Chapter 1

General Introduction

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"*I will not attempt any definition of instinct. A little dose [...] of judgement or reason often comes into play, even in animals very low in the scale of nature.*"
Charles Darwin in *On the Origin of Species* (1859)

In recent history many animal species, if not most, have been facing rapid changes in their environment by habitat destruction, exploitation of their resources, climate change, or a combination (Tilman *et al.* 2001; Butchart *et al.* 2010; Leadley *et al.* 2010). Currently, human-induced environmental change proceeds at unprecedented rates (e.g. IPCC 2014). To develop adequate measures that help existing ecosystems to prosper, a deeper understanding of how populations react to changing circumstances is needed more than ever.

The connection between populations and their environment is shaped by evolution through natural selection (Darwin 1859). The phenotype adjusts to environmental change by selection of adaptive variation over generations, but also by plastic (West-Eberhard 2003) and flexible (Piersma & van Gils 2011) development of the individual phenotype. This can be any phenotypic trait, but the most directly observable interaction with the environment, in many organisms, is through behaviour. Behavioural choices influence whether the individual thrives or dies, which in turn is a basic ingredient of natural selection. Many different approaches are being used to study the relationship between populations and the environment, all uncovering different aspects of its stunning complexity. This thesis contains five studies from a behavioural perspective, which I hope will contribute as well, if only a bit.

Using behaviour to study ecological interactions: the optimality approach

Conventional wisdom has it that, contrary to humans who make conscious decisions, other animals simply act by 'instinct'. It implies that animal habits are the expression of a genetically orchestrated behaviour, whereas humans at least to some extent have the ability to anticipate and to choose rationally. However, there is no biological evidence for any such distinction. As implied in the above quote by Darwin, it should always be considered that behaviour involves decision making. Animals must make decisions whenever alternatives appear (McFarland 1977). When and where to breed, where and when to forage, what food to search for, all must be decided. What sources are used to inform these decisions, and how they are judged, has been shaped by evolution. It cannot be expected that animals measure all available information, that they necessarily measure it correctly, or even that the best decision is always made when all information is measured. But it is to be expected that animal senses have evolved to gather available information that is necessary to choose the fitness-maximizing option (Schmidt, Dall & van Gils 2010). That implies that fitness questions can be investigated by asking which information influences animal decisions, and how this information is perceived. This is the basis of 'optimality models' (reviewed in McNamara, Houston & Collins 2001). Optimality models provide a way to generate quantitative hypotheses on how animals will respond to changes in environmental variables; behaviourally, developmentally and evolutionarily.

In search of a population with an easy fitness currency

A considerable difficulty in the application of optimality models has been the search for a 'currency' in which fitness consequences should be measured, on the basis of which to compare alternative options (Stephens & Krebs 1986). Animals must consume enough of the right nutrients, reproduce, avoid to be consumed or to fall ill, and provide the best

possible circumstances for their offspring to do the same. All these factors may influence what is the best option, but not all are always relevant (Owen-Smith 1993). For example, the life cycle of migratory birds includes the distinction between the breeding season and the non-breeding season. Especially in species that do not provide parental care outside the breeding season, the main determinant of fitness then is to survive, and to be ready for the next breeding season. The important decisions then primarily concern habitat selection and diet selection. Although a crude simplification, the animal's habitat selection may be understood by assuming that the animal needs to consume a certain daily amount of energy, and that it will choose its foraging location such that it is able to reach these requirements, at the least possible risk of mortality. At this location, its general diet selection may be understood by assuming that it chooses to forage on that mix of resource types that offer the highest intake rate of the necessary nutrients, thereby minimizing the time needed for foraging. We have now entered the realm of 'optimal foraging theory' (MacArthur & Pianka 1966; Stephens & Krebs 1986; Piersma & van Gils 2011).

