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Untying the knot

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Chapter 10

The many dimensions of knots

THE INTEGRATION OF A PHENOTYPE

Allert Bijleveld

The main goal of the research presented in this thesis was gaining a deeper understanding of the spatial distribution of social predators. Questions that we asked were: Do knots use public information to find their hidden food? Do individuals differ in the way they search for food? Can we predict the spatial distribution of knots based on the spatial distribution of their prey? 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?

In this final chapter, I will highlight some of our findings and at the same time seek directions for future studies. In line with the thesis structure, I have divided this general discussion into different sections. First, I will briefly discuss sampling methodology and the importance of estimating spatial autocorrelation functions for understanding spatial distributions. Second, I consider the sociality of knots. In this section I will reflect on the information benefits of social foraging and communal roosting, as well as the interference-costs that are associated with social foraging and how these relates to spatial distribution modelling. Third, I will discuss individuality. In particular how differences between individuals may drive spatial distributions, and the ecology and evolutionary background of animal personalities. Fourth, I will tie the knot together and propose an ecological-evolutionary framework for the development of personality differences between knots. Finally, I will briefly summarise our main findings and suggest some future research directions.

SAMPLING METHODOLOGY

Quantifying the spatial distribution of species is essential to understand the underlying mechanisms (Thrush 1991, Legendre et al. 1997). One way to quantify the spatial distribution of a species is by estimating how spatial autocorrelation varies with distance, the so-called spatial autocorrelation function. For bivalves, few studies investigate the spatial autocorrelation function explicitly (e.g., Thrush et al. 1989, Hewitt et al. 1996, Hewitt et al. 1997a, Hewitt et al. 1997b, Legendre et al. 1997, Kraan et al. 2009a, Kraan et al. 2009b). Studies that investigate spatial autocorrelation in combination with predation are especially rare (e.g., Boldina and Beninger 2013).

The novel sampling design that we propose in Chapter 2 allowed for accurately estimating spatial autocorrelation. Even though the finding itself is not novel (e.g., Huxham and Richards 2003, Kraan et al. 2009a, Boldina and Beninger 2013), by estimating the spatial autocorrelation function we revealed that cockles cluster in patches both at small spatial scales (Fig. 8.2 and 8.3), as well as large spatial scales (Fig. 9.4 and Appendix Fig. A9.5). What is more novel is our use of the spatial autocorrelation function to demonstrate that predation by knots substantially homogenized the spatial distribution of cockles (Fig. 8.3).

The spatial autocorrelation function can also be used to predict (map) the spatial distribution of prey. These maps can, for instance, be used to understand the distribution of predators (Chapter 9). For the predators, spatial autocorrelation might convey informa-

tion to find their prey more efficiently (Nolet and Mooij 2002, Klaassen et al. 2006a, van Gils 2010). For instance, if knots are unsuccessful in finding prey, large spatial autocorrelation implies that they also won't be more successful nearby; they better move elsewhere. To maximise the probability of finding prey, they should move at least a distance equal to the spatial range of the autocorrelation function (Klaassen et al. 2006a), i.e. the distance at which the autocorrelation reaches zero (Fig. 8.3 and Appendix Fig. A9.5). Moreover, positive spatial autocorrelation in prey abundance (i.e. patchiness) allows knots to benefit from the sampling behaviour of others, for instance, through local enhancement (Chapter 6, Pöysä 1992, Danchin et al. 2008, Beauchamp 2014).

SOCIALITY

Information benefits of social foraging

Animals live in uncertain and variable environments in which information on resources can increase foraging success and efficiency (Stephens and Krebs 1986, Dall et al. 2005, Stephens et al. 2007, Danchin et al. 2008). Especially for foragers that have a limited time window to gather their food, such as tidal foragers, information on prey distributions can be important for survival. Foragers could gather such information by trial and error (e.g., by sampling the environment) or by monitoring the behaviour of others, i.e. by using public information (Valone 1989, Valone and Templeton 2002, Danchin et al. 2004, Valone 2007, Danchin et al. 2008). Public information covers all information that is not private and thus accessible to others (Chapter 6, Wagner and Danchin 2010). Animals from a wide range of species are reported to use public information and the literature on public information use is still growing (see Valone 2007, Blanchet et al. 2010, Rieucau and Giraldeau 2011).

