ADAPTIVE INDIVIDUAL DIFFERENCES

The Evolution of Animal Personalities

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The Evolution of Animal Personalities

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Chapter 1

General introduction

Individual differences in behaviour are a ubiquitous phenomenon within animal populations. Great tits (*Parus major*), for example, differ in the speed with which they explore a novel object (Verbeek *et al.*, 1994), three-spined sticklebacks (*Gasterosteus aculeatus*) differ in their aggressiveness towards territorial intruders (Huntingford, 1976), and mice (*Mus musculus*) and rats (*Rattus norvegicus*) differ in how quickly they solve a maze problem (Benus *et al.*, 1987). Quantitative behavioural differences such as these play an important role in this thesis, but in themselves are hardly surprising. After all, for most quantitative traits, phenotypic differences are to be expected, for example due to noise in the development of the phenotype or stochastic state differences among individuals (e.g., in energy reserves). At first sight, these differences do not seem to call for a deeper explanation.

Two basic observations suggest, however, that there may be more to behavioural variation than meets the eye (Sih *et al.*, 2004b). First, behavioural differences are often stable for some period of time. A great tit that explores a novel object faster than a conspecific will tend to be faster also several weeks later (Verbeek *et al.*, 1994). Similarly, the rank order in the level of aggression that individuals show towards territorial intruders tends to remain stable throughout the breeding cycle in sticklebacks (Huntingford, 1976).

Second, behavioural differences often extend to a range of different situations and contexts (sensu Sih *et al.*, 2004a) in a systematic way. The faster a great tit approaches a novel object, for example, the faster it explores a novel environment, the more aggressively it behaves towards conspecifics, the quicker it forms rigid foraging habits and the more willing it is to take risks (Groothuis & Carere, 2005). Similarly, the more aggressively a stickleback behaves towards a conspecific territorial intruder during the breeding cycle, the more aggressive it is also towards a heterospecific intruder and the bolder it is when approaching a predator at non-breeding times (Huntingford, 1976).

Such findings are surprising. If behavioural differences were solely due to random factors such as noise in the development of the phenotype, such differences should be uncorrelated, both through ontogeny and across different situations and contexts. The above findings, however, indicate that behavioural differences are often much more structured. Behavioural differences that are maintained through time and across contexts are termed personalities in humans (Pervin & John, 1999) and, in analogy to this, the term animal personalities (also: coping styles, Koolhaas *et al.*, 1999; temperament, Reale *et al.*, 2007; behavioural syndromes, Sih & Bell, 2008) has been adopted in the literature (Gosling, 2001). Throughout this thesis I will follow this usage, using the term animal personalities to refer to behavioural differences that are (i) stable through part of the ontogeny of individuals and (ii) correlated across a range of situations and contexts.

MOTIVATION

My thesis is concerned with the study of animal personalities. This is a fascinating and important topic, in particular because it can be seen as the continuation of a rich research tradition that aims to develop an integrated and holistic view of the behavioural phenotypes of animals (Tinbergen, 1963; Gould & Lewontin, 1979; West-Eberhard, 2003; McNamara & Houston, in press). I provide two examples.

Behavioural phenotypes as integrated and coadapted entities. In order to understand the behavioural phenotype of an animal, this phenotype is often decomposed into smaller components which are each investigated in isolation. In particular, this process often isolates the behaviour shown in a particular context (e.g., territory defence, foraging, mating or predator avoidance) or ontogenetic stage from that shown in other contexts and stages. The existence of personalities suggests that a more holistic approach is needed. To put it simply, if the behaviour of an individual in context A depends on what it did in context B, any approach that tries to understand the behaviour in context A while neglecting context B can only provide incomplete explanations. Similarly, if the behaviour of an individual is affected by its behavioural history, ultimately this history has to be taken into account when explaining current behaviour.

Integration of function and mechanism. Ultimate explanations of behaviour often overlook the proximate mechanisms underlying behaviour. To understand the behavioural interdependencies characteristic of personalities, however, we have to investigate the factors underlying these interdependencies and how these factors are shaped by natural selection. Such factors are often found in the architecture of behaviour, that is in the proximate mechanisms underlying behaviour (e.g., genetic, physiological or cognitive systems). One important cause of behavioural associations across situations, contexts and time is that multiple traits are often share a common mechanism within this architecture. Such common mechanisms include pleiotropic genes (Mackay, 2004), hormones (Ketterson & Nolan, 1999), neurotransmitters (Bond, 2001), behavioural rules (Todd & Gigerenzer, 2000) and emotions (Rolls, 2000) that affect multiple traits at the same time.