RED KNOTS

This thesis is concerned with the foraging behaviour of red knots *Calidris canutus* during the winter season. Red knots are medium sized migratory shorebirds that breed in the High Arctic and spend the winter in temperate and tropical regions (Fig. 1.1), where they fully rely on intertidal mudflats and forage mainly on small mollusc prey during the low tide (Piersma & Davidson 1992). They ingest their prey whole, and digest them in their specialized muscular stomach, the gizzard (Piersma, Koolhaas & Dekinga 1993). In the breeding area they feed mostly on insects, but regularly also include plant material in their diet (leaves and berries; J.A. van Gils and J. Wilson, personal communication). Also during staging, red knots occasionally forage on plant material (e.g. in Gdańsk Bay, J.A. van Gils, personal communication). At Banc d'Arguin, red knots feed on seagrass rhizomes at a rate that has been increasing in recent years (van Gils *et al.* 2016), acting as a secondary resource when mollusc availability is low (van Gils *et al.* in prep). Six subspecies are distinguished worldwide (Buehler, Baker & Piersma 2006), all threatened in their existence by climate change in the breeding areas and destruction of the intertidal areas that they rely on during migration and in the winter (Piersma 2007; Ma *et al.* 2014; Piersma *et al.* 2016; van Gils *et al.* 2016).

Wintering red knots are particularly suited for the study of behaviour under natural conditions with the use of optimal foraging theory, for several reasons. Firstly, their wintering range is confined to a well-defined, accessible and readily observable habitat: intertidal mudflats (Piersma 2012). The mollusc prey that they forage on are largely sessile, and can be sampled and quantified accurately through time and space using specialized sampling methods (Beukema 1976; Piersma, de Goeij & Tulp 1993; Bijleveld *et al.* 2012). Secondly, red knots comprise one of the few vertebrate species that are still being found in their natural habitat, with much of the food web complexity that it had in pre-industrial times, even in Western Europe. This offers the possibility to study the intricate
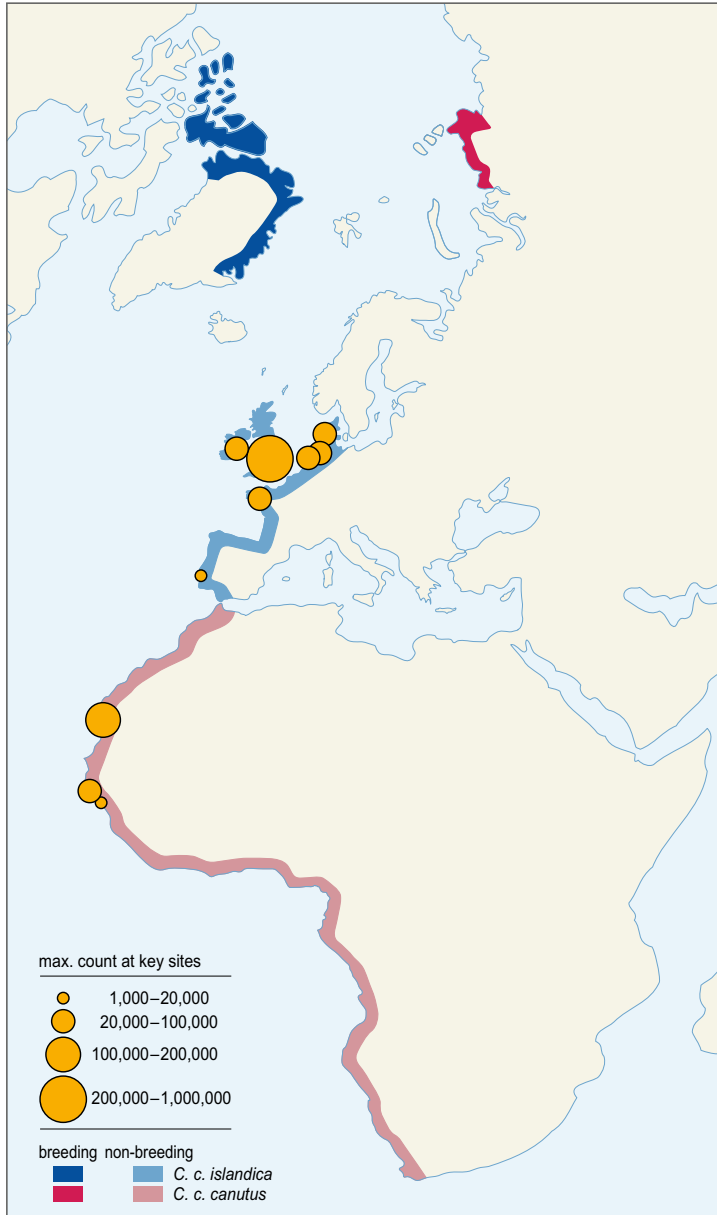
Figure 1.1 Winter distribution of red knots *C.c. islandica* and *C. c. canutus*. The red knot subspecies *islandica* (in blue) breeds in N Greenland and NE Canada, and winters along the W European coast, mainly the Wadden Sea. Subspecies *canutus* (in red) breeds in N Siberia, and winters on the W African coast, and mainly Banc d'Arguin. *Canutus* red knots stage in the Wadden Sea during migration, where they then co-occur with the *islandica* red knots. Nonetheless, individuals virtually never switch migration scheme. Shown are the estimated red knot numbers in the period 2010–2014 (van Roomen *et al.* 2015). Breeding and non-breeding areas reproduced from Davidson & Piersma (2009) and Bijleveld (2015).

