FORAGING DECISIONS IN A MARINE TOP-PREDATOR, THE RED KNOT (*CALIDRIS CANUTUS*)

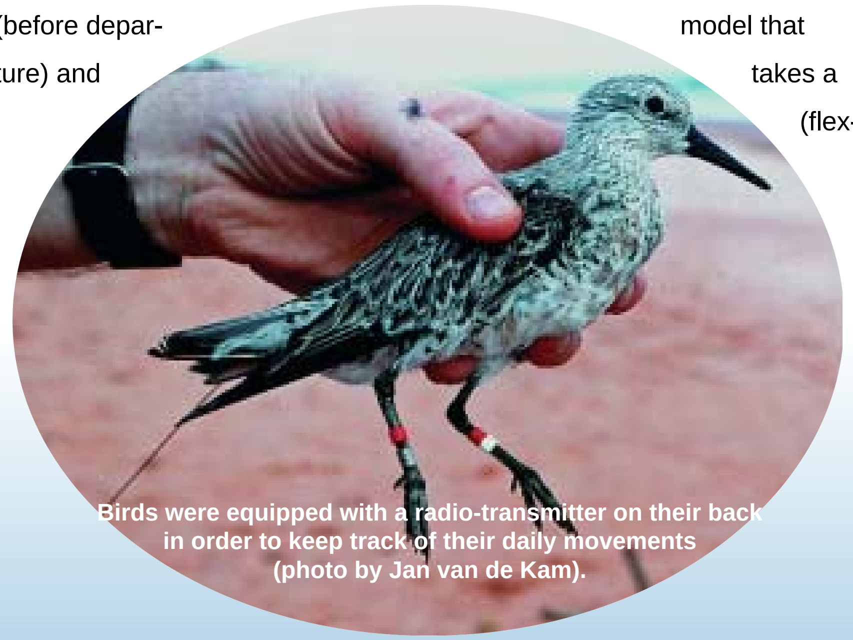
Jan van Gils, Theunis Piersma, Anne Dekinga & Bernard Spaans.*

In our department, the red knot (*Calidris canutus*) is used as a model organism to investigate the role of top-predators in marine ecosystems. In this context, the present study aimed at understanding the knot's basic feeding habits. The application of ultrasonography enabled us to estimate stomach size and revealed that knots adjusted the size of their digestive system to the quality of their intertidal prey. However, at times with only poor quality prey around, knots with the smallest stomachs were the ones most likely to die.

Ultrasonography was used to estimate gizzard (stomach) size in live knots (photo by Maurine Dietz).

During their non-breeding season, red knots are typically found at intertidal mudflats, where they mainly feed on bivalved shellfish like cockles, which they swallow whole! Knots possess a relatively large muscular stomach or 'gizzard', which allows them to crush their hard-shelled prey internally. This way of feeding comes at a price as a large gizzard requires large transport and maintenance costs. However, knots seem to have found a way out by flexibly reducing the size of their gizzard (and other nutritional organs) at times when feeding is impossible, such as during their long-distance flight (5,000-16,000 km) between their arctic breeding grounds and their coastal wintering grounds in temperate and tropical zones. However, such reductions (before departure) and enlargements (upon arrival) of the digestive system take time and therefore knots in their migratory period often have too small gizzards to (re)fuel at full speed. How red knots cope with this problem is the main theme of this work.

By applying a diet model that takes a (flex-



Birds were equipped with a radio-transmitter on their back in order to keep track of their daily movements (photo by Jan van de Kam).

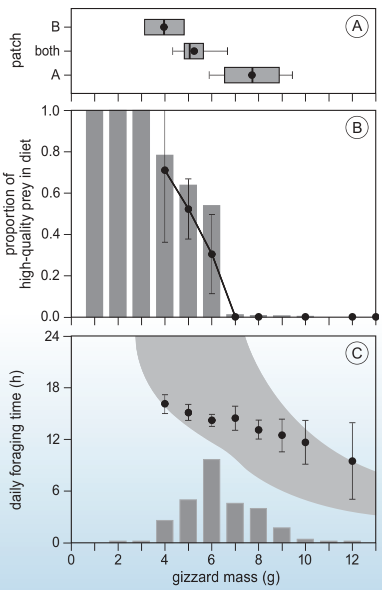
*Corresponding author: theunis@nioz.nl

ible) digestive constraint into account, we predicted knots with relatively small gizzards to feed on easy-to-digest, soft-bodied prey (crustaceans) and knots with larger gizzards to feed on more abundant but harder-to-digest, hard-shelled prey (bivalves). As the model predicted birds with the smallest gizzards to obtain the lowest intake rates, we expected those birds to make the longest working days. The use of ultrasonography enabled us to estimate gizzard mass in live knots and to test these gizzard-size dependent diet-predictions.

Indeed, knots lived up to our expectations. Radio-marked, free-living knots that had relatively small gizzards (i.e. those that were about to depart or had just arrived) were found in soft-bodied food patches, while birds with the largest gizzards were found in hard-shelled food patches. Diet composition varied accordingly (measured by detailed analysis of the faeces), with the softest diets found in knots with the tiniest gizzards. Finally, length of the foraging day declined with gizzard mass, with birds possessing the smallest gizzards stretching their working day to almost 17-h (by moving along with the tide in an eastward direction).

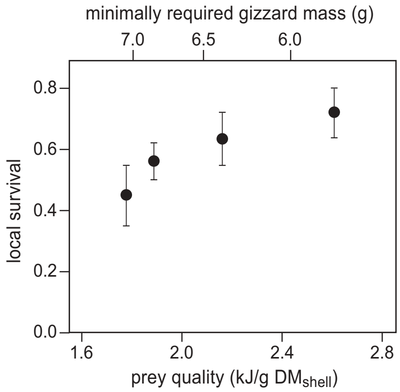
By reversing the equations of the diet model we expected and indeed found that knots fine-tuned the size of their gizzard to the local quality of the prey (both within and between years and between sites).

Individual colour-marking was used to estimate annual survival rates. This particular bird was banded near Texel in spring 2002 and was resighted in the UK in winter 2003/2004 (photo by Chris Kelly).



(A). Birds with small gizzards only visited the patch containing the soft-bodied prey (patch B containing shrimps and crabs), while birds with large gizzards only visited the patch containing hard-shelled prey (patch A containing cockles). Birds with intermediate gizzard sizes visited both patches. (B). Proportion of soft-bodied food in the diet declined as a function of gizzard mass (dots ± SE-bars), in line with theoretical expectations (grey bars). (C). Daily foraging time declined with gizzard mass (dots ± SE-bars), with birds possessing the smallest gizzards just being able to balance their energy budget (lower boundary of grey surface). On the contrary, birds with the largest gizzards hit the upper limit to daily metabolizable energy intake (upper boundary of grey surface). Grey bars give frequency distribution of gizzard mass during late summers.

Knots possessed large gizzards when their bivalve prey contained little amounts of flesh relative to the amount of shell material, while they possessed smaller gizzards when prey contained relatively good amounts of flesh. However, we observed limits to these flexible adjustments of gizzard size. We calculated that in years with low prey quality the required size adjustments would be too large for some birds to be able to cope. In



The local survival rate (year-1) of colour-banded red knots increased with prey quality (defined as the amount of metabolizable energy per gram shell mass). Bars give SE.

accordance with this prediction, our colour-marking programme revealed (i) that birds with too small gizzards disappeared and likely died after such years, and (ii) that the proportion of birds that did not disappear (i.e. those that survived) increased with local prey quality. We were able to show that mechanical cockle-fisheries were the direct cause of the observed decline in prey quality in the western Dutch Wadden Sea.