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Untying the knot

Bijleveld, Allert Imre

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Chapter 1

General introduction

KNOTS

Allert Bijleveld



KNOTS – PART I

Walking the mudflats of the Dutch Wadden Sea fuels one's fascination for nature. Twice a day, vast areas of mudflat are exposed for a few hours. In this short time-window, many thousands of birds need to find food to survive. Most birds feed on small worms and shellfish that live buried in mudflats that, at first glance, appear to show little variation. Only when one digs in the mud, one realises that some parts of the mudflats contain much more food than others. Likewise, on some mudflats birds clump together in flocks of several thousand individuals, while on others a handful of birds are widely spread out. This makes one wonder how the birds find their scattered and concealed food on mudflats that look so uniform. Do they use each other to find food? Are some individuals more successful in finding their prey than others? Why did they choose to forage there, and not elsewhere?

Questions like these highlight the focus of my thesis and are fundamental to ecologists, scientists that study the interactions between organisms and their environment. I will stand on the shoulders of giants (Table 1.1) and continue three decades of research on red knots *Calidris canutus islandica* (Fig. 1.1, hereafter called knots) in an effort to identify and untie the mechanisms that drive their foraging decisions and spatial distributions in the field. Even though this research mainly concerns knots, the mechanistic understanding that we pursue is certainly not limited to this single species. In fact, knots serve as a model

Table 1.1 The shoulders of giants that I stand on. This Table shows the different PhD students and theses on knots and their prey, which have been defended at the University of Groningen.

Year	Auteur	Title
1994	Theunis Piersma	Close to the edge: energetic bottlenecks and the evolution of migratory pathways in knots
1997	Leo Zwarts	Waders and their estuarine food supplies
2004	Jan A. van Gils	Foraging decisions in a digestively constrained long-distance migrant, the red knot (<i>Calidris canutus</i>)
2006	Wouter K. Vahl	Interference competition among foraging waders
2007	Jeroen Reneerkens	Functional aspects of seasonal variation in preen wax composition of sandpipers (Scolopacidae)
2008	Deborah M. Buehler	Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants
2010	Casper Kraan	Spatial ecology of intertidal macrobenthic fauna in a changing Wadden Sea
2010	Piet J. van den Hout	Struggle for safety: adaptive responses of wintering waders to their avian predators
2011	Jutta Leyrer	Being at the right place at the right time: interpreting the annual life cycle of Afro-Siberian red knots
2012	Eelke O. Folmer	Self-organization on mudflats
2013	Matthijs van der Geest	Multi-trophic interactions within the seagrass beds of Banc d'Arguin, Mauritania: a chemosynthesis-based intertidal ecosystem



Figure 1.1 Group of foraging knots (*Calidris canutus islandica*) on intertidal mudflats in the Dutch Wadden Sea. Note that some birds have found a cockle (*Cerastoderma edule*) that they are about to swallow whole. Photo courtesy by Jan van de Kam.

allowing us to understand principles that are commonly found in nature, including human nature. Such an understanding is of general interest from a basic scientific perspective (the intrinsic value of understanding the world around us), as well as from an applied science or conservation perspective. Especially in light of a rapidly changing world (e.g., due to climate change, land reclamations, natural resource extraction, etc.), the need for nature conservation managers to predict animal spatial distributions is growing, which requires an understanding of species distributions.

FORAGING THEORY

Foraging theory is central to ecology and has been studied and refined over many decades (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Charnov 1976, Pyke et al. 1977, Clark and Mangel 1984, Lima 1985, Mangel and Clark 1986, Stephens and Krebs 1986, Krebs 2001, Stephens et al. 2007). A forager's survival and reproductive success (fitness) will depend on how well they can acquire food (energy and nutrients). Food intake rate is, therefore, often assumed to be correlated with fitness (Kacelnik et al. 1992). Foraging theory has provided a deep understanding of how forager's decide what to eat, where to eat it, and when to look somewhere else to feed. At the base of foraging theory is the functional response that describes a forager's intake rate as a function of prey density

(Holling 1959). The exact shape of the functional response depends on how searching and handling time limit intake rate. The most widespread is the ‘type II’ functional response (Fig. 1.2) that shows a decelerating increase in intake rate to a plateau that is set by handling time, i.e. at high prey densities foragers almost immediately find their prey and are continuously handling them.