HUMAN PERSONALITIES

Compared to the study of animal behaviour, human psychology has long history of personality research (Winter & Barenbaum, 1999). Others have discussed this huge literature extensively (Pervin & John, 1999); here I will limit myself to summarizing a few basic facts on human personalities.

Personality research is, almost by definition, concerned with those traits that show some stability through ontogeny, since the term personality refers to "those characteristics of individuals that describe and account for consistent patterns of feeling, thinking, and behaving" (Gosling, 2001). This is not to say, however, that personality characteristics are thought to be absolutely stable throughout ontogeny. In fact, human personality traits are known to differ in their stability and to undergo systematic changes with age, maturational events and social-contextual transitions (Caspi *et al.*, 2005; Roberts *et al.*, 2006).

What are the basic dimensions of human personality differences? The "currently most widely accepted and complete map of personality structure" (Gosling & John, 1999) is the so-called Five Factor Model of human personalities (Costa *et al.*, 2001). This descriptive model is based on the following approach. Subjects are asked to rate people they know according to a long list of adjectives describing personality characteristics (other studies are based on self-ratings). These ratings are then distilled into a smaller set of variables using a factor analysis. The consensus from a large number of studies that have followed this approach (Digman, 1990) appears to be that behavioural variation can be described along five independent axes: extraversion, agreeableness, conscientiousness, neuroticism and openness. Each of these axes subsumes a large number of traits that tend to be correlated with each other. Individuals that score high on the extraversion axis, for example, tend to be talkative, assertive, active, energetic, outgoing, outspoken, dominant, forceful, enthusiastic, sociable, adventurous, noisy and bossy (John & Srivastava, 1999).

A number of studies have shown that an individual's personality score predicts outcomes in his or her life, such as juvenile delinquency, performance in school and at work, psychopathology and longevity (Pervin & John, 1999). Twin studies have fairly consistently reported heritabilities in the range of 0.4 to 0.6 for each of the five axes (Bouchard & Loehlin, 2001).

ANIMAL PERSONALITIES

The study of personalities non-human animals has a short history. An early landmark was a set of studies by Nobel Laureate Ivan Pavlov, in which he identified three temperamental types in dogs (Pavlov, 1928, pp. 363-364):

> "Finally, we have been able to distinguish several definite types of nervous systems. To one of these types, then, I take the liberty to direct your attention. This type of dog is one which judging by his behaviour (especially under new circumstances) every one would call a timid and cowardly animal. He moves cautiously, with tail tucked in, and legs half bent. When

> we make a sudden movement or slightly raise the voice, the animal draws back his whole body and crouches on the floor. … As I gradually analysed the types of nervous systems of various dogs, it seemed to me that they all fitted in well with the classical description of temperaments, in particular with their extreme groups, the sanguine and the melancholic. … Between these extremes stand the variations of the balanced or equilibrated type, where both the process of excitation and the process of inhibition are of equal and adequate strength, and they interchange promptly and exactly."

Yet, despite several other seminal contributions (Yerkes, 1939; Hebb, 1946; Huntingford, 1976; Stevenson-Hinde & Zunz, 1978; Stevenson-Hinde *et al.*, 1980), research on animal personalities was almost non-existent for most of the 20th century.

Several explanations are offered for this in the literature. Clark and Ehlinger (1987, p. 2) attribute the neglect of individual differences to the focus of early ethologists on stereotyped, species-typical behaviours and the assumption of comparative psychologists (behaviourists) – in search of general laws of learning and cognition – that variation in their subjects' responses results from uncontrolled factors in the environment. Wilson (1998a, p. 199) emphasizes the historical trend in the use of natural selection to explain differences between organisms at increasingly finer scales, ranging from the explanation of differences between genera and higher-level taxa to differences between closely related species in the 1960s (which had been controversial in the 1940s) to explanations of differences among subpopulations in the 1980s. Several other authors point to a rigid refusal to 'anthropomorphize'(e.g., Hebb, 1946; Griffin, 1992; Bouchard & Loehlin, 2001; Gosling, 2008).

