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METHODS AND PRELIMINARY RESULTS FOR EXPERIMENTAL STUDIES OF FORAGING IN SHOREBIRDS

by J.P. Myers, S.L. Williams and F.A. Pitelka

The issue of prey availability plagues any study of foraging ecology, be it on waders, pipits, mammals or fish. How does measured prey density correspond to what the foraging animal experiences? We have set out to explore this matter using laboratory experiments with Sanderlings (Calidris alba), focussing on the importance of different factors controlling prey availability. Here we report briefly on our methods and some preliminary results. We hope that by describing our work at this early stage we shall encourage other research groups to attack related problems. Further clarification of these issues is critical to continued and more refined work on shorebird ecology. Sanderlings, surprisingly, are remarkably tractable laboratory animals, and other shorebird species living in open habitats such as beaches and mudflats may prove similar in this respect.

Methods

Sanderlings were caught in the course of banding operations at Bodega Bay, California. Upon capture, they were banded and placed in a 3x5x1.75 m (tall) indoor aviary where they subsequently have been maintained on commercial catfood, mealworms, and an assortment of natural prey from the field (especially beach crustaceans). Their weights, monitored since capture, have remained at or above weights of Sanderlings caught periodically in the field.

Experimental apparatus

The observation chamber for experiments on prey availability is a 1.75x0.5x0.5 m (tall) box with a screened top and plexiglass front. Observers sit behind a black plastic screen hung in front of the cage approximately 50 cm from the foraging bird. The bird forages on a tray of fine wet sand 1x0.5 m. Sand, to a depth of 35 mm, sits in the tray on a porous shelf through which water can be drained or injected into the feeding tray. This allows us to manipulate the water content of the substrate.

The prey used are frozen and thawed Excirolana linguifrons and Excirolana kincaidi, two local beach isopods which figure importantly in Sanderling's diets around Bodega Bay (Myers et al. 1979). The isopods are separated into different size classes before the experiments by sieving them through a stack of Tyler mesh screens. This allows us to present the Sanderlings with a single size class or known mixture of prey size classes.

The tray is divided into 10 25x20 cm units and each unit is divided into a 1.4 cm grid by laying a plastic screen over it with a 1.4x1.4 cm size mesh. Using this grid system we place each individual prey item in a known position on the tray, varying prey density and relative position according to the experiment (see below).

Prey placement

With one exception (see proximity experiment below), prey are placed in the tray in a stratified random distribution. Each 20x25 cm tray unit receives the same number of prey; within each unit, prey are distributed randomly relative to one another by selecting coordinates in the 1.4 cm grid randomly, save that only one prey is placed per 1.4 cm mesh unit.

Depth of prey is controlled by using a plunger to make a hole of known depth for each prey item. After each hole is made, we gently press the prey to the bottom and cover it with sand. After all the prey are placed, the plastic screen grid is removed and the tray is slowly filled by percolating water up through the porous shelf. Once saturated, the sand surface is gently but thoroughly reworked with a comb to eliminate all visual clues of prey position. At this point we can manipulate sand penetrability by banging the tray to varying degrees: increased jostling causes increased compacting and makes the sand less penetrable. Substrate penetrability can then be measured using a penetrometer.

The prey do not move throughout this process because they are dead. Moreover, we have verified that they are not displaced by recovering individual prey from the tray.

Observations

Birds are allowed to forage on the tray until they eat a predetermined number of prey items. While foraging we monitor total time, the number of foraging events, and the amount of time the bird is actually probing.

During early experiments we simply timed these with two stopwatches. Now we use an automated keyboard (an SSR, Stephenson and Roberts 1977) which puts a signal onto magnetic tape that can be decoded directly by computer. This keyboard allows us to track the bird's position as well as recording the times and durations of foraging events.

After a bird forages on the tray we determine whether each prey item was captured by coring prey locations on the 1.4 cm grid. Further, because Sanderling probe marks remain on the sand following the experiment, we can determine whether the bird probed within the 1.4 cm mesh unit within which each prey was placed. By scoring whether each prey item's mesh unit was probed by the bird, and whether the prey was found, we can examine how different variables affect an isopod's risk of being captured. We define risk (see Figures 2-4) as the ratio of the number of prey captured to the number of prey whose mesh unit was searched.