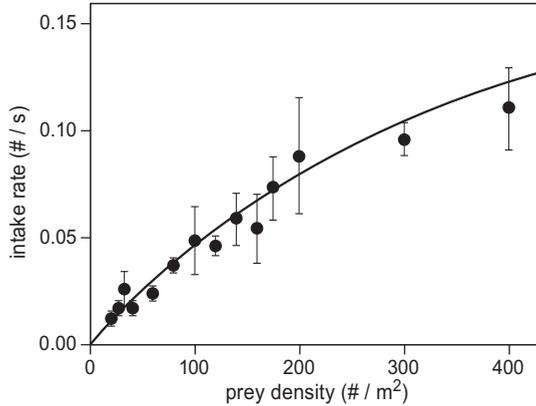


Figure 1.2 The functional response of knots feeding on Baltic tellins (*Macoma balthica*) and edible cockles (*Cerastoderma edule*). These data were gathered from captive knots in controlled experiments (Piersma et al. 1995), and pooled for both prey species as the functional response parameters were indistinguishable. The dots represent means and bars represent standard errors. The solid line represents Holling’s disc equation: $IR = a \times N / (1 + a \times N \times T_h)$, where a forager’s predicted numerical intake rate is given by IR ($n\ s^{-1}$), searching efficiency or area of discovery by a ($5.7\ cm^2\ s^{-1}$), prey density by N ($n\ m^{-2}$), and prey handling time by T_h (3.8 s). We reproduced this graph from van Gils (2004, Box II).

PREDICTING SPATIAL FORAGING DISTRIBUTIONS

Prey are often distributed in patches where prey density is higher than the surrounding area (Kraan et al. 2009a). Assuming that animals aim to maximize intake rate (fitness), one would expect foragers to aggregate in those patches with the highest prey densities (Sutherland 1983, Tregenza 1995). Clearly, predators are found much more spread out, and the question is why not all foragers are found in the patch with the highest prey density? As predators aggregate they increasingly interfere with each other, which decreases their intake rate (Goss-Custard 1980, Johnson et al. 2004, Vahl et al. 2005b, Smallegange et al. 2006). When predators aggregate even more, their intake rate drops below the intake rate that they could acquire on a different patch with lower food density but also with less competition (Fig. 1.3). Ultimately, foragers will distribute themselves in such a way that they all experience a similar intake rate, i.e. they obey what is known as the ‘ideal free distribution’ (Fretwell and Lucas 1970). Ideal-free distributions are null-models that are built on simplifying (and hence usually unrealistic) assumptions. For

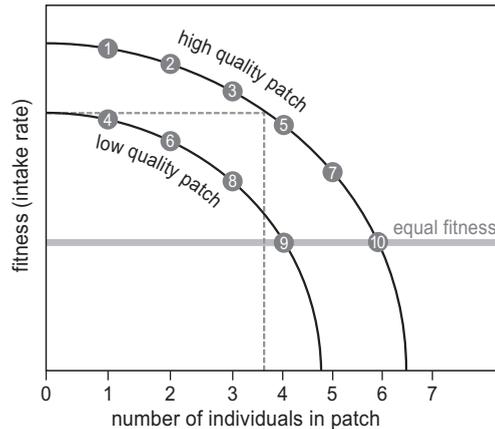


Figure 1.3 The ‘ideal free distribution’. The two solid curves represent two food patches, one of low and one of high quality in terms of intake rates. The numbers in grey circles indicate the order in which 10 foragers will choose between patches. Foragers are expected to go to the patch that maximises their intake rate (fitness). They will, therefore, first go to the high quality patch. As the group size of foragers increases, their intake rate will decrease. At a group size of between 3 and 4 foragers, the intake rate in the high quality patch drops below that of the low quality patch (without foragers). The fourth forager will therefore go to the low quality patch where its interference-free intake rate will be highest at that time, and so forth. Finally, six foragers will gather on the high quality patch and four on the low quality patch; all of them with the same intake rate (as indicated by the horizontal grey bar).