behavioural responses that red knots have evolved in interaction with the ecologically highly complex environment that they inhabit. Thirdly, red knots show not only highly variable habits across the world and even within populations (van Gils *et al.* 2005a; van Gils *et al.* 2006; Piersma 2007), but also a highly flexible physiology that closely interacts with behavioural variability (Dekinga *et al.* 2001; Piersma 2002). This enables the study of individual variation in (non-)behavioural traits, and the interactions between behavioural decisions and the environment.

Last, but certainly not least, red knots are a superb study species because so many studies have already been performed, and much of their basic ecology, the important physiological parameters and behavioural details have been uncovered. Worldwide logistics are currently in place that allow an active international research community to study their wintering and staging areas worldwide, especially in the subspecies *C.c. islandica*, *C.c. canutus* and *C.c. rufa* (Piersma 2007).

Red knots wintering in the Wadden Sea

Red knots wintering in the Wadden Sea belong to the subspecies *C.c. islandica*, maintaining a migratory connection via Iceland with their breeding grounds in N Greenland and NE Canada (Fig. 1.1; Davidson & Wilson 1992). This population has received by far the most attention of all. No fewer than 12 PhD theses involving red knot foraging behaviour have been defended at the University of Groningen (all listed in Bijleveld 2015, except the newest; de Fouw 2016). The current thesis draws heavily on them all, and particularly on the first, the third and the eleventh (Piersma 1994; van Gils 2004; Bijleveld 2015). Piersma (1994) provided the ecological foundation, describing general basic foraging ecology and diet of the red knot, the significance of its migration, energetic bottlenecks and physiology, with particular attention to the gizzard and its relation to the diet. Van Gils (2004) provided a solid basis for the use of optimal foraging theory and diet choice experiments to clarify the functional relationship between the observed variability in gizzard mass and the diet and habitat selection of red knots in the Wadden Sea. Bijleveld (2015) introduced the study of consistent individual variation in physiology and habitat- and diet selection, focussing on personality differences as a cause rather than an effect of physiomorphic differences. In addition, it provided the ins and outs of radio tracking red knots, with a spatially explicit resource sampling scheme underlying it.

Red knots wintering at Banc d'Arguin

The work in this thesis focusses on the red knot subspecies *C. c. canutus*, wintering at the other major wintering site along the East Atlantic flyway, the Banc d'Arguin in Mauritania (Fig. 1.1). In a practical sense, this work comprises not much more than previously successful research techniques in the Wadden Sea, applied to the red knots at Banc d'Arguin. These red knots breed in Siberia and meet the *islandica* subspecies in autumn during stopover in the Eastern Dutch and German Wadden Sea and the Baltic coast, before continuing to the wintering grounds of W Africa, and mainly the Banc d'Arguin (Dick, Piersma & Prokosch 1987). The total population size there was estimated reliably for the first time in 1980 and estimated at 350,000 individuals (Altenburg *et al.* 1982). Since then,
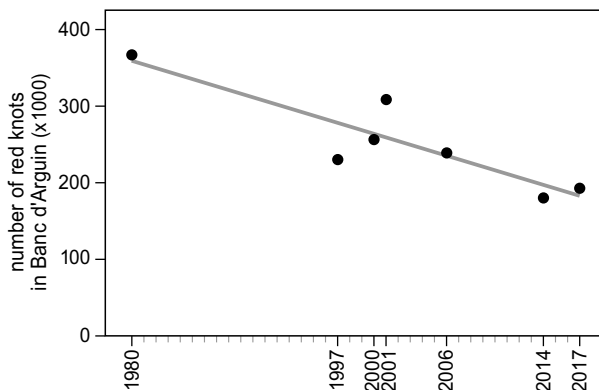
Figure 1.2 The number of red knots counted in all complete winter counts of Banc d'Arguin. Grey line shows the linear regression ($F_{1,5}$ = 20.3, R^2 = 0.76, p = 0.004). Counts were performed in January or early February. Data by courtesy of Parc National du Banc d'Arguin, SOVON, Birdlife International and Wetlands International.

