshore area to the safe offshore area is higher than the probability to move from the safe offshore area to the dangerous nearshore area.

To account for the expected increase with age in dominance rank (Sarova et al. 2013) and/or the ability to cope with toxic prey (van Gils et al. 2013; Oudman et al. 2014), that is, to investigate interactions of “age” and “differential survival” or “directional movement”, we additionally considered an effect of age on the probabilities of survival and movement from dangerous to safe area, distinguishing 2 (juvenile vs. older birds) age classes. To assess the relative roles of “differential survival” and “directional movement” in explaining the observed relationship between age and distance of foraging sites to obstructive cover along the shore, we used multistate mark-recapture modeling techniques. We applied model selection to evaluate the fit of competing models to the data (Burnham and Anderson 2002).

METHODS

Species and study area

Red knots are specialized molluscivores that during the nonbreeding season forage on wide-open off-shore mudflats, generally in large flocks (Piersma 2007, 2011). Red knots of the subspecies *C. c. canutus* usually spend their first 2 winters in West Africa and start migrating to the breeding grounds in north-central Siberia in their third calendar year (Piersma et al. 1996).

The Banc d'Arguin, the main nonbreeding area of *C. c. canutus*, is an area of shallow water and islands connected by 500 km² of intertidal flats along the northern coast of Mauritania, bordering the Sahara desert from about 20°50'N, 16°45'W to 19°20'N, 16°28'W. The fieldwork was carried out on and around the peninsula of the village Iwik (19°53'N, 16°17'W, Figure 1). Here, of a total area of 50 km², approximately 22 km² is occupied by tidal mudflats largely covered by seagrass, *Zostera noltii* (Folmer et al. 2012). We divided the study area into sites (Figure 1) and spread observation effort equally across these sites. The mudflats are bordered by saline flats, the sabkhas, in most places separated by a 1-m high and 20–40-m wide ridge of low dunes that (especially at sites 1, 2, and 3) are used by large falcons (lanner, *Falco biarmicus*; barbury, *Falco peregrinoides*; and peregrine falcon, *Falco peregrinus*) as cover for surprise attacks. The central part of the peninsula consists of bare, 15-m high hills used by the falcons as perching sites and points of departure for attacks. A large surface of sea grass meadows is separated from the peninsula across the entire tidal cycle by 0.1–1.5-km wide channels. Site 8 harbors a narrow dune ridge of approximately half a meter in height and an observation tower commonly used as a perching place by 1 or 2 falcons throughout the nonbreeding season of shorebirds (see Electronic Supplementary Material S.1 for more details about the study area).

Field methods

Between 2002 and 2013, during yearly 3-week study periods in winter (November–December), we captured, marked, and resighted red knots around the Iwik Peninsula, Banc d'Arguin. Birds were trapped with mist-nets around the New Moon spring tides (Piersma and Spaans 2004; van Gils et al. 2013). In the hours after capture, the birds were aged as 1st winter, 2nd winter, or older than 2nd winter and marked with unique combinations of 4 color-rings and a “flag” (Leyrer et al. 2006; van den Hout et al. 2008). The age of birds older than 2nd winter cannot be told apart (Prater et al. 1977). This means that for individuals older than 2nd winter at ringing, their age in subsequent years must be considered relative