Results

These experiments are still in progress and the results reported here are preliminary. They do, however, already show clear trends.

Experiment 1: the effect of prey density on foraging rate

All prey in this experiment were 10 mm beneath the surface and all were 8 mm long (surface area of 18 mm^2). Sanderling foraging rate varied directly with prey density, increasing over the entire range of prey densities used to date (Figure 1, $P < 0.001$). We are currently extending the range of high densities used in order to determine whether we can reach a definite asymptote in the relationship between density and rate.

Experiment 2: the effect of prey size on risk

At a constant prey density, how does prey size affect the probability that a prey item will be encountered? Although the sample is still small, the results clearly indicate that small prey are at lower risk than large prey (Figure 2). This means that the foraging rate at a constant prey density will depend heavily upon the distribution of size classes in the prey population.

We do not correct here for the possibility of preferences for larger prey animals, something well documented in visually foraging shorebirds (Goss-Custard 1979). The necessary controls are in progress. Nevertheless, given that our birds are foraging tactually and that prey handling time is small compared to the time required to find prey, we do not think that the preference is important in this system.

Experiment 3: the effect of prey depth on risk

At a constant prey density, how does prey depth affect the likelihood that a prey item will be encountered? Figure 3 shows that prey risk decreases with depth (ANOVA $F_{3,16} = 15.3$, $P < 0.001$). Down to 10 mm risk was high and relatively constant: about 60% of the prey were found once the bird probed their areas. But below 10 mm the risk decreased sharply, falling to 10% by a depth of 25 mm. This trend corresponds well to Sanderling bill lengths, which for our birds range between 21.5 and 24.5 mm (tip to the rear of the nares).

Experiment 4: the effect of proximity on risk

This question is more directly related to how prey should behave. The question is: can a prey affect its risk by varying its spatial position relative to other prey within the same patch? More precisely, once the prey's nearest neighbour is captured, how does its risk vary as a function of distance to that neighbour? As Figure 4 shows, at very close distances its risk is greatly elevated above what it would be were there no relationship between risk and distance. But the effect decays sharply, so that by 4.5 cm there is no difference between observed (solid circles) and expected (open circles) risk. The overall effect of distance on risk is highly signficant (ANOVA $F_{3,15} = 9.096$, $P < 0.002$). These results imply that Sanderling foraging within a patch is concentrated around each site of prey capture.

Conclusions

Through experimental manipulations we have begun to tease apart various factors that affect prey availability to foraging Sanderlings. Few of the general patterns we have found so far are surprising - students of wader biology expect prey density, depth, or size to affect foraging behaviour (e.g. Reading and McGrorty 1978, Goss-Custard 1979). What is important is that we can examine detailed features of the relationships among these variables and prey availability. Understanding such interactions is a central prerequisite to advancing basic knowledge of the foraging ecology of different wader species and is pertinent to a number of theoretical issues in population and behavioural ecology.

This research is also relevant to many applied aspects of studies on waders. Nowhere could this be more evident than in work on the effects of oil pollution. The crude effects of pollution arise from large-scale habitat destruction and direct mortality. But what of more subtle and more pervasive influences? How do low levels of oil contamination, for example, affect the foraging efficiencies of waders taking prey from oiled substrates? Our experimental procedures offer one approach to these questions. We hope that groups involved in such research consider them. They - especially the Outer Continental Environmental Assessment Programs in Alaska and elsewhere - are logical choices to lead, encourage and fund research in this area.

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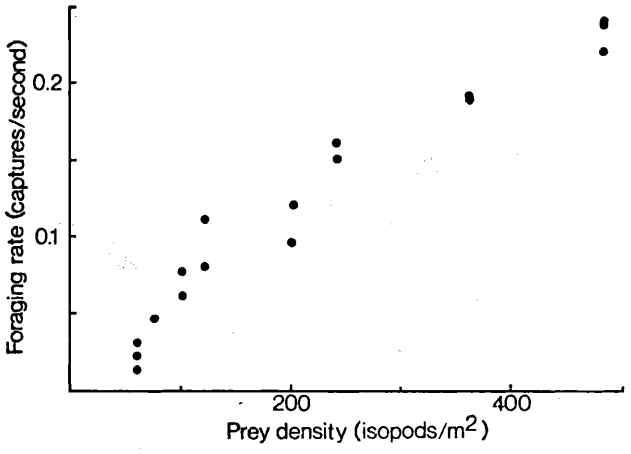

Figure 1. Foraging rate (captures/second) as a function of prey density (isopods/m^2).