instance, foragers are assumed to have perfect knowledge about the possible intake rates across all patches that are available to them, and to incur no costs for moving between patches. Nevertheless, such null-hypotheses help us understand spatial distributions (Sutherland 1983, Parker and Sutherland 1986, Bautista et al. 1995, Sutherland 1996, van der Meer and Ens 1997, van Gils et al. 2006b).

BENEFITS OF SOCIALITY

As discussed above, a main cost of foraging in groups is competition for resources. Group foraging (social foraging) is beneficial as well and animals are often attracted to each other (Folmer et al. 2012). The benefits of group foraging include increased safety in numbers (Pulliam 1973), increased time that could be spent foraging rather than on anti-predation vigilance (Lima 1995), and the accessibility of foraging information (Clark and Mangel 1984, Valone 1989, Danchin et al. 2004, Dall et al. 2005, Valone 2007, Giraldeau and Dubois 2008). Animals face tremendous uncertainty in nature. Information gained from others can help individuals make more accurate and faster estimates of patch resource density (Clark and Mangel 1984, 1986, Valone 1989), which allows foragers to maximise their intake rate by wasting less time in unprofitable patches (Charnov 1976, Templeton and Giraldeau 1996, Smith et al. 1999, van Gils et al. 2003b). Information from others can

also indicate the location of food (local enhancement, Thorpe 1956, Pöysä 1992). Many different species use local enhancement to select where to eat (Galef and Giraldeau 2001), which is especially beneficial when food is clumped and patches are large enough not to be monopolized (Beauchamp 1998); if patches are small, dominant foragers can exploit food discoveries of subordinates (Vahl and Kingma 2007).

INDIVIDUAL VARIATION

Within species and populations, individuals differ in their behaviour, which can affect foraging decisions that drive spatial distributions (Parker and Sutherland 1986). Based on foraging theory there should, however, be one optimal foraging decision that maximises intake rate and thus fitness (Stephens and Krebs 1986). The observed between-individual variation in foraging behaviour was often seen as noise around an animal's calculated optimal behaviour, i.e. 'the raw material on which natural selection acts, rather than as the end product of natural selection' (Wilson 1998). However, individuals of many species have been shown to vary consistently in their behaviour across contexts, yielding the notion of 'animal personalities' (Koolhaas et al. 1999, Gosling 2001, Dall et al. 2004, Sih et al. 2004a, Sih et al. 2004b, Réale et al. 2007, Carere and Maestripieri 2013). An animal's personality is commonly quantified on the basis of standardized measurements of aggressiveness, boldness, exploration, sociability and activity (Réale et al. 2007). These personality traits have been shown to relate to ecologically relevant traits such as social dominance (Armitage and Van Vuren 2003, Dingemanse and de Goede 2004), risk-taking (Bell 2005, Bell and Sih 2007), social information use (Kurvers et al. 2010b), habitat use (Boon et al. 2008, Minderman et al. 2010, van Overveld and Matthysen 2010), and foraging behaviour (Wilson and McLaughlin 2007). Only recently, animal personality research has become firmly grounded in evolutionary ecology and life-history theory (Réale et al. 2007, Stamps 2007, Wolf et al. 2007, Biro and Stamps 2008, Careau et al. 2008, Réale et al. 2010a, Réale et al. 2010b, Wolf and Weissing 2010, Dall et al. 2012, Wolf and McNamara 2012). Nonetheless, the evolutionary origin and maintenance of phenotypic variation in animal personality is still intensely debated (Dingemanse and Réale 2005, Dingemanse and Wolf 2010, Dall et al. 2012, Wolf and McNamara 2012).