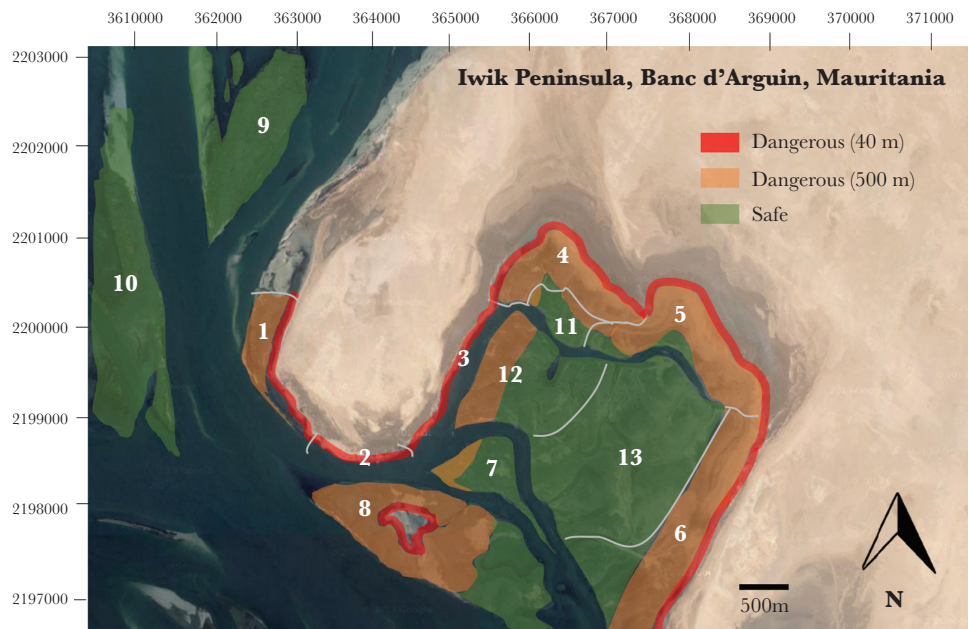


Figure 1

The details of the study area within the Parc National du Banc d'Arguin, Mauritania, showing the subsites. Coordinates are in UTM. Red and orange area shows the dangerous foraging zones of 40 m and 500 m from shore. For the analysis with a 40-m danger zone boundary, orange and green are safe area; for the analysis with a 500-m danger zone boundary, only green area is safe.

from the 3rd year onward. In the analysis, we additionally included color-banded red knots that were similarly marked during their stage in the Wadden Sea in The Netherlands and Germany (see Dick et al. 1987). In the Wadden Sea, we started color-banding red knots as early as the mid-1990s, so that the dataset includes individuals up to 18 years of (relative) age. We used observations from 2004 onwards.

Annual survival was calculated from winter to winter, where winter i was defined as July in year i until June in year $i + 1$. Although we used resightings made during the entire nonbreeding period (late August through April), the vast majority of resightings (96%) were performed in November–January. Observations of 11 adult (3 years or older) and 13 first-year red knots radio-tagged (and color-ringed) in December 2006 were included in the analysis. To be sure that only active foragers were included in the dataset, for some near-shore sites where birds tended to assemble just prior to roosting (sites 1, 4, 5, 6, and 11) we restricted the observations to 2 h before and after low tide. Exclusion of these high tide aggregations should not lead to an observation-bias towards an age class. The dataset consisted of 1232 uniquely color-marked individuals. On average, across the entire study period, an individual bird was resighted 3.1 times (range: 2–42 times).

Observation sessions covered a single period of time (1–3 h) spent by one observer that moved around in a sub-area within the study area (henceforth called “sites”). With a detection distance of 200 m for reliable observations of color-marked birds, the instantly observed diameter around an observer was 400 m. Depending on a danger zone boundary of 40 m or 500 m from shore (further explained below), 438 and 188 sessions took place in “safe offshore areas”, and 183 and 433 in “dangerous nearshore areas” (Table 1). All sites contained safe offshore areas, except sites 2 and 3, which were entirely dangerous. Depending on the danger zone (40 or 500 m) sites were entirely dangerous, partly dangerous, or entirely safe. The boundaries between dangerous and safe areas within a site

were assessed by eye. When no observations were done in a dangerous part of a site, this site was considered entirely safe, and vice versa. In Table 1, danger levels are classified per site. The numbers of different individuals observed at each site are summarized in Electronic Supplementary Materials S.2 and S.3. Note that a study in Scotland suggested that colour-ringing does not affect predation mortality of waders (Cresswell 2007).

Assessing levels of predation danger

Lank and Ydenberg (2003) explained why we should distinguish “risk” from “danger”. Predation risk, the probability of being depredated, is under some degree of control by an animal (behaviorally, by keeping away from predators, or physically, for example, by lowering body mass), whereas predation danger, as an attribute of the environment, is not. A number of studies on birds from open habitats have identified that proximity to obstructive cover is a major determinant of predation danger (Cresswell 1994; Dekker and Ydenberg 2004; Pomeroy 2006; van den Hout et al. 2008, 2014; Cresswell et al. 2010). In the context of this paper, when talking about dangerous or safe, we refer to predation danger rather than risk, implying that if behavioral responses to predation danger, the so-called “non-lethal effects” of predation, are inadequate, it may result in direct mortality (“lethal effects” of predation).

Distances to shore were defined as the shortest distance to shoreline from the midpoint of a site. Like most gregarious shorebirds, red knots typically engage in socially coordinated escape manoeuvres when attacked (Lima 1993). For timely recruitment of enough flock members for a coordinated escape with the advantages of risk dilution and confusion of the predator (Krause and Ruxton 2002), they should be able to detect an approaching predator from a relatively large distance (van den Hout et al. 2010). Therefore, near-shore zones with obstructed view from the horizon must be most dangerous and should generally be avoided (van den Hout et al. 2014). This should be reflected in vigilance, being higher in these

Table 1
Number of observation sessions per year and danger status (DS)