Public information use

Mudflats appear, at first glance, uniform and featureless. To estimate local densities of their buried prey, knots need to probe and sample the mudflat. Due to spatial heterogeneity in elevation of food patches and variation in the timing and level of low water, the availability of food patches is variable (e.g., van Gils et al. 2005b, Piersma 2012). Hence, socially foraging knots are likely candidates for using public information to increase foraging success. Knot distributions in the field were found consistent with the assumption of 'ideal free distribution' models that foragers have complete information on the possible intake rates at different locations (van Gils et al. 2006b). The question remained whether knots can acquire such information socially.

In Chapter 6 we show that knots can indeed monitor the foraging success of their flock mates, and that they choose their foraging locations accordingly. By incorporating pubic information a knot's intake rate increased proportionally with group size.

Socially foraging individuals can search for food themselves (so-called producers) or search for the food discovered by others (so-called scroungers) (Barnard and Sibly 1981, Barnard 2004, Beauchamp 2014). In Chapter 6 we also show that the use of producer or

scrounger tactics differs consistently between individuals: some knots searched for prey, while others exploited these efforts. Similar findings were reported for barnacle geese *Branta leucopsis*. Barnacle geese differed in their use of public information, which was negatively correlated with their boldness, i.e. their readiness to explore novel objects (Kurvers et al. 2010a, Kurvers et al. 2010b). Until recently, the use of public information in relation to personality has received little attention (Kurvers et al. 2010b). In fact, at the time of the public information experiments we were unaware that knots consistently differed in their exploratory behaviour (Chapter 7). We believe that future investigations on links between exploratory behaviour and information use will clarify spatial foraging distributions of knots and of social foragers in general.

Public information on communal roosts

Communally roosting birds are spectacular to watch, especially their seemingly coordinated flights and sudden drops towards the ground. Communal roosting has also stimulated spectacular scientific debates (e.g., Mock et al. 1988, Richner and Heeb 1995). Particularly on the idea that information benefits provide the primary evolutionary origin and maintenance of communal roosting (Ward and Zahavi 1973). Four decades after publication, the Information Centre Hypothesis remains controversial.

In Chapter 5 we show that there is empirical support for communal roosts as information centres. Whether this is the primary evolutionary cause driving communal roosting is a question that is hard to answer. Because many species roost communally, we think it is particularly interesting to focus on the information benefits that individuals could gain from roosting communally. The original information centre hypothesis states that information transfer must be active. We suggest that inadvertent public information is widely available at communal roosts and this is a more likely source of information. The information conveyed inadvertently is acquired at lower costs compared to trial-and-error sampling, and might even be unavailable when roosting solitary.

The difficulty of unequivocally testing hypotheses on information use at communal roosts probably reflects their controversy. Especially in the field, it is difficult to identify whether individuals have used information from each other on a roost. However, the ongoing developments of small tracking devices that are capable of collecting high resolution spatial and temporal data (Chapter 3, Bouten et al. 2013, Klaassen and Reneerkens 2014) could provide a means to study information use at communal roosts.

Cultural evolution

Natural selection acts through the interaction of an organism with its environment (West-Eberhard 2003, Duckworth 2009, Piersma and van Gils 2011, Odling-Smee et al. 2013). Through so-called 'niche construction' (Odling-Smee et al. 2013), individuals can to some extent control the environment that they encounter, which feeds back on their fitness (Laland et al. 2013, Laland 2014). By roosting communally, knots create their own environment in which different types of public information are available. In a group, the sum of information as well as traditions can be defined as culture (Danchin et al. 2004). I like to

propose that through public information use, communal roosting may allow cultural evolution (Laland et al. 2000).

Slowly the similarities between cultural and genetic transmissions are becoming recognised (Mesoudi et al. 2004, Jablonka et al. 2005). Culture consists of non-genetic, heritable differences among populations and requires overlapping generations that allow transmission of phenotypic traits (Danchin et al. 2004). The main difference between cultural and genetic selection is that cultural traits have the property to be passed on between unrelated group members.

Within communal roosts many types of information are available (Chapter 5). The spread of this public information might lead to a roost culture and perhaps eventually to cultural evolution. For instance, through public information use, free-living great tits (*Parus major*) acquired novel foraging techniques that rapidly spread through the whole population (Aplin et al. 2014). A study on communally breeding northern gannets (*Morus bassanus*) revealed that competition in combination with public information on foraging locations probably caused segregation in foraging area use between nearby colonies (Wakefield et al. 2013). Likewise, public information on communal roosts could drive spatial segregation on foraging areas and consequently drive cultural evolution. Note that the socially acquired behaviour is not necessarily the most optimal or adaptive behaviour, i.e. informational cascades (Giraldeau et al. 2002). An 'informational cascade' occurs when an individual's decisions are predominantly based on the behaviour of others instead of its own. Therefore, through informational cascades, cultural evolution might not always select for beneficial traits.