KNOTS – PART II

Knots are migratory shorebirds (Fig. 1.4) that breed on large territories in High-Arctic tundras between June and July (Davidson and Wilson 1992, Piersma 2007). During the non-breeding season they live in tidal areas of Western Europe (Piersma 2007, Quaintenne et al. 2010, Piersma 2012). Around high tide, they aggregate (roost) on exposed areas in large and dense flocks (Piersma et al. 1993a). Around low tide, they search for food in large groups of up to several thousand individuals (Piersma et al. 1993a). Over short time-scales (weeks) their foraging locations tend to be unpredictable,

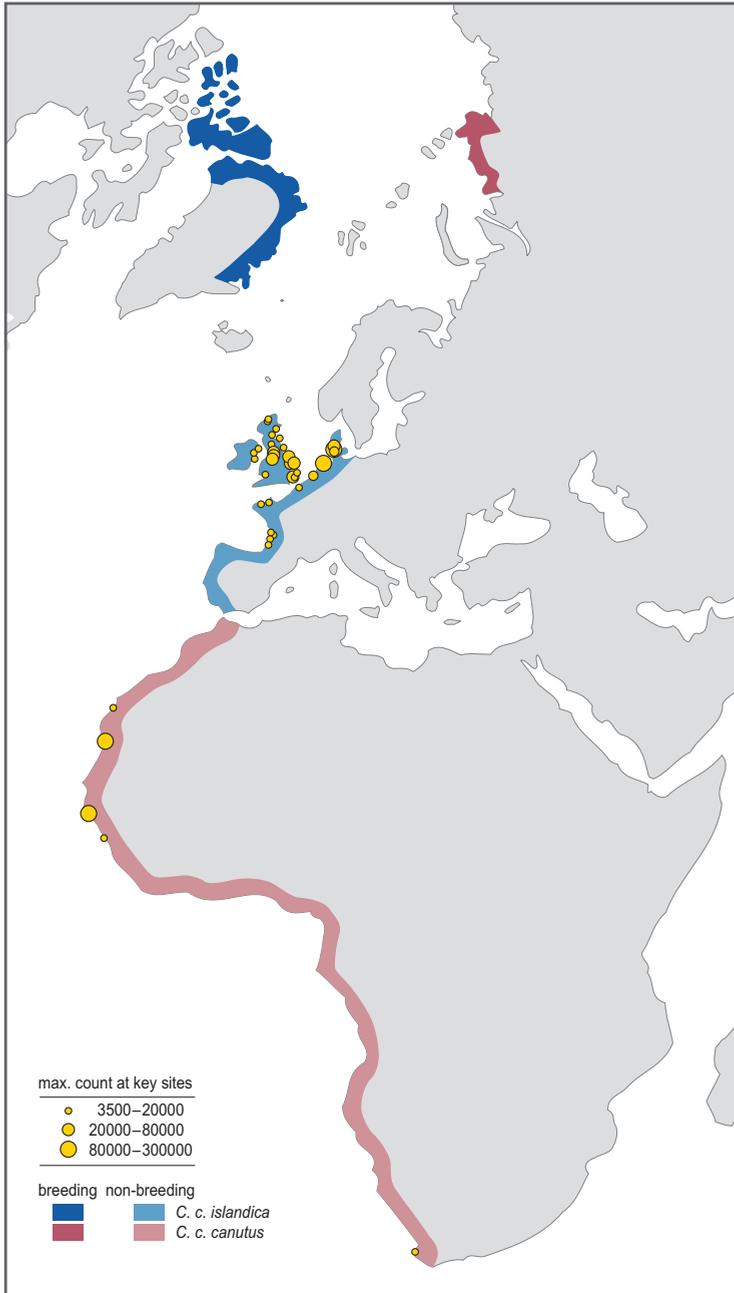


Figure 1.4 Spatial distribution of two subspecies of knots: *Calidris canutus canutus* and *islandica*. The *canutus* subspecies can be found in the Dutch Wadden Sea during periods of migration between their breeding sites in Siberia and their overwintering sites in Africa. The *islandica* subspecies breeds in Greenland and Canada and overwinters in mudflats across Western Europe, including the Dutch Wadden Sea. The work that we present in my thesis focusses on the *islandica* subspecies. This figure was reproduced from Davidson and Piersma (2009).