Site	DS (40 m)	DS (500 m)	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	Total
1	D/S	D	4	1	9	2	0	0	0	1	0	0	17
2	D	D	2	1	15	0	3	0	0	1	2	11	35
3	D	D	18	12	29	29	11	8	6	3	9	3	128
4	D/S	D	0	0	0	1	0	0	0	0	1	1	3
5	S	D	0	0	0	1	0	0	1	1	0	2	5
6	S	D	0	0	1	3	0	3	4	2	0	0	13
7	S	S	4	5	0	0	0	9	3	3	7	8	39
8	S	D	1	0	31	4	8	6	5	24	16	25	120
9	S	S	4	2	5	3	7	9	4	12	5	4	55
10	S	S	5	7	22	11	11	4	3	3	2	4	72
11	S	S	0	0	0	0	0	6	1	1	1	4	13
12	S	D	0	5	21	3	11	15	8	14	11	24	112
13	S	S	0	0	0	0	0	3	1	3	1	1	9

Note that sites 1 and 4 encompass both dangerous and safe areas. Last column shows the total number of observation sessions per site. D = Dangerous; S = Safe.

nearshore zones (Beauchamp 2015b). To account for uncertainties in the way that the danger gradient was perceived by the birds, we chose to vary the threshold between the dangerous and the safe areas. Although—as we pointed out—vigilance behavior is not a direct measure of danger, we can nevertheless use vigilance as an informed guess of how birds *perceive* danger with respect to distance from shorelines.

The first danger threshold was based on measurements of head-up rates collected in winter and spring of 2005 at a high spatial resolution covering 0–100 m from the shoreline. These head-up rates were estimated by observing a randomly chosen focal bird through a telescope for 4 min, and counting the number of head-ups during that period with a hand-held counter. We limited the possibility of multiple observations on the same individual by spreading the observations as much as possible across the entire study area. A head-up was defined as raising the head from a foraging down position to at least a horizontal position (Metcalf 1984). As we kept a safe distance from a focal bird, we felt confident that the behavior of the bird was not disturbed by our presence. As flock sizes may affect vigilance (Beauchamp 2015a), these were recorded as well, and controlled for in analyses. Distance to shore was estimated by eye, with a 10-m resolution. Head-up rate declined from 10–50 m from shore when it plateaued at its lowest value, so the zone within the first 40 m of the shore were considered as dangerous, and the area beyond as relatively safe (see Results; Figure 2, panel a). To account for the possibility that the danger zone may actually be much wider, we carried out an additional analysis with a danger threshold of 500 m from shore, the distance at which the time spent vigilant (head-up duration) reached its lowest plateau value (van den Hout et al. 2014; Figure 2, panel b).

In the analyses, the type of site where an individual was located (i.e., either the safe offshore or the dangerous nearshore site) was considered as a “state”. To determine an individual’s state in a particular year, we had to estimate whether a bird spent more time in dangerous nearshore or in safe offshore foraging area. To do so, for each site we first calculated the proportion of observation sessions in which the individual was actually observed (see Online Supplementary Materials S.2 and S.3, for a summary of site-specific bird observations for the 40-m and 500-m danger zones). To determine the “relative presence” in the dangerous and safe areas, we then averaged these site-specific proportions over all dangerous and safe sites where the individual was seen at least once, thereby assuming that only these sites were part of its home range. At Banc

d’Arguin, red knots of all age classes are very faithful to their foraging locations at low tide (Leyrer et al. 2006; Leyrer et al. 2012; Oudman et al. 2016). Tracking observations using Time Of Arrival tags (MacCurdy et al. 2011; Piersma et al. 2014) revealed that the mean distance between foraging locations across low tide periods was only 800 m (SD = 500 m; Oudman et al. 2016). A diameter of 800 m would generally cover at most 1–2 sites (see Figure 1). If a bird was only observed at a dangerous site in a particular year, its state was defined as “dangerous”. Similarly, if a bird was only observed at safe sites, its state was “safe”. When a bird was observed at both safe and dangerous sites, its state was determined by selecting the state in which it had the highest “relative presence”. The fact that birds move very little between sites (and thus states) was also supported by the fact that those birds that were observed multiple times in the same winter were generally observed in either safe or dangerous areas, seldom in both (Figure 3).

Multistate capture–recapture modelling approach

Multistate capture–recapture models can be used to separate the estimation of survival in, and movement between, states (Brownie et al. 1993; Lebreton and Pradel 2002), while accounting for potential differences in resighting probabilities between states. The approach has been widely used to estimate movements between sites (Hestbeck et al. 1991), but is equally suitable to estimate transition probabilities between other kinds of states, such as behavioral or reproductive states (Nichols et al. 1994).

A common problem with multistate models is that the number of parameters can easily become large, particularly when all possible probabilities are allowed to vary over time. Given the amount of data, estimating many different parameters would lead to poor inference on any of the parameters. Based on previous work (Leyrer et al. 2012; van Gils et al. 2013), we included year-to-year variation in resighting probabilities in all models. As we were primarily interested in testing several a priori hypotheses about differences in survival and movement probabilities in relation to the state of danger, taking into account the limited amount of data on birds in the dangerous state, we decided to exclude temporal (year-to-year) variation in survival and movement. We expect a much higher resighting probability in dangerous area, given its relatively small surface and easy accessibility (by foot, instead of by boat) compared to the majority of safe area. We corrected for this built-in bias by modelling resighting probability as a function of state.