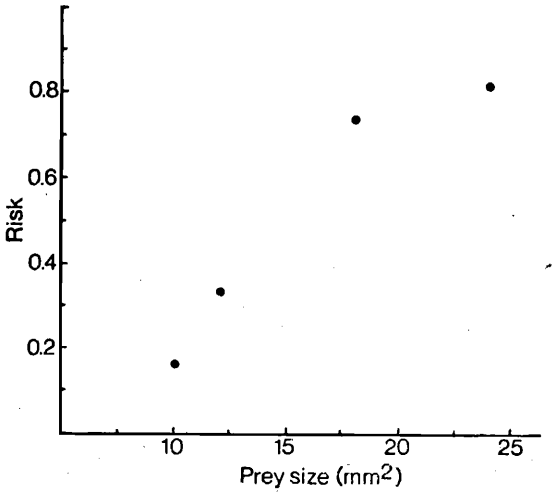

Figure 2. Risk of capture by a foraging Sanderling for isopods of different sizes. See text for definition of risk.

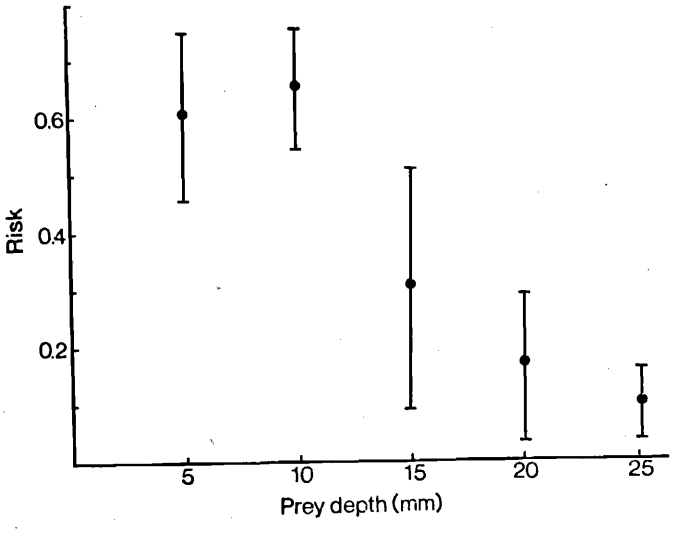

Figure 3. Risk of capture by a foraging Sanderling for isopods at different depths. See text for definition of risk. Vertical lines are 95% confidence limits.

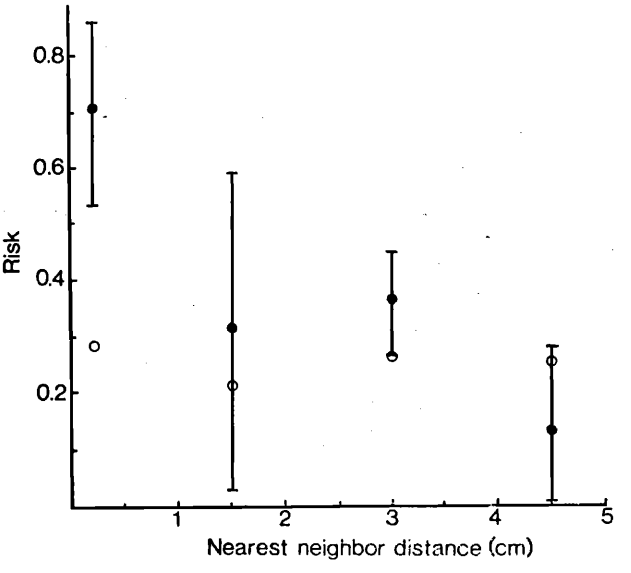

Figure 4. Risk of capture by a foraging Sanderling for isopods as affected by their distance to nearest neighbour, once the nearest neighbour has been captured. See text for definition of risk. Closed circles, observed risk, open circles, expected risk if risk unrelated to proximity. Vertical lines are 95% confidence limits.

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