which is attributed to their strong social attraction (Folmer et al. 2010), mobility (van Gils et al. 2005b), and the large spatial extent of foraging opportunities (Kraan et al. 2009a). Within each low-tide period, knots fly tens of kilometres across exposed mudflats in search of buried hard-shelled molluscs, such as Baltic tellins *Macoma balthica* and edible cockles *Cerastoderma edule* (Zwarts and Blomert 1992, Piersma et al. 1993a, van Gils et al. 2005b). Knots have pressure sensitive organs in the tip of their bill, which enable them, by repeatedly inserting their bill in soft wet sediments, to remotely touch-sense hard-shelled prey over a distance of several cm (Piersma et al. 1998). When found, knots swallow their prey whole and are, therefore, limited to ingesting prey smaller than 16-18 mm (Zwarts and Blomert 1992, Piersma et al. 1993a). To crush the shells, they require a strong muscular stomach that is known as a gizzard (van Gils et al. 2003a, Battley and Piersma 2005). With an ultrasound scanner, gizzard mass can be measured in living birds (Dietz et al. 1999, Dekinga et al. 2001). Under controlled experimental conditions, gizzard mass was found to be flexible within individuals and changes in response to the ratio of flesh to shell mass of their prey (prey quality). The size of the gizzard sets an upper limit to the amount of shell mass that can be processed and thus limits daily intake rates (van Gils et al. 2003a). The lower the prey quality, the larger the gizzard must be to process the ballast shell material necessary to uphold their required energy intake rates.

THESIS OUTLINE

My thesis is divided into four sections. In the first section we develop methodology that we build on subsequently. Monitoring programmes can have multiple objectives with conflicting demands on the optimal sampling design. In **Chapter 2**, we develop a novel sampling method that allows for estimating temporal and spatial changes, as well as accurately mapping macrobenthic prey densities on intertidal mudflats. In order to track the small-bodied knots at fine spatial and temporal scales across nonbreeding habitats, in **Chapter 3** we report on the development of a novel light-weight tracking method. In the second section we untie the effects of sociality on the foraging behaviour of knots. In **Chapter 4**, we first show the costs of social foraging, which differ between dominant and subordinate knots. Then we investigate the information benefits of social foraging. In **Chapter 5**, we dust-off the controversial information-centre hypothesis from the 1970s and show how knots could use high-tide roosts to gain inadvertent information on where, on what and with whom to forage. In **Chapter 6**, we show that knots indeed use the foraging success of their flock mates to decide where to forage and that social foraging increases their foraging efficiency proportional to flock size. We also show that knots consistently differ in the effort they put into searching for food patches and that some individuals readily and consistently exploit the searching effort of their flock mates.

This leads up to the third section of my thesis in which we show how individual variation in both predators and prey is crucial for understanding foraging decisions and distributions. In **Chapter 7**, we experimentally establish that knots have personalities. They consistently differ in their exploratory behaviour; some readily explore a novel environ-

ment while others are more sedentary. We also show how variation in exploratory behaviour drives variation in gizzard mass and explained their spatial distribution in the wild. Then, in **Chapter 8**, we switch from the predator's perspective to that of the prey and show the effect that predation by knots has on the density, length, and body composition of cockles and discuss their potential for adaptive anti-predation responses. In **Chapter 9**, we illustrate that due to negative density-dependence among cockles, knots are faced with a trade-off between prey quantity and quality. Opposing the common notion that predators achieve the highest intake rate at the highest prey densities, we predicted that knots would achieve the largest intake rates at intermediate prey densities. By sampling prey quantity and quality and tracking the spatial distributions of knots in the wild, we indeed show that knots selected locations with intermediate prey densities. I conclude my thesis with the fourth section that contains **Chapter 10**. Here, I highlight some of our findings that I discuss in a broader context and suggest avenues for future research.

Section I

Methodology