Interference and spatial distribution modelling

When resources are distributed in patches, as they frequently are (Levin 1992), behavioural ecologists often use ideal free distribution models to predict foraging distributions across these patches (Goss-Custard 1980, Sutherland 1983, Ens and Goss-Custard 1984, Holmgren 1995, Moody and Houston 1995, Tregenza 1995, Stillman et al. 1996, van Gils and Piersma 2004, Smallegange and van der Meer 2009, van der Meer and Smallegange 2009, Quaintenne et al. 2011). In order to get realistic predictions on spatial distributions, the choice of the interference model should have a strong biological underpinning. Especially because subtle differences in the selected interference mechanisms result in qualitatively different predictions of the spatial distribution of foragers (van der Meer and Ens 1997). Understanding the mechanisms of interference competition is therefore of paramount importance (Skalski and Gilliam 2001, Vahl et al. 2005b, Smallegange 2007, Folmer 2012).

In Chapter 4 we show that the intake rates of knots decline with group size, but that the common mechanisms of interference competition also declined or were virtually absent. We found that the main mechanism of interference was due to avoiding encounters with conspecifics, so-called 'cryptic interference'. Note that cryptic interference is more than a state of avoidance behaviour that reduces the available searching time (Stillman et al. 1997, Smallegange and van der Meer 2009). With increasing group size, knots increasingly

divert their attention between searching for prey and avoiding interactions with conspecifics, which additionally reduces their searching efficiency (Goss-Custard 1976, Cresswell 1997, Dukas and Kamil 2001, van Gils et al. 2015).

Interference models that are based on behaviour (so-called mechanistic interference models) are preferred from a scientific point of view (van der Meer and Ens 1997). However, if they don't incorporate the key interference behaviour, the resulting aggregative response will be flawed. Perhaps phenomenological interference models (that are based on a statistical fit between intake rate or searching efficiency, and competitor density) are not so bad after all *because* they fit the data and don't assume and possibly miss underlying behaviours (Sutherland 1983). Even though there has been substantial progress since Fretwell and Lucas (1970) proposed the 'ideal free distribution' as a null model, there is no grand unified theory to predict forager distributions based on the distribution of food and basic foraging behaviour. Ecology is a much less deterministic science than chemistry or physics. The interactions between an individual and its environment are determined by a wealth of different state dependent behaviours. Perhaps, therefore, a 'grand unified theory' is not possible (Tregenza 1995). Moreover, mechanistic 'ideal free distribution' models assume that all individuals are 'aimless billiard balls' and equal which is obviously not true. They thus are best seen as helpful null-models to come to grips with distributional problems (e.g., Bautista et al. 1995, van Gils et al. 2006b, Leyrer et al. 2012).

INDIVIDUALITY

All individuals are equal but some are more equal than others
Within species, individuals differ in their morphology and behaviour, which can both affect foraging decisions and spatial distributions (Parker and Sutherland 1986, le V. dit Durell 2000). For instance, morphology (e.g., bill length) affects the costs and benefits that are associated with a particular behaviour, which will affect where individuals will forage (Mathot et al. 2007, Catry et al. 2012, Duijns et al. 2014). How behaviour affects the spatial distribution of foragers has also been investigated, but only for the limited number of behaviours that were thought to directly affect fitness, e.g. dominance (Réale et al. 2007). A well-known example is the phenotype-limited distribution introduced by Parker and Sutherland (1986). They altered the assumption of 'ideal free distribution' models that all individuals should be equal and allowed individuals to vary in their susceptibility to interference. The prediction is that intake rates can differ between patches and that competitively dominant individuals should be found on the highest quality territories. Such phenotype-dependent spatial distributions can have important consequences for population dynamics (le V. dit Durell 2000, Bolker et al. 2003). In addition to dominance, animals differ in many more behaviours that could affect their spatial distribution.