Times have changed and during the last decade animal personalities have been the subject of considerable scientific interest. A survey by (Gosling, 2001) counted personality studies in 64 species from a wide range of vertebrate and invertebrate taxa, including mammals, fish, birds, reptiles, amphibians, arthropods and molluscs. The research questions in these studies are diverse, addressing methodological issues (e.g., assessment of the reliability and validity of particular behavioural tests), the structure of personalities (e.g., what traits are correlated with each other? How stable are these correlations through ontogeny?) and the causes and consequences of personalities (e.g., what are the physiological correlates of personalities? How does experience affect personalities?). Reviews of this huge and growing literature are provided elsewhere (Clark & Ehlinger, 1987; Boissy, 1995; Gosling & John, 1999; Koolhaas *et al.*, 1999; Gosling, 2001; Sih *et al.*, 2004b; Dingemanse & Reale, 2005; Groothuis & Carere, 2005; Reale *et al.*, 2007; Biro & Stamps, 2008; Sih & Bell, 2008; Smith & Blumstein, 2008) and I limit myself here to a brief introduction of two common (i.e., to some extent universal) behavioural characteristics of animal personalities which will figure prominently in this thesis. I will then turn to the main topic of the thesis, the causes of animal personalities.

The boldness-aggression syndrome

The term 'boldness-aggression syndrome' refers to a positive correlation between individual differences in boldness (e.g., in the response to a predator, in exploring a novel environment) and levels of aggression towards conspecifics. To my knowledge, such differences were first described by Huntingford (1976) in three-spined sticklebacks. Huntingford found that: (i) within the breeding cycle, male sticklebacks differed significantly in their aggressiveness towards territorial intruders; (ii) the rank order of aggressiveness remained stable both when confronted with different types of intruders and throughout the breeding cycle; and (iii) individuals that were more aggressive towards territorial intruders during the breeding cycle tended to be bolder in response to a predator outside the breeding cycle.

Since Huntingford's (1976) stickleback study, the boldness-aggression syndrome has been described for a variety of other taxa (Sih *et al.*, 2004b), including birds (Groothuis & Carere, 2005) and rodents (Koolhaas *et al.*, 1999). At present, the boldness-aggression syndrome is one of the most reported findings in the animal personality literature (Dingemanse *et al.*, 2007; Sih & Bell, 2008; Smith & Blumstein, 2008). Having said this, it is far from universal. Even within a single species, the three-spined stickleback, population comparisons have shown that the boldness-aggression syndrome is present in populations that are under strong predation pressure, but not in their counterparts in safe environments (Bell, 2005; Dingemanse *et al.*, 2007; Bell & Sih, 2007b).

Responsiveness to environmental stimuli

Individual differences in responsiveness to environmental stimuli are a second behavioural characteristic of animal personalities that appears to have some universality. While some individuals appear to be very responsive to stimuli and readily adjust their behaviour to the prevailing conditions, others show more rigid, routine-like behaviour. Consistent differences in responsiveness (also termed coping style, reactivity, flexibility, plasticity) have been documented in several taxa including birds (Groothuis & Carere, 2005), rodents (Koolhaas *et al.*, 1999), pigs (Hessing *et al.*, 1994) and humans (Aron & Aron, 1997).

In both mice and rats (Benus *et al.*, 1987), for example, individuals differ substantially in their responsiveness to environmental changes in a maze task. Some individuals quickly form a routine, are not influenced by minor environmental changes and perform relatively badly when confronted with a changing maze configuration. Others do not form a routine, are strongly influenced by minor changes and perform relatively well when confronted with changing maze configurations. Similarly, some great tits readily adjust their foraging behaviour to a change in the feeding situation while others stick to formerly successful habits (Verbeek *et al.*, 1994).

EXPLAINING PERSONALITIES

This thesis is concerned with the causes of animal personalities. As will be discussed in detail in Chapter 2, any explanation of personalities has to account for at least three basic behavioural phenomena: behavioural differences among individuals, time-consistency of behaviour and behavioural correlations across situations and contexts. To give a concrete example, why do individual sticklebacks differ in their aggressiveness towards territorial intruders, why are such differences stable both throughout the breeding cycle and when confronted with different types of intruders and why are such differences associated with differences in the boldness shown to a predator (Huntingford, 1976)? As with any biological phenomenon, the question of causation can be answered on different levels (Tinbergen, 1963).

