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Untying the knot

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Summary



The main goal of the research presented in this thesis was to gain a deeper understanding of the spatial distributions of social predators. In order to gain such understanding, I built on three decades of research on red knots (*Calidris canutus islandica*, hereafter called knots). Knots are medium-sized shorebirds that feed on hard-shelled molluscs living in intertidal mudflats. Even though this research mainly concerns knots, the understanding that we have gained is certainly not limited to this single species. In fact, knots could serve as a model for a wider range of species, perhaps including humans.

Questions that we asked are: Do knots use public information to find food? Can we predict the spatial distribution of knots based on the spatial distribution of their prey? Do individuals differ in the way they search for food? Do individual knots have distinct 'personalities' with reference to movement and foraging decisions, and if so, can we explain how and why they consistently differ in behaviour?

We studied knots outdoors on the intertidal mudflats of the Dutch Wadden Sea as well as indoors, i.e. under captivity in the unique experimental shorebird facility at NIOZ Royal Netherlands Institute for Sea Research. These experiments in artificial, controlled conditions allowed disentangling the mechanisms that drive their behaviour. Their decisions in the wild are what we finally try to comprehend. In order to gain an understanding of the mechanisms that drive the spatial distributions of social predators, one needs to combine both methods.

My thesis is divided into four sections that I will summarise consecutively. For the study of interactions between prey and predator their abundances need to be sampled. In the first section we develop a methodology for sampling both prey and predator distributions. In the second section we study aspects of behaviour between knots (their so-called sociality). Here we untie the effects that conspecifics have on an individual's foraging success. Then we switch to individuality. In this third section we show how individual variation in knots is crucial for understanding their foraging decisions. We also show that the spatial distribution of knots can be explained by individual differences in prey. In the fourth section I tie the knot together by discussing some of our findings in a broader context and suggest directions for further research.

SAMPLING METHODOLOGY

Sampling spatial and temporal distributions of a species is central to ecologists, as well as to conservation biologists that are concerned with advising policy makers. In order to maximize effectiveness at minimal costs, these sampling efforts should be optimised.

In **Chapter 2** we develop an optimal sampling design for monitoring programmes with objectives that have conflicting demands on the sampling design. These objectives were: (1) estimate changes in abundance, (2) predict abundances at unsampled locations, or (3) estimate spatial autocorrelation model parameters. With Monte-Carlo simulations, we compared five popular sampling designs: simple random sampling, grid sampling, two types of transect sampling, and our novel grid sampling design with additional random sampling stations. We compared these sampling designs at four levels of naturally occur-

ring spatial autocorrelation, i.e. the level of spatial clustering. Grid sampling with a number of random samples placed on gridlines catered best for all three objectives combined, and can therefore be widely applied.

Knots feed on hard-shelled molluscs buried in the sediment, e.g., Baltic tellins (*Macoma balthica*) and edible cockles (*Cerastoderma edule*). Having developed a sampling design that allows accurately mapping prey densities, we also needed a new methodology to sample spatial distributions of knots. The miniaturisation of tracking technology proceeds at a high speed and has begun to provide tools to ecologists that require the monitoring of large numbers of individuals. Unfortunately, many of these new tools are inapplicable to many species due to mass, cost and energy constraints, leaving gaps in our understanding.

In **Chapter 3** we present a new technique with small transmitters, which is capable of automatically gathering position data for large numbers of animals over long timescales. Relative to current methods, this technique offers ecologists unprecedented amounts of data with accurate position estimates at a high frequency (every second). Moreover, it can be broadly applied to species that were previously too small for automated tracking systems, and due to reduced tracking costs, the numbers of individuals that can be tracked is large.

SOCIALITY

When resources are distributed in patches, as they frequently are, behavioural ecologists often use ideal free distribution models to predict foraging distributions across these patches. When predators aggregate in the best food patches, they increasingly interfere with each other. Consequently, they suffer reduced intake rates. When predators aggregate even more, their intake rate drops below the intake rate that they could have acquired on a different patch with lower food density but also with less competition.