Animal personalities
The study of animal personalities (i.e. consistent among-individual differences in behaviour) has become popular among ecologists and evolutionary biologists. Probably because

personalities are commonly found among many different species across the animal kingdom (Verbeek et al. 1994, Gosling and John 1999, Gosling 2001, Sih et al. 2004b, Réale et al. 2007, Bell et al. 2009). The ecological implications of personality can be substantial (Wolf and Weissing 2012). For instance, animal personality can affect species interactions and population dynamics (Bolnick et al. 2003), and habitat use (Werner et al. 1981, Boon et al. 2008, Minderman et al. 2010). Populations composed of a diversity of personality types should also be less vulnerable to (human induced) environmental changes (Bolnick et al. 2011, Sih et al. 2012, Wolf and Weissing 2012). The presence of animal personality signifies that behavioural flexibility is limited and that, when the context changes, individuals may not always behave optimally (Sih et al. 2004a, Sih et al. 2004b). Because natural selection favours optimal behaviour, a major puzzle in evolutionary and behavioural ecology is how and why animal personalities persist over evolutionary time.

In recent years, there has been substantial progress to explain animal personalities from proximate as well as ultimate points of view (e.g., Koolhaas et al. 1999, Dall et al. 2004, Koolhaas et al. 2007, Wolf et al. 2007, Biro and Stamps 2008, Careau et al. 2008, McNamara et al. 2009, Bergmüller and Taborsky 2010, Dingemanse and Wolf 2010, Réale et al. 2010b, Wolf and Weissing 2010, Wolf and McNamara 2012, Carere and Maestripieri 2013). As discussed in Chapter 7, most of the adaptive (ultimate) explanations of behavioural consistency involve between-individual variations in state. State is defined as any feature of an individual that affects the cost and benefits of its behaviour (Houston and McNamara 1999). State variables that underlie consistent among-individual differences in behaviour may be fixed (e.g., structural body size in adults), but they may also be flexible (e.g., body mass). Provided that among-individual differences in state are maintained via positive feedback between an individual's state and their state-dependent behaviour (e.g., Dingemanse and Wolf 2010, Wolf and Weissing 2010, Sih et al. 2015). Positive feedback mechanisms combine proximate (e.g., neurophysiology, hormone concentrations, maternal effects, social interactions) with ultimate explanations (fitness consequences) to understand the maintenance of animal personality (Sih et al. 2015).

Because the densities of high quality prey are low, competition for high quality prey could force individual knots to feed on particular resource qualities (Chapter 9, Van Valen 1965, Bolnick et al. 2003, Araújo et al. 2011). Positive feedback between an individual's resource specialisation, experience, and physiology could then account for consistency in their behaviour (Bergmüller and Taborsky 2010, Dall et al. 2012). For instance, an individual that feeds on high quality prey learns about their scattered distribution, and adapts its gizzard mass to increase processing efficiency. Both factors make it easier for this animal to continue to forage on high quality prey (e.g., Marchetti and Price 1989). Such positive feedbacks would then reinforce an individual's resource specialisation and exploratory behaviour.

An animal's personality develops during ontogeny by continuous interactions between the environment (e.g., climate, competition, predation pressure, resource availability, and resource quality), genes, and prior phenotypic expression itself (Koolhaas et al. 1999, Turner 2009, Stamps and Groothuis 2010a, Groothuis and Trillmich 2011). Individuals

have the capacity to develop in a variety of different ways that can have a profound influence on how they respond to conditions later in life (e.g., Bateson 2005). Under variable but predictable conditions, an animal's phenotype can thus be well adapted to the local environment.

During ontogeny initial differences in state interact with the environment. These interactions can have cascading effects on other parts of an animal's phenotype and drive consistent adaptive behaviour (West-Eberhard 2003, Stamps and Groothuis 2010a, Stamps and Groothuis 2010b, Groothuis and Trillmich 2011). Natural selection and phenotypic plasticity can thus reduce costs associated with an individual's behaviour enforcing correlations between behaviour, physiology and morphology (Chapter 7, Dingemanse et al. 2007, Sih et al. 2010, Carere and Maestripieri 2013). For instance, exposure to predation generated a correlation between aggression and exploration in sticklebacks *Gasterosteus aculeatus* (Bell and Sih 2007). We found that exploratory knots were smaller and had larger flight capabilities than non-exploratory knots (Box 10.1), which could reduce an individual's costs associated with an exploratory lifestyle (e.g., metabolic costs of flight, exposure to predation, see Chapter 7).

From an adaptive (ultimate) perspective the ontogeny of animal personality has so far received little attention (but see Stamps and Groothuis 2010a, Stamps and Groothuis 2010b). Perhaps, this is because of the complexity in disentangling the continuous interactions and feedbacks between developing phenotypic traits and environments. Nonetheless, to aid our understanding of the ecology and evolution of animal personalities, we need to study the interactions between the environment and phenotypic traits during ontogeny together with their fitness consequences (Groothuis and Trillmich 2011, T. Piersma pers. comm.).