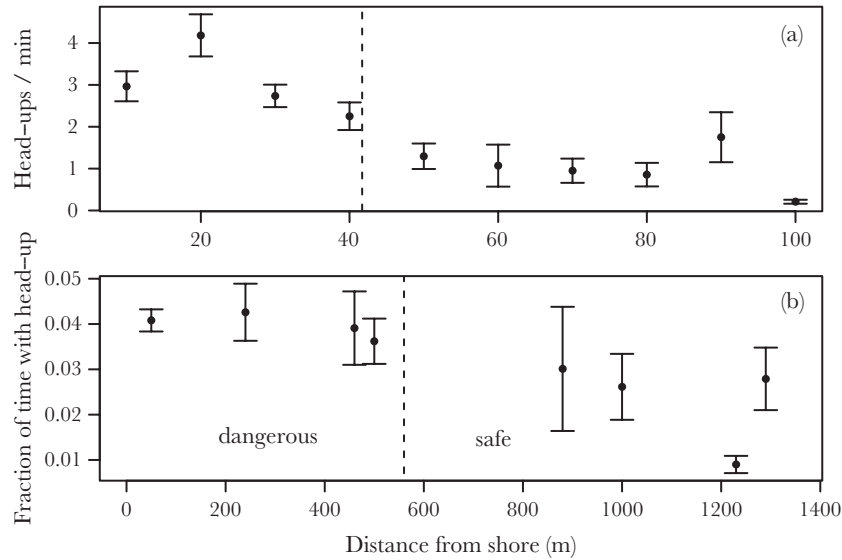


Figure 2

Vigilance measures, with 2 methods applied: recording head-up rates (a) and time spent with head-up (b). (a) Head-up rates (number of head-ups per minute \pm SE) in red knots observed in the distance range of 0–100 m from shore near Iwik on Banc d’Arguin in spring 2005. A distance of 40 m from shore was chosen to delineate relatively safe from relatively dangerous foraging area (see text). (b) Head-up time (expressed as a fraction of the total time budget) observed at a larger scale of 0–1500 m from shore, during the winters of 2002/2003 to 2008/2009 and 2010/2011 (adapted from Van den Hout et al. 2014). A distance of 500 m was used as an alternative transition between relatively dangerous and relatively safe area, to be used in an additional analysis, testing the sensitivity of the model to a specific threshold between dangerous and safe area.

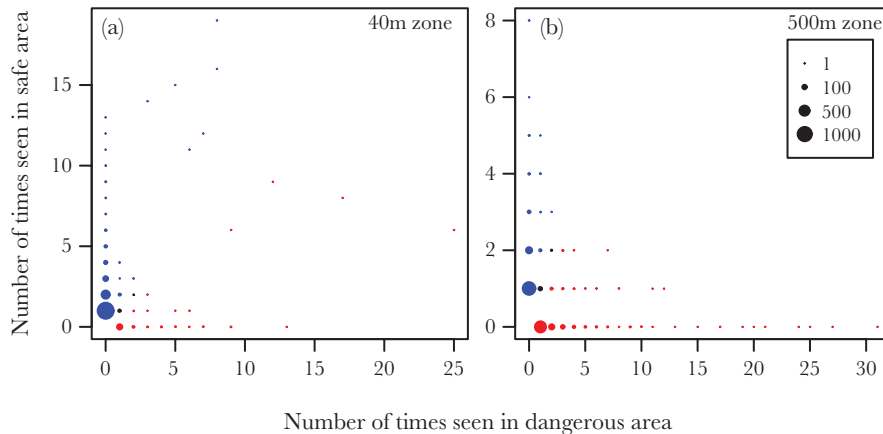


Figure 3

Number of individuals that were observed in nearshore dangerous and offshore safe habitat, shown for the 40-m and 500-m danger zone boundaries. Dot size reflects the number of individuals. Red dots are birds assigned to the dangerous state, blue dots birds assigned to the safe state. Note that axes ranges differ between plots.

We only used resightings for our analyses, as from captures it cannot be assessed whether a bird is foraging in dangerous or safe habitat. This means that we excluded birds that died shortly after the capture event, as well as transients that immediately left the study area after capture. Moreover, we excluded the considerable amount of the resightings performed during the period of arrival at roosting sites. Although doing resightings during this period is efficient in terms of the number of color-banded individuals that could be observed, it provides no information on where these individuals had been foraging (in safe or dangerous area). Due to standardized activities in our annual expeditions (see above) we can safely assume constant resighting effort across years and areas.