PROXIMATE EXPLANATIONS

Behavioural differences

At the proximate level, the behavioural phenotype of an individual is caused by its architecture of behaviour, that is the genetic, physiological, neurobiological and cognitive systems underlying its behaviour. Any differences among individuals in this architecture can give rise to behavioural differences. Such architectural differences between individuals are common, for example genetic differences (Van Oers *et al.*, 2005; Fidler *et al.*, 2007), differences in the stress-response system (Korte *et al.*, 2005; Ellis *et al.*, 2006) and differences in basal metabolic rates (Careau *et al.*, 2008). It should be noted that behavioural differences are expected even in the absence of architectural differences, since the expression of behaviour is subject to processes that give rise to stochastic variation around some target value.

A second well-known factor underlying behavioural differences among individuals are differences in experience (Gilbert, 2001; Oyama *et al.*, 2001; Stamps, 2003). The incubation temperature of a lizard's eggs, for example, can affect the antipredator behaviour of the later hatchling (Downes & Shine, 1999), experiences in enriched environments can affect mating behaviour (Dukas & Mooers, 2003) and the social environment experienced during development can affect various social behaviours (Rodd & Sokolowski, 1995; White *et al.*, 2002).

Consistency across time, situations and contexts

As indicated above, the architecture of behaviour can give rise to trait correlations across time, situations and contexts whenever several traits are affected by a common underlying mechanism within this architecture (Sih *et al.*, 2004b; Sih & Bell, 2008). Pleiotropic genes (Mackay, 2004), hormones (Ketterson & Nolan, 1999), neurotransmitters (Bond, 2001), behavioural rules (Todd & Gigerenzer, 2000) and emotions (Rolls, 2000) affecting multiple traits at the same time are examples of such mechanisms.

It has been shown, for example, that the positive correlation between aggressiveness at different points during ontogeny in the three-spined stickleback is caused in part by pleiotropic genes (Bakker, 1986). Pleiotropic genes are also thought to be responsible (Riechert & Hedrick, 1993; Maupin & Riechert, 2001) for the positive correlation between agonistic behaviour, antipredator behaviour and superfluous killing in the American desert spider (*Agelenopsis aperta*). The negative correlation between mating effort and parental effort in several bird species is mediated by the hormone testosterone (McGlothlin *et al.*, 2007). To give a final example, the fearfulness of an individual affects its reaction to a multitude of potentially threatening situations, including persistent dangers in its ecology, novelty and interactions with conspecifics (Boissy, 1995).

Differences in experience among individuals can give rise to long-lasting behavioural differences in suites of correlated behavioural traits (Stamps, 2003; Sih *et al.*, 2004b). Differences in maternal care, for example, give rise to stable individual differences in the stress reactivity, fearfulness and maternal behaviour of female offspring in rats (Meaney, 2001). Similarly, differences in maternal-deprivation experience during infancy give rise to consistent differences in stress reactivity, exploration behaviour and fearfulness in rhesus monkeys (Suomi, 1997).

ULTIMATE EXPLANATIONS

Proximate explanations provide only a partial understanding of animal personalities. Behavioural differences among individuals may be caused by architectural differences, but why did the evolutionary process give rise to such differences and how are these differences maintained in the population over evolutionary time? Likewise, behavioural correlations across time, situations and contexts may by caused by common mechanisms within the architecture of behaviour, but why did evolution lead to such an inflexible architecture in the first place?

The present thesis is concerned with ultimate, adaptive explanations of animal personalities. The guiding question throughout can be formulated as follows: Can behavioural differences among individuals that are consistent across time, situations and contexts be understood in terms of adaptive evolution? There have been some attempts to answer this question in the literature (e.g., Clark & Ehlinger, 1987; Buss, 1991; Wilson *et al.*, 1994a; MacDonald, 1995; Wilson, 1998b; Bouchard & Loehlin, 2001; Rands *et al.*, 2003; Dall *et al.*, 2004; Dingemanse *et al.*, 2004; McElreath & Strimling, 2006; Nettle, 2006; Stamps, 2007; Wolf *et al.*, 2007a; Biro & Stamps, 2008; McNamara *et al.*, 2008; Pruitt *et al.*, 2008; Wolf *et al.*, 2008b; McNamara *et al.*, 2009a), but the evolution and the potential adaptive value of personalities is still a poorly understood phenomenon.