RETYING THE EXPLORATORY KNOT

In the past decades, our research group has gathered a wealth of information on the evolutionary ecology of knots and the interaction with their environment (e.g., Piersma 1994, Zwarts 1997, van Gils 2004, Vahl 2006, Reneerkens 2007, Buehler 2008, Kraan 2010, van den Hout 2010, Leyrer 2011, Piersma and van Gils 2011, Folmer 2012, van der Geest 2013). This provides us with a unique opportunity to use the knot as a model species and synthesize an empirically-based evolutionary-ecological conceptual framework for the development and maintenance of personality variation. Though this conceptual framework is speculative, it may aid future studies on knot personalities and perhaps provide some interesting thoughts for animal personality research in general.

Integrating knot personality development with adaptive evolutionary ecology

During ontogeny, the interaction between an individual's genes and the environment result in an adaptive phenotype (Monaghan 2008). Animals have different ways of responding to environmental variation. Based on the speed of this response, we have characterized three adaptive trait categories (Fig. 10.1): 'behavioural', 'physiomorphic', and
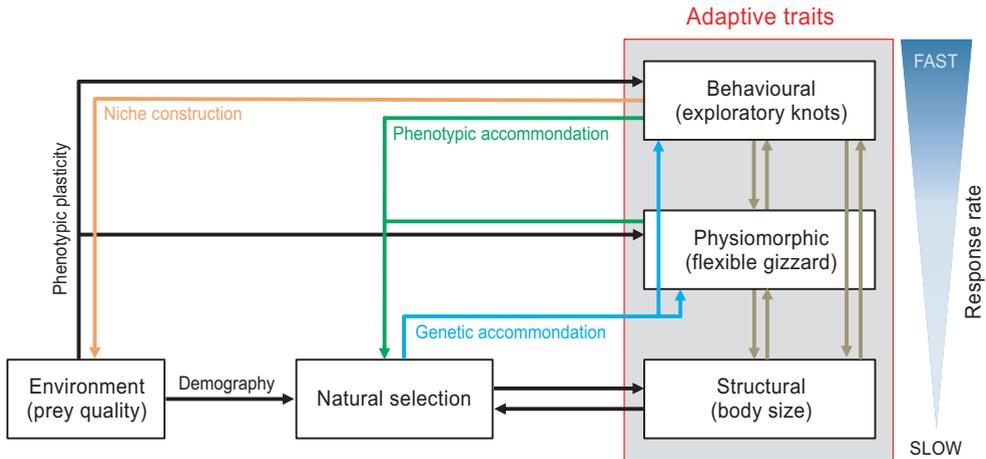
Figure 10.1 Evolutionary-ecological framework of personality development between knots. The grey area highlights the combinations of '*adaptive traits*' that depict a knot's phenotype. Note that with the term '*physiomorphic*' we indicate physiological traits, as well as flexible morphological traits such as gizzard mass, body mass, etc.. Through '*phenotypic plasticity*', variability in the environment will induce an adaptive phenotypic response that can be immediate ('*behavioural*'), or requires time ('*physiomorphic*'). The slowest adaptive response to environmental change is via structural traits such as body size ('*structural*'). For a structural phenotypic response, the environment is a direct agent of natural selection through mortality and reproduction, i.e. '*demography*'. An individual's adaptive phenotypic response can also feed back to the environment, i.e. '*niche construction*' or niche picking. An explorative knot, for instance, explores large areas in search of high food quality thus creating its own prey quality environment. An individual's adaptive phenotypic response will affect whether an individual will survive in its environment ('*phenotypic accommodation*'). If this phenotypic variance is partly due to genetic variation among individuals, phenotypic accommodation can lead to '*genetic accommodation*'. This conceptual framework expands on the positive feedback that we introduced in Chapter 7 (Fig. 7.6). In this feedback loop, capable of maintaining personality variation, exploratory behaviour allows access to high-quality prey through niche construction. Therefore, exploratory birds will acquire small gizzards through phenotypic plasticity, which enforces exploratory behaviour through their digestive constraint, i.e. they require high quality prey to achieve a sufficiently high intake rate. This illustration was inspired by Fig. 1 in Lister (2014).

