

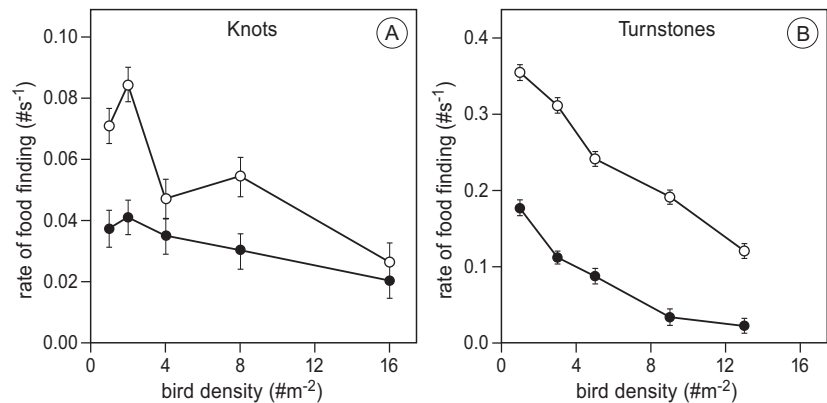
FIGHTING FOR FOOD

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Intertidal areas such as the Dutch Wadden Sea have an important function as wintering grounds for migratory waders (shorebirds). But how many waders can winter in a certain intertidal area? This question interests biologists for both applied (nature management) as well as fundamental (population dynamics) reasons. It seems clear that the maximum number of waders will depend on the amount of food in the area. Perhaps less obvious, the (aggressive) behaviour of the waders themselves is also of importance.

Wintering waders are thought to compete with each other. Competition may be indirect, through the depletion of resources, but also direct, through behavioural interactions such as fights or mutual avoidance. Because time and energy spent on behavioural interactions cannot be used to search for food, competition may lower the condition and survival of wintering waders. The extent to which wintering waders suffer from competition, however, strongly depends on the way in which they compete.

To study whether and how wintering waders compete for food, we performed a series of experiments in the indoor aviaries of NIOZ (the 'Experimental Shorebird Facility'). Use of the aviaries enabled us to study the behaviour of known individuals at experimentally determined combinations of food and forager density, whereas variables that often confound field observations (such as weather, predation risk, level of satiation etc.) are in control. As study species we used



The rate of food finding of knots (A) and turnstones (B) at initial prey densities 50 (black) and 200 (white). Both species found less food items when foraging at higher forager densities.

red knots (*Calidris canutus*) and ruddy turnstones (*Arenaria interpres*), two medium-sized waders that differ strongly in their foraging behaviour. Knots are, for instance, more specialised in their food preferences than turnstones. The two species differ in their social behaviour too: there is a much clearer dominance hierarchy in turnstones than in knots.

In a first experiment we found that both knots and turnstones find less food when foraging at higher densities. This negative effect did, however, not result from the steal-

ing of food items (kleptoparasitism), the mechanism that is generally assumed to underlie competition. Follow-up experiments suggested that foraging waders may instead suffer from competition through resource monopolisation. We found that when food was distributed in clumps (as it is naturally), dominant foragers are able to monopolize the food, thereby achieving a much higher intake rate than their subordinate competitors. An experiment on the beaches of New Jersey, USA, in which we studied the foraging

behaviour of free-living turnstones, indicated that resource monopolisation can indeed be a mechanism that underlies competition in the field.

Our results reveal the importance of knowledge of competition mechanisms. When foraging waders compete with each other through the monopolisation of clumps of food, it no longer suffices to know the overall density of food to predict the maximum number of waders that can winter in an intertidal area; the (small-scale) distribution of food should also be known. Moreover, we found that social dominance strongly and consistently affected the intake rate of foraging individuals. This implies that individual differences need to be accounted for in studies of the maximum number of waders that can be sustained in intertidal areas.



Close-up of a ruddy turnstone (*Arenaria interpres*) searching for food on an experimental foraging arena. Food in this experiment was covered by a layer of seaweed to resemble the natural foraging situation of turnstones.



Design of one of the experiments performed in the 'Experimental Shorebird Facility' of NIOZ. In this experiment two patches were offered to foraging turnstones; only one of them contained food (the left one). The behaviour of the foraging waders was recorded with video cameras. Note that the floor of the aviary is covered with water; this ensured that the experimental birds always used one of the experimental patches.



Free-living ruddy turnstones (*Arenaria interpres*; 7 individuals) and sanderlings (*Calidris alba*; 2 individuals) searching for food on the beaches of Delaware Bay (USA). While most individuals are searching for food, two of the turnstones are engaged in an aggressive interaction. Interactions like these are thought to reduce the rate of food intake.