Chapter 2 of this thesis will present an in-depth discussion of the factors and mechanisms that can contribute to an adaptive explanation of animal personalities. I limit myself here to a brief sketch of the main factors involved in such explanations.

Behavioural differences

Adaptive explanations of behavioural differences underlying personalities can resort to a large body of well-developed theory addressing the evolutionary emergence and persistence of variation (detailed references to this literature are provided in Chapter 2). There are three basic factors underlying adaptive variation: frequency-dependent selection, spatiotemporal variation in the environment and state differences among individuals.

Time-consistency of behaviour

The adaptive value of time-consistent behaviour has been discussed to some extent in the literature (e.g., Clark & Ehlinger, 1987; Wilson *et al.*, 1994a; Wilson, 1998b; Rands *et al.*, 2003; Dall *et al.*, 2004; McElreath & Strimling, 2006; Stamps, 2007; Wolf *et al.*, 2007a; Biro & Stamps, 2008; McNamara *et al.*, 2008; Wolf *et al.*, 2008b; McNamara *et al.*, 2009a), but a coherent framework of adaptive behavioural consistency is still lacking. A promising family of explanations is based on state differences (McNamara & Houston, 1996; Houston & McNamara, 1999) among individuals (e.g., differences in physiology and experience). Since the costs and benefits of behavioural actions are affected by an individual's state, stable state differences may account for consistent differences in behaviour. But why should state differences be stable over time? One prominent line of explanation is based on feedbacks (Sih *et al.*, 2004b; Sih & Bell, 2008): state differences give rise to behavioural differences among individuals that act to reinforce initial state differences. Such reinforcement might, for example, act through learning or training (Rosenzweig & Bennett, 1996), or through behaviour-induced changes in an individual's condition (Rands *et al.*, 2003; Stamps, 2007).

Correlations across situations and contexts

As with time-consistent behaviour, until recently the adaptive value of behavioural correlations had received little attention in the literature (but see, e.g., Clark & Ehlinger, 1987; Wilson *et al.*, 1994a; MacDonald, 1995; Wilson, 1998b; Dall *et al.*, 2004; McElreath & Strimling, 2006; Stamps, 2007; Wolf *et al.*, 2007a; Biro & Stamps, 2008; McNamara *et al.*, 2008; Pruitt *et al.*, 2008; Wolf *et al.*, 2008b). There are three families of explanations for adaptive behavioural correlations. First, behavioural correlations could reflect an architecture of behaviour in which limited plasticity is adaptive. Second, state differences among individuals could give rise to adaptive behavioural correlations, since states often affect the costs and benefits of multiple behaviours at the same time. Third, adaptive behavioural correlations could arise in a population whenever individuals follow an adaptive behavioural rule (or convention) that favours the association of these traits.

THIS THESIS

The main part of this thesis begins with the conceptual **Chapter 2** in which we review the main mechanisms that can contribute to an adaptive explanation of personalities. In particular we discuss how natural selection can give rise to the three key behavioural aspects of personalities: behavioural differences among individuals, consistency of behaviour over time and behavioural correlations across situations and contexts.

The remainder of the thesis presents a series of conceptual evolutionary models. Methodologically, these models are based on analytical methods from evolutionary game theory (Weibull, 1995) and adaptive dynamics (Geritz *et al.*, 1998) in combination with individual-based computer simulations. The models presented are conceptual in nature; their purpose is not to give a complete and realistic description of natural situations but rather to investigate isolated features of those situations that may be important in shaping adaptive animal personalities.

I aim to address behavioural aspects of animal personalities that appear to have some universality, in that they occur in a range of animal species. As discussed above, at present there seem to be at least two candidates that meet this condition; these two candidates form the focus of the remainder of this thesis.

Chapters 3 and 4 deal largely with the boldness-aggression syndrome and **Chapters 5 and 6** with individual differences in responsiveness.

Chapter 3 is based on the observation that traits such as boldness and aggressiveness are risky traits in the sense