'structural'. The 'physiomorphic' category includes physiological traits (e.g., hormone levels, immunity, crushing power by gizzards, digestive enzymes), as well as flexible morphological traits (e.g., fat stores, muscle and gizzard sizes, Piersma and van Gils 2011). Through day-to-day decisions, behaviour allows the fastest response to the environment (Duckworth 2009). Physiomorphic traits have an intermediate response rate, e.g., the gizzard mass of knots take one to two weeks to adjust to a change in diet (Dekinga et al. 2001). The 'structural' category refers to traits that, compared to a behavioural response, are thought to be more fixed throughout an adult's life, such as body size. For a structural response, the environment acts as a direct agent of natural selection through demographic rates (reproduction and survival) (e.g., Kraan et al. 2009b, Kentie et al. 2013, Lok et al.

2015, Rakhimberdiev et al. 2015). Those individuals that survive will live to reproduce and their phenotypic traits will increase in (gene) frequency. The combinations of all three trait categories depict a knot's adaptive phenotype (the grey area in Fig. 10.1).

The negative correlation that we found between exploratory behaviour and gizzard mass (Fig. 7.1B) suggests a trade-off between an individual's behavioural and physiomorphic response (Fig. 10.2A). Moreover, both an individual's exploratory behaviour and gizzard mass were correlated with structural traits (i.e. body size, Box 10.1), which suggests that an individual's structural traits mediate behavioural and physiomorphic responses (Fig. 10.1). A proximate explanation for such trade-offs could be that large non-exploratory knots with large gizzards have reduced flight capacity (Box 10.1) and probably increased travelling costs that are associated with exploratory behaviour (Piersma et al. 2003). Likewise, small knots with small gizzards could experience increased risk of starvation due to the digestive constraint that is associated with small gizzards (van Gils et al. 2003a).

In Chapter 7 we show that exploratory behaviour does not correlate with survival probability, which suggests that combinations of exploratory behaviour, gizzard mass, and body size reflect alternative strategies with equal fitness, i.e. the combined phenotype is an adaptive response to the environment (Fig. 10.2B). Whether it is exploratory versus non-exploratory behaviour, a small gizzard versus a large gizzard, or small bodies versus large bodies, these contrasts may all reflect extreme phenotypes on a continuum of combinations between behavioural, physiomorphic, and structural responses to environmental conditions. The levels of an individual's behavioural, physiomorphic and structural response depend on the exact costs and benefits of the combined responses, which will change continuously in interactions with the environment (Bateson 2005). Small differences in any of the traits could ultimately lead to lasting personality variation (Sih et al. 2015).

Across generations, a species will evolve towards having combinations of behavioural, physiomorphic, and structural traits that are the most adapted to the past environment. On the shorter timescales within an individual's lifetime, phenotypic plasticity can drive combinations of these traits and allow knots, during their ontogeny, to maintain their adaptive response to their experienced environment (phenotypic accommodation, Fig. 10.1). Phenotypic accommodation (through physiomorphic as well as behavioural traits) may well precede changes in gene frequencies (Wcislo 1989, West-Eberhard 2003, Jablonka et al. 2005, Duckworth 2009, Piersma and van Gils 2011). If the degree or pattern of phenotypic accommodation is partially genetically coded and if there is variation among individuals, natural selection can enforce changes in frequencies of the relevant genes ('genetic accommodation', West-Eberhard 2003, West-Eberhard 2005).