Based on our a priori hypotheses, we defined a candidate model set of 45 models combining different parameterizations for survival,

movement and resighting probabilities (Table 2). In the most parameterized “umbrella” model, survival and movement probabilities were a function of age class (distinguishing hatch-year and older birds), state and their interaction. Resighting probability was a function of state, year, and their interaction: $\Phi_{\text{state} \cdot \text{a}2} \Psi_{\text{state} \cdot \text{a}2} P_{\text{state} \cdot \text{year}}$. Goodness-of-fit of the umbrella model was tested, using the median \hat{c} test in program MARK (White and Burnham 1999). A slight lack of fit (overdispersion) was estimated in both models ($\hat{c} = 1.03$ and $\hat{c} = 1.09$ for the 40-m and 500-m zone, respectively). Model selection was based on Akaike’s information criterion taking into account small sample sizes and adjusting for the estimated level of overdispersion (QAICc; Akaike 1973; Akaike 1974; Burnham and Anderson 2002). We considered models with $\Delta\text{QAIC}_c < 2$ to have similar support, except for those containing uninformative

parameters (Arnold 2010). To account for model selection uncertainty, we used model averaging to derive parameter estimates and confidence intervals (Burnham and Anderson 2002). Models were constructed in R v. 2.13.0 (R Core Team 2011) using package RMark (Laake 2013) and run using program MARK (White and Burnham 1999).

Animal Welfare

Although no government permits were required to catch and handle red knots at Banc d'Arguin, Mauritania, research permits were issued by the scientific committee of the Parc National du Banc d'Arguin. Note that captured birds were handled exclusively by experienced and well-trained persons, applying the protocols granted by the Dutch Animal Care committees to ensure that as little discomfort was inflicted on the birds as possible.

RESULTS

Head-up rates decreased with distance from shore (LM on ln transformed data, $N = 341$, $R^2_{\text{adjusted}} = 0.30$, $P < 0.001$). This relationship was not affected by flock size ($P = 0.36$), nor by age class ($P = 0.18$). Head-up rate tended to plateau at lowest values beyond a distance of approximately 40 m from shore (Figure 2). Head-up rates from 10 m to 40 m (mean = 2.87) did not differ from each other but were different from the rates at 50 m and farther (mean = 0.82; 2-sample t -test, $t_{354.9} = 9.4637$, $P < 0.001$). This distance to shore of 40 m was used to delineate the “dangerous nearshore area” from the “safe offshore area” (see Methods). Likewise, on the larger scale, mean of head-up proportions within 500 m from shore (mean = 0.05) differed from those farther offshore (mean = 0.02; 2-sample t -test, $t_{174.9} = 5.2902$, $P < 0.001$).

For danger zone boundaries of both 40 m and 500 m, the percentages of birds observed in safe foraging area increased with age and extended well beyond the transition from 1st to 2nd winter (Figure 4); the effect was strongest at the 40-m danger zone boundary. This age-specific pattern was mainly driven by movements between years from dangerous to safe area (with probabilities of 0.71–0.76 and 0.26 for the 40-m and 500-m danger zone boundaries, respectively) rather than vice versa (probabilities of 0.04 and 0.14; Table 3). There was some support for adults being more likely to move from dangerous to safe, than juveniles (Table 3). A difference in movement probability to explain the age-related distribution was strongly supported, as for both boundaries the movement probability was a function of state in all models with $\Delta\text{QAIC}_c < 2$ (Tables 4 and 5). The data are thus consistent with Prediction 2 (“the probability to move from the dangerous to the safe area was higher than the probability to move from the safe to the dangerous area”).

With the danger zone boundary set at 40 m, there was no evidence for differences in survival between birds foraging in dangerous and safe area (survival was 0.78–0.79 in dangerous and 0.76–0.79 in safe area; see Table 3 for more detail and Table 4 for the Model selection results). Adding a state effect on survival increased the QAIC_c by 1.98 (Table 4); hence, this parameter should be considered uninformative (Arnold 2010). Similarly, there was only limited support for state-dependent survival when the danger zone boundary was set at 500 m. Although there was some support for an interaction between state and age on survival, where juveniles had higher survival in the safe area (0.85 vs. 0.78) and adults had higher survival in the dangerous area (0.79 vs. 0.77—for more detail see the model-averaged estimates in Table 3 and Table 5 for Model selection results), the model with constant survival had