the population has been showing a significant decline that seems to be continuing to this day (Fig. 1.2), with the current best estimate being 200,000 (van Roomen *et al.* 2015, Oudman *et al.* 2017). The causes are probably multiple. A decline in resource availability in the Wadden Sea, the main important stopover area during migration, may have contributed in the recent past (van Gils *et al.* 2009; Kraan *et al.* 2010). Reasons may also be found in the Arctic. There, rising spring temperatures are causing a mismatch between egg-hatching and the peak in insect abundance potentially causing high mortality in juveniles during migration and on the wintering grounds, where bivalve availability to juveniles is lower, presumably due to shorter bills (van Gils *et al.* 2016). Changes in red knot habitat also take place at Banc d'Arguin, which can be explained by cyclical ecosystem dynamics, but do point out a high sensibility to ecosystem disturbance (de Fouw *et al.* 2016). Disturbance is indeed taking place, e.g. by the recent increase in the harvesting of several ray species (mainly Lusitian cownose ray *Rhinoptera marginata* and blackchin guitarfish *Rhinobatos cemiculus*; Sidi Yahya Cheikhna Lemrabott, personal communication), whose population sizes have been greatly reduced by intense harvesting in the 1980s and 1990s.

Hence, *canutus* red knots face environmental change in all the ecosystems that they connect. This provides an important practical purpose for investigations on their ecology. It also provides a highly appealing ecological study system: what are the complex behavioural mechanisms that have allowed them to persist until now?

STUDY OUTLINE

The studies in this thesis are specifically aimed at a further understanding of the foraging decisions of *canutus* red knots wintering at Banc d'Arguin, taking the foraging decisions of *islandica* red knots in the Wadden Sea as a reference. In **Chapter 2** we set out to deter-

mine the factors that influence red knot diet composition, focusing on the two main prey types of red knots in Banc d'Arguin, *Loripes lucinalis* and *Dosinia isocardia*. Based on knowledge from the Wadden Sea red knots, we expected that Banc d'Arguin red knots would ignore any other food type than *Loripes*. This prediction highly contrasted the actual diet, a mix of *Loripes* and other mollusc species. We hypothesized that this discrepancy is a consequence of the peculiar metabolism of *Loripes*, involving sulfide-oxidizing bacteria and causing a toxic effect due to the ingestion of sulphur compounds. This hypothesis was tested in an experiment with captive red knots in Mauritania. In **Chapter 3** we extend the diet choice predictions of Banc d'Arguin red knots to the field, by implementing the toxin constraint into the digestive rate model, which was previously designed to test diet choice of Wadden Sea red knots (Hirakawa 1995; van Gils *et al.* 2005b). We tested whether this addition is necessary to explain winter survival of red knots, based on annually measured winter densities of *Loripes* and *Dosinia*. In **Chapter 4** we perform another diet experiment to test another expected consequence of the toxin constraint, which is that a larger gizzard mass should increase the maximum intake rate of non-toxic *Dosinia*, but not of toxic *Loripes*. This has the implication that individuals with larger gizzards are expected to prefer a lower proportion of *Loripes* in the diet. In **Chapter 5**, we put the consequently expected causal relation between individual gizzard mass and diet preferences to the test in the wild, using an automated radio tracking system to record patch residence times (MacCurdy, Gabrielson & Cortopassi 2012; Piersma *et al.* 2014; Bijleveld *et al.* 2016). In **Chapter 6** we use the obtained residence patch locations to compare space use of tagged red knots to similarly tagged conspecific counterparts in the Dutch Wadden Sea (Bijleveld *et al.* 2016). Based on two extensive benthos sampling schemes, we tested whether red knots adjusted the degrees of aggregation and site fidelity to differences in the resource landscape. In **Chapter 7**, I place the implications of these studies in a broader context. I emphasize the potential role that the observed behavioural decision processes may have on population dynamics and the development of the individual phenotype. This is of immediate relevance for an understanding of the evolutionary forces that shape the red knot and the intricate relationship with its environments; environments that it shares with us.