Phenotypic plasticity itself may also be reflected in the genotype. Genetic variation for plasticity has been demonstrated, which suggests that adaptive phenotypic plasticity can evolve through natural selection (West-Eberhard 2003). In unpredictable environments, natural selection may favour phenotypic plasticity, including phenotypic flexibility (e.g., Moran 1992, Piersma and Drent 2003, Piersma and van Gils 2011). There may, however,
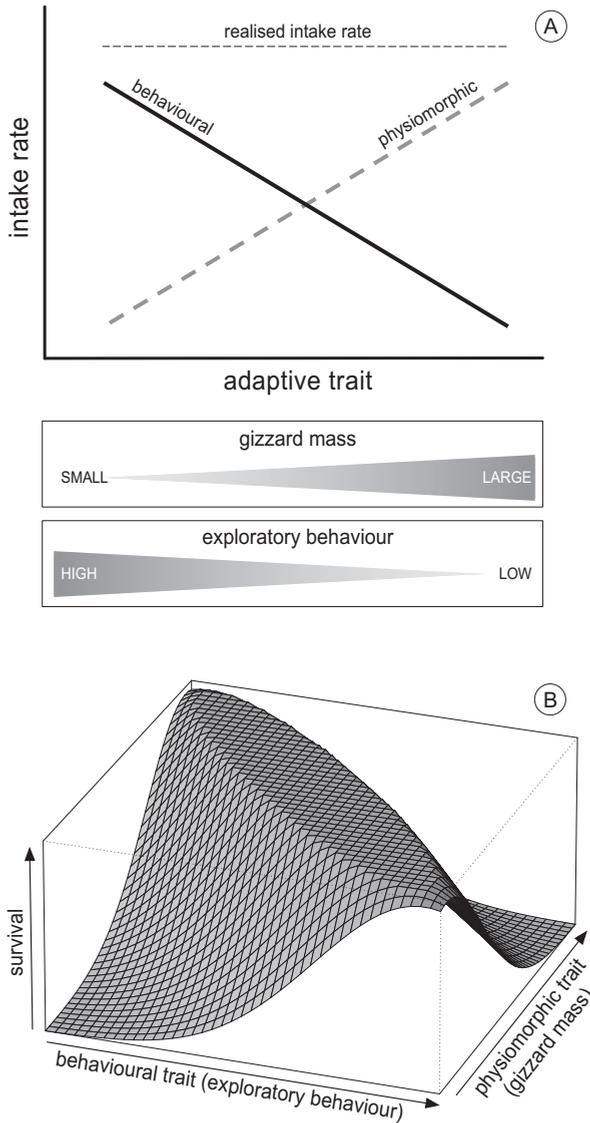
Figure 10.2 Trade-offs between adaptive traits. The negative correlation that we found between gizzard mass and exploratory behaviour (Fig. 7.1B) suggests a trade-off between an individual's physiomorphic and behavioural traits. In panel (A), we represent this trade-off. For the sake of argument, we assume that all knots aim for the same intake rate. In order to realise this intake rate, knots can permit different combinations of gizzard mass and exploratory behaviour. In panel (B), we schematically show how the trade-off between physiomorphic and behavioural traits result in equal survival (fitness) that is shown on the z-axis.
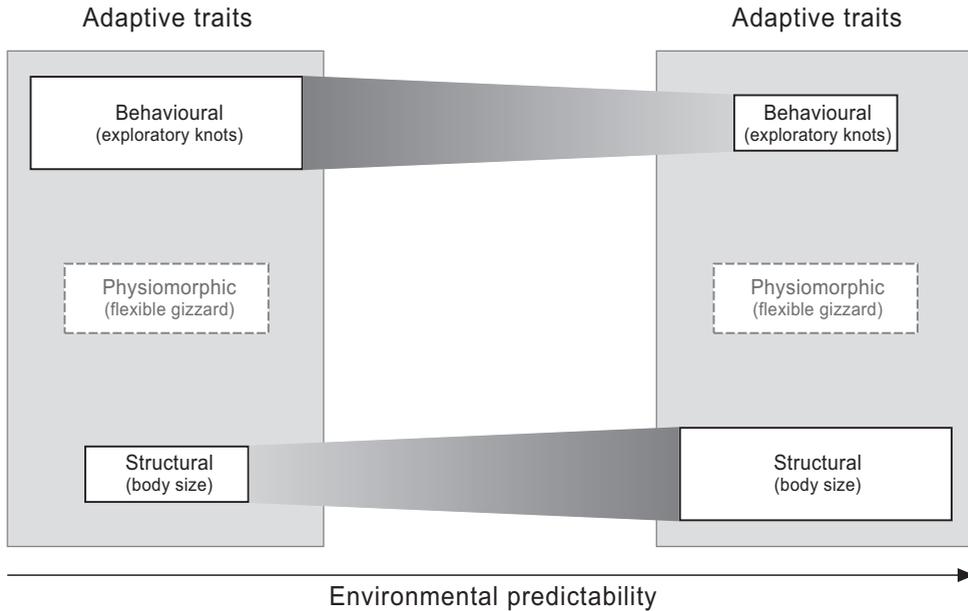
Figure 10.3 The hypothesized effect of enviromental predictability on the adaptive response of an individual. Here we built on Fig. 10.1 and added an axis of environmental predictability. Assuming that phenotypic plasticity has some cost, we examplify the extremes of an individual's adaptive response to the environment, i.e. a behavioural and structural response. The box-size of an individual's behavioural and structural traits reflect their relative weight in either an unpredictable (left) or predictable environment (right). Unpredictable environments will favour adjustments based on phenotypic flexibility rather than based on the natural selection of structural traits, and *vice versa*.

also be costs associated with phenotypic plasticity (Bateson 2001, Dall et al. 2004). Once a phenotype is 'fully' formed, during a change in local conditions it may be difficult and costly to switch to another, better adapted, phenotype (Bateson 2001). The predictability of the environment in combination with the costs of behavioural, physiomorphic, and structural plasticity will therefore determine whether such adaptive traits become genetically accomodated (Baldwin 1896, Crispo 2007). Assuming that plasticity has some cost, individuals living in predictable environments will adapt with structural traits that are more or less fixed during a lifetime. Likewise, individuals living in unpredictable environments will adapt with the more plastic physiomorphic and behavioural traits (Fig. 10.3).