Understanding how intake rate decreases as a function of the number of competitors is of paramount importance to predicting spatial distributions of foragers. Especially because subtle differences in these interference functions may result in qualitatively different predictions. Moreover, resource competition and interference competition are hard to separate as both their negative effects increase with an increase of group size. In an attempt to exclude resource depletion and study interference competition in isolation, we designed an experimental setup with moving patches. Because of the moving patches, new prey became available and prey density remained constant.

In **Chapter 4** we show that the intake rates of knots declined with group size, but surprisingly the common interference mechanisms also declined or were virtually absent. The main mechanism of interference competition among knots is avoiding encounters with conspecifics, so-called 'cryptic interference'. Cryptic interference reduces the available searching time and, because knots divert their attention between searching for prey and avoiding interactions with conspecifics, reduces their searching efficiency. To accurately predict intake rates and model foraging distributions, we need to account for the possibility of cryptic interference.

Foraging together can also be beneficial to individuals. These benefits include increased safety in numbers, increased time that could be spent foraging rather than on anti-predation vigilance, and the accessibility of foraging information. In 1973 Peter Ward and Amotz Zahavi proposed that communal roosting (the grouping of more than two individuals resting together) evolved primarily as centres where individuals *actively* advertise foraging information such as the location of patchily distributed foods. Their proposal has stimulated fierce debates and has not been widely accepted.

In **Chapter 5** we review this controversial ‘information centre hypothesis’ and summarize studies that demonstrate behaviours consistent with the predictions of the hypothesis. Whether actively sharing foraging information is the primary evolutionary cause driving communal roosting is a question that is hard to answer. Because communal roosting is widespread, we think it is particularly interesting to focus on the information benefits that individuals could gain from roosting communally. We suggest that inadvertent information transfer, rather than active information exchange, predominates in communal roosts. To illustrate how testable predictions can be generated, we propose a conceptual model on communally roosting knots. In particular, we illustrate how roost arrival timing may convey inadvertent information on intake rate, prey density, forager state (i.e. digestive processing capacity) and food quality. Unsuccessful foragers could use such information in order to select with whom to leave the roost at the subsequent foraging opportunity. Thus increasing their foraging success.

Information gained from others can help individuals to make better estimates of patch resource density enabling foragers to increase their intake rate, e.g., by wasting less time searching for food in unprofitable patches. The presence of other foragers can also indicate the location of food, so-called local enhancement, which is commonly used by many species.

In **Chapter 6** we show that socially foraging knots also use public information. By monitoring the foraging success of their flock mates they were able to find food faster. In fact, the time needed to locate a food patch decreased proportionally to group size.. Another interesting finding was that knots differed in their search strategy: some individuals consistently exploited the searching efforts of others.

INDIVIDUALITY

Individuals of many species have been shown to vary consistently in their behaviour across contexts. This variation is referred to as ‘animal personality’. Animal personality indicates that behavioural flexibility is limited and that, when the context changes, individuals may not always behave optimally. Because natural selection favours optimal behaviour, a puzzle in evolutionary and behavioural ecology is how and why animal personality persists over evolutionary time. Most of the adaptive (ultimate) explanations of behavioural consistency involve between-individual variations in state. An individual’s state is defined as any feature of an individual that affects the cost and benefits of its behaviour. Recently, variation in the size of metabolic organs has been suggested to cause and main-

tain variation in personality. Large metabolic organs require bold and explorative behaviour that allow for the acquisition of large amounts of energy necessary to sustain these metabolically expensive organs.