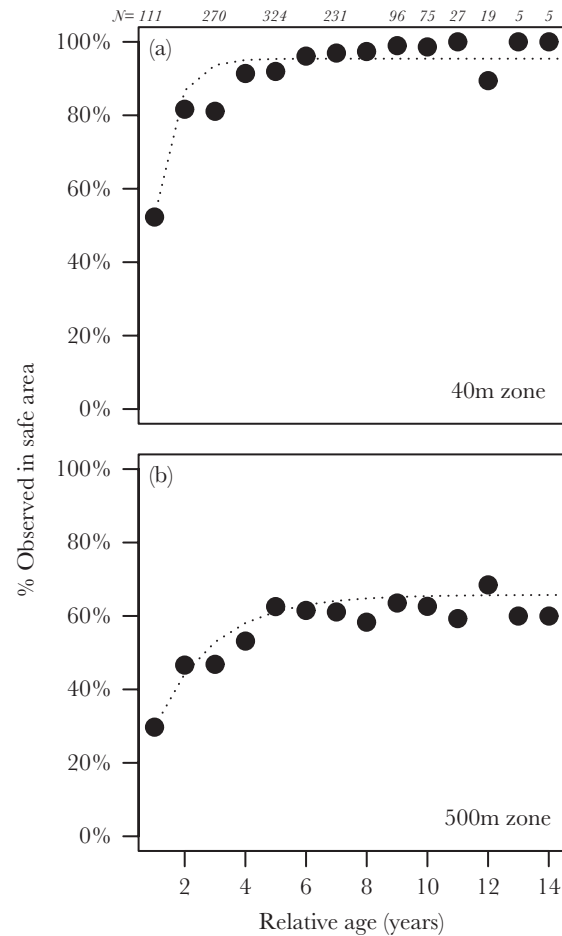


Figure 4

The percentage of birds that were observed in safe area (dots) as a function of relative age, for the 2 danger zone boundaries of 40 m (panel a) and 500 m (panel b). The age is a minimum and relative as the true age is unknown for birds aged as 2 years or older upon capture. The dotted lines show the predicted age-dependent area use, starting from the observed proportion of juveniles in the dangerous area, and then calculating the expected proportions of birds in dangerous and safe area in subsequent age classes using the estimated age-independent probabilities to move from dangerous to safe area (76% and 26% for the 40-m and 500-m danger zone) and from safe to dangerous (4% and 14%, respectively) from the most parsimonious models. N refers to the number of observations involved in each age class. Relative age classes 16 and 18 were left out as each of them had only 1 observation, they were excluded from this graph.

similar support with fewer parameters. Therefore, overall, we found very limited evidence in agreement with Prediction 1 (“survival chances will be higher in safe (offshore) foraging areas than in dangerous (nearshore) foraging areas”).

We also found very limited evidence for age-specific survival and age-specific movement probabilities. For the 40-m danger zone boundary, adding an age effect on survival or movement increased QAIC_c , hence the age parameter was uninformative. As mentioned before, with a danger zone boundary of 500 m, there was some support for an interaction between state and age on survival, but the model with constant survival was more parsimonious. For both 40 m and 500 m, the temporal variation in resighting probabilities differed between birds foraging in dangerous and safe areas. Model-averaged estimates of survival, transition, and resighting probabilities are shown in Table 3.

Table 2
List of a priori models

Parameterizations	Description
Survival (Φ)	
.	Survival does not differ between states or age classes
a2	Survival differs between first-year and older birds
state	Survival differs between birds in dangerous versus safe state
state + a2	Survival differs between birds in dangerous versus safe state and between first-year and older birds
state·a2	Survival differs between birds in dangerous versus safe state and this difference varies between first-year and older birds
Movement (Ψ)	
.	Probability to move from dangerous to safe state is the same as the probability to move from safe to dangerous state
state	Probability to move from dangerous to safe state is different than to move from safe to dangerous state
d·a2 + s	Probability to move from dangerous to safe state differs between 1st winter and older birds; probability to move from safe to dangerous state does not depend on age
Resighting (P)	
state + year	Probability of resighting is different for birds in dangerous versus safe state and varies from year to year (in a similar way for the 2 states)
d + s·year	Probability of resighting is different for birds in dangerous versus safe state and only varies from year to year for birds in the safe state
state·year	Probability of resighting is different and varies differently from year to year for birds in dangerous versus safe state

Each combination of parameterizations is tested, resulting in 45 models. As to “Survival”, a2, this involves lower survival of first-year birds, but similar for dangerous and safe area, as juveniles trade-off reduced intake rates as a result of interference competition with adults (and inability to find food in seagrass or higher toxin constraint) against predation risk. As to “Movement”, complementary to the first statement is the probability to stay in the dangerous state is the same as the probability to stay in the safe state.