THE ENDLESS KNOT

The work presented in this thesis provides us with a better understanding of the spatial distribution of knots. We have established that knots use public information to find their hidden prey, which increases their foraging success. Even though knots rarely fight and are seemingly peaceful birds, we found that knots do engage in serious forms of interference. Interference that is not clearly expressed and thus 'cryptic'. Currently, models to predict the spatial distributions of foragers do not incorporate such interference mechanisms.

In the field, we have shown that knot predation can have substantial influence on cockle densities, and that, by selecting high quality cockles, knots exert strong selection pressures on cockles to defend themselves and have thick shells. In fact, these selection pressures are amongst the highest reported in the literature. By measuring individual prey as well as predator characteristics, we found that knots maximise their energy intake rates at intermediate prey densities. This makes prey density alone a poor predictor of intake rates, a statement that counters most of what you would read in the pertinent literature. It is an important finding as it affects how we model spatial distributions and carrying capacity. Another noteworthy finding was that knots have personalities too, i.e. they consistently differ in their exploratory behaviour. Even though a knot's gizzard is flexible, it is behaviourally constrained due to consistent prey ingestion. Knots with different exploratory behaviour and gizzard masses have equal survival. These traits thus reflect different foraging strategies that result in equal fitness.

As usual each answer leads to new questions. We found that knots consistently differed in their social foraging tactics. Some knots consistently exploited the searching efforts of others. Public information use in relation to personality differences has, so far, received little attention in the literature. A promising next step could be to investigate whether non-explorative birds rely on the searching effort of exploratory birds. In the field, it is difficult to identify whether individuals use public information while foraging or roosting. Hopefully, further technological advances could provide a means to study information use in the wild. Studies on the ecological implications of animal personality in the wild are currently rare. Especially, studies that combine ecological feedbacks with the ontogeny of animal personalities are lacking. They are, nonetheless, necessary to gain a thorough understanding on the evolutionary origin and maintenance of personality variation. Rather than to only focus on the evolution of personality, we need to understand the proximate ecological mechanisms as well. Perhaps the framework we proposed that centres on the whole organism (Fig. 10.1) can aid future research. Disentangling the continuous interactions and feedbacks between phenotypic traits and the environment is, however, no easy task, as it requires the disentangling of an endless knot.

Box 10.1 Exploratory birds are smaller and have larger flight capacity than non-exploratory birds

In Chapter 7 we found that exploratory birds have smaller body masses than non-exploratory birds. This was partly due to the fact that they had smaller energy stores, but also because they were structurally smaller: exploratory behaviour was negatively correlated with the first principal component of body-size traits (intercept = −0.64, 95% CI [−1. 26; −0.02], slope = −1.08, 95% CI [−1.61; −0.72], r = −0.42, P = 0.046, Fig. B10.1A). With ultrasound, we also measured the (transversal) height of an individual's pectoral muscle (Dietz et al. 1999). We did this one day after capture, which therefore reflected the birds' muscle mass while free-living. The mass of the pectoral muscle relates to an individual's flight capacity (Dietz et al. 2007). Following Dietz et al. (1999), we derived its weight (g) as −10.9 + 31.7 × transversal height (cm). We found that pectoral muscle mass was not correlated with exploratory behaviour (r = 0.23, P = 0.31). However, because total body mass was negatively correlated with exploratory behaviour, an individual's flight capability (i.e. the pectoral muscle as fraction of total body mass) was positively correlated with exploratory behaviour (intercept = −1.25, 95% CI [−1.34; −1.16], slope = 0.16, 95% CI [0.11; 0.24], r = 0.47, P = 0.03, Fig. B10.1B).

Figure B10.1 Standardised major axis regressions of an individual's exploratory behaviour with (A) body size, and (B) relative pectoral muscle mass. Exploratory behaviour is the logit of the fraction of time spent searching (see Chapter 7). Body size was estimated by extracting the first principal component of wing length (mm), tarsus length (mm) and total head (mm, i.e. the length between the back of the head and tip of the bill) (see Appendix of Chapter 7). Relative pectoral muscle mass was calculated as the fraction of an individual's body mass. Note that we analysed logit-transformed relative pectoral muscle masses.