In **Chapter 7** we examine this hypothesis. We showed that exploratory behaviour of captive knots was negatively rather than positively correlated with digestive organ (gizzard) mass. In a follow-up experiment we reciprocally reduced and increased an individual's gizzard mass and found that its exploratory behaviour was unaffected. Few studies show how personality traits measured under controlled environments in the laboratory relate to behaviour in the wild. In order to test whether the experimental quantification of exploratory behaviour was representative of this behaviour in the field, we tagged and released the experimental birds with unique combinations of colour-rings and estimated local resighting probabilities. Birds that were not resighted locally, over the 19 months after release, had higher exploration scores than birds that were resighted. Moreover, a long-term mark-recapture effort on free-living knots with known gizzard masses at capture confirmed that local resighting probability (an inverse measure of exploratory behaviour) was correlated with gizzard mass without detrimental effects on survival. We conclude that personality drives physiological adjustments, rather than the other way around, and suggest that physiological adjustments mitigate the survival costs of exploratory behaviour. Our results show that we need to reconsider hypotheses explaining personality variation based on organ sizes and differential survival.

From individual variation among knots we then switch to individual variation among their prey, the cockles. Selective predation can lead to natural selection in prey populations and may also alleviate competition among surviving individuals. The processes of selection and competition can have substantial effects on prey population dynamics, but are rarely studied simultaneously.

In **Chapter 8** we study the processes of selective predation and competition in the wild. We measured densities, patchiness, morphology, and body composition (shell mass and flesh mass) of cockles before and after predation in three similar plots of 1 ha each. Two of these plots experienced predation, and one plot remained unvisited in the course of the short study period and served as a reference. We showed that predation by knots substantially reduced cockle densities and homogenised their spatial distribution. Moreover, knots selected those individual cockles that allowed them to maximise their energy intake rates, i.e. juvenile cockles with large flesh mass and little shell mass. By this selective predation knots imposed a strong selection pressure on cockles to grow fast with thick shells and little flesh mass. The calculated selection gradients are among the highest reported in the literature. We also found that cockle body composition declined with cockle density (negative density-dependence) possibly through intra-specific competition.

The effects of density dependence are generally studied within trophic levels. However, density dependence within a trophic level may also have implications for higher levels. Until now the idea is that a predator's intake rate always increases with prey density. Large prey densities should thus attract many predators. However, the presence of negative density-dependence among prey challenges this prediction.

In **Chapter 9** we investigate negative density-dependence among cockles and its implications for the energy intake rate of knots. With the method that we present in Chapter 2, we sampled the density and quality of cockles across 50 km² of mudflat. Simultaneously, we tracked the spatial distribution of knots with the novel time-of-arrival methodology that we introduce in Chapter 3. We show that, due to negative density-dependence in the flesh mass of cockles, knots are faced with a trade-off between prey quantity and quality. At low prey densities predators have difficulty finding prey, but those prey have relatively large energy content. At high densities prey are easier to find, but have relatively low energy content. Contrasting the current viewpoint, knots do not necessarily maximise their energy intake rates at the highest prey densities. Resource-selection modelling revealed that the tagged knots indeed avoided areas with the highest cockle densities. They preferred foraging on areas with intermediate cockle densities where they could maximise energy intake rate given their phenotype-specific digestive constraints (as indicated by gizzard mass).

Because negative density-dependence is common for many different (prey) species, we oppose the current consensus and suggest that predators will often maximise their energy intake rates at intermediate prey densities. Prey density alone may thus be a poor predictor of intake rates, carrying capacity and spatial distributions of predator populations.

RETYING THE KNOT

The work presented in this thesis provides us with a better understanding of the spatial distribution of knots. The mechanisms that we unraveled can be relevant for studies on foragers in general.

In **Chapter 10** I highlight some of our findings and discuss them in a broader context. Such as the importance of estimating spatial autocorrelation functions for understanding spatial distributions, the possibility of cultural evolution at communal roosts, how ‘cryptic interference’ relates to spatial distribution modelling, how consistent differences between individuals may drive spatial distributions, and the phenomenon of animal personality. Finally, I propose a framework for the development of adaptive personality differences between knots. This framework may contribute to future studies on knot personality and provide some interesting thoughts for animal personality research in general.