DISCUSSION

This study shows that the age-related foraging distribution of red knots on the mudflats of Banc d’Arguin was primarily explained by the higher probability to move from the dangerous nearshore area to the safe and open offshore area, rather than by differential survival between birds using dangerous versus safe areas. In the course of their lives, red knots increasingly used the safer offshore feeding areas. We cannot distinguish whether the higher movement probability from dangerous to safe area was driven by a proactive decision of adult birds to move to safer foraging grounds, or by random redistribution of adults, since the surface of dangerous foraging grounds was considerably smaller than that of safe foraging grounds (Figure 1). However, the fact that the proportion of juveniles among the foraging red knots was considerably higher in dangerous nearshore areas than in safe offshore areas shows that at least juveniles are not distributing randomly in their first year of settlement, but instead are “forced” (e.g., by interference competition and physiological constraints) to forage close to the shore. Our conclusion that the age-related foraging distribution was primarily driven by the birds moving toward safe area (whether by random redistribution or not) from the first to the second year (as movement probabilities were similar for juveniles and older birds, Table 3) instead of driven by lower survival rates of birds foraging nearshore will therefore be unaffected.

This conclusion was upheld for the 2 thresholds of distance to shore (40 m and 500 m). The 40-m danger zone boundary, that we defined to delimit an area with high danger perception and short detection times (based on Figure 2), closely matches the findings of Cresswell et al. (2010) who observed that attack success rates of sparrowhawks *Accipiter nisus* exponentially declined with distance to predator-concealing cover. Using both danger zone boundaries, the age segregation, expressed as the yearly estimates of age-related site use (dots in Figure 4a and b), was best explained by the model that predicts a constant chance to move from the dangerous to the safe zone between years (fitted lines in Figure 4a and b). This means that the movement probability did not change with age.

Table 3
Model-averaged parameter estimates for the datasets with a 40-m and 500-m danger zone boundaries

Parameter	40-m danger zone		500-m danger zone	
	Estimate	95% CI	Estimate	95% CI
$\Phi_{d,juv}$	0.78	(0.62–0.88)	0.78	(0.59–0.89)
$\Phi_{d,ad}$	0.76	(0.69–0.82)	0.79	(0.74–0.83)
$\Phi_{s,juv}$	0.79	(0.63–0.90)	0.85	(0.52–0.97)
$\Phi_{s,ad}$	0.76	(0.74–0.79)	0.77	(0.73–0.80)
$\Psi_{d \rightarrow s, juv}$	0.71	(0.41–0.89)	0.26	(0.16–0.41)
$\Psi_{d \rightarrow s, ad}$	0.78	(0.62–0.89)	0.26	(0.21–0.33)
$\Psi_{s \rightarrow d}$	0.04	(0.02–0.09)	0.14	(0.11–0.18)

For year-specific resighting rates, see Electronic Supplementary Table S.4.

That movements from dangerous to safe area were less pronounced with a danger zone boundary of 500 m rather than 40 m suggests that the perceived danger gradually decreases with distance, with a considerable proportion of adults (ca. 40%, see Figure 4) accepting the somewhat higher predation danger between 40 and 500 m. That we did not find differences in survival between safe and dangerous area suggests a predator–prey foraging game where knots equalize foraging reward (relative to their requirements, which may differ between juveniles and adults) per unit of predation danger (Gilliam and Fraser 1987; Brown et al. 1999). In this game, juvenile knots do best when they forage nearshore. By avoiding offshore eelgrass beds, they suffer less interference from adults, avoid areas where the ratio of toxic to nontoxic prey is highest (van Gils et al. 2013; Oudman et al. 2014), while they compensate for the greater danger close to shores by foraging longer and allocating more time to vigilance (van den Hout et al. 2014). When they get older they increase both their dominance status and their abilities to forage on toxic prey, so offshore eelgrass beds become more valuable. These offshore areas are also safer because the falcons seldom hunt far from shore (van den Hout et al. 2014); they seem “anchored” (Sih 2005) to shorelines, requiring shoreline cover for hunting success. Not having to

Table 4**Model selection results for the 45 candidate models using a danger zone boundary of 40 m, adjusted for overdispersion ($\hat{c} = 1.03$)**

Φ	Ψ	P	K	ΔQAIC_c	$\Delta\text{QDeviance}$	Akaike weight
.	State	state:year	21	0.00	3.60	0.24
.	d:a2+s	state:year	22	0.60	2.15	0.18
a2	State	state:year	22	1.37	2.92	0.12
state	State	state:year	22	1.98	3.53	0.09
a2	d:a2+s	state:year	23	2.13	1.62	0.08
state	d:a2+s	state:year	23	2.56	2.06	0.07
state + a2	State	state:year	23	3.26	2.75	0.05
state:a2	State	state:year	24	3.95	1.39	0.03
state + a2	d:a2+s	state:year	24	3.97	1.41	0.03
state:a2	d:a2+s	state:year	25	4.62	0.00	0.02
.	d:a2+s	d+s:year	14	5.30	23.19	0.02

Φ = apparent survival; Ψ = movement probability; P = resighting probability; K = number of parameters; d = dangerous state; s = safe state; a2 = age class, distinguishing hatch-year and older birds. Only the models with an Akaike weight of more than 0.01 are shown. Deviance = 991.40; QAIC_c = 4380.30.

Table 5**Model selection results for the 45 candidate models using a “safety border” of 500 m, adjusted for overdispersion ($\hat{c} = 1.09$)**

Φ	Ψ	P	K	ΔQAIC_c	$\Delta\text{QDeviance}$	Akaike weight
.	state	state:year	21	0.00	6.12	0.22
state:a2	state	state:year	24	0.05	0.01	0.21
state	state	state:year	22	0.86	4.94	0.14
a2	state	state:year	22	1.63	5.70	0.10
.	d:a2+s	state:year	22	2.05	6.12	0.08
state:a2	d:a2+s	state:year	25	2.10	0.00	0.08
state + a2	state	state:year	23	2.55	4.56	0.06
state	d:a2+s	state:year	23	2.92	4.94	0.05
a2	d:a2+s	state:year	23	3.67	5.69	0.03
state + a2	d:a2+s	state:year	24	4.60	4.56	0.02

Only the models with an Akaike weight of more than 0.01 are shown. Φ = apparent survival; Ψ = movement probability; P = resighting probability; K = number of parameters; d = dangerous state; s = safe state; a2 = age class, distinguishing hatch-year and older birds. Deviance=1369.97; QAIC_c = 4687.21.

be so vigilant, older birds can forage more efficiently on the offshore eelgrass beds (van den Hout et al. 2014). Thus, our results provide evidence for an ontogenetic niche shift that operates through a foraging game, that is, an ideal free distribution that accounts for predation danger, equalizing survivorship across age classes. In this system juveniles manage danger using time allocation (see Figure 2), whereas adults manage danger mostly by habitat selection.

Apart from the fact that offshore eelgrass beds become more valuable for older birds as they can better deal with toxic prey, another consideration may explain why most red knots move to safer offshore areas with age: the need of older birds to elevate food intake rates to build up body store for northward migration (Zwarts et al. 1990). Young birds do not require this extra energy as they mostly remain at Banc d'Arguin during the northern summer (Cramp et al. 1983). Increased requirements may necessitate foraging in the safer offshore areas (van den Hout et al. 2014).

That a learning curve may be involved in such ontogenetic niche shifts is consistent with studies demonstrating the long-term development of foraging skills (Caldow et al. 1999; Jaeger et al. 2014), competitive ability (Fretwell and Lucas 1969; Cresswell 1994; Bautista et al. 1995; Minderman et al. 2006), or both (Caldow et al. 1999). Among these studies, only Caldow et al. (1999) could underpin the finding with longitudinal observations on individuals. They showed that in the small communities of oystercatchers the rate at which juveniles learn to forage on mussel beds on the most profitable prey types may be hindered by the interference from adults (Goss-Custard and Le V. dit Durell 1987a, 1987b).

At Banc d'Arguin, red knots live in small communities too. The small home ranges and site-faithfulness of individual red knots at Banc d'Arguin (Leyrer et al. 2006, 2012; Oudman et al. 2016, and see Harrington and Leddy 1982, for beaches in Florida) indicate that foraging flocks act as closed communities with newcomers having to compete to get access (see discussion in Leyrer et al. 2012).

Ontogenetic shifts mediated by predation danger do not necessarily follow a transition from dangerous to safe habitat. Juvenile bluegill sunfish *Lepomis macrochirus* restricted themselves to safe but poor habitats and only entered the dangerous but food rich habitats when they were large enough not to be susceptible to largemouth bass *Micropterus salmoides*, a gape-limited predator (Werner et al. 1983). Likewise, juvenile snowshoe hares *Lepus americanus*, under the threat of great horned owls *Bubo virginianus*, get forced by older, more dominant animals into dangerous, but food-rich habitat. This allows them to maximize growth rate and force their way into safer areas (Fitzgerald and Keith 1990; Rohner and Krebs 1996).

The degree to which either “differential survival” or “directional movement” leads to habitat segregation between age-classes, may be expected to correlate with the extent to which predator-prey dynamics are either “mortality-driven” or “fear-driven” (Brown et al. 1999). That is, the less predators are capable of controlling the prey population through mortality particularly in the early stages of life (i.e., the more predator-prey dynamics are “fear-driven”), the more scope there would be for ontogenetic shifts in spatial behavior. Yet, as the system of owls and snowshoe hares shows, even in systems that are typically considered as “mortality-driven”, fear appears

to mediate habitat choice of young and old animals (Rohner and Krebs 1996). In view of the ubiquity of systems where behavioral responses to predation are more important than mortality effects (Preisser et al. 2005; Cresswell 2008), such patterns leading to age-related spatial distribution may be more common in animals than hitherto acknowledged, particularly in animals living in groups.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by van den Hout PJ et al (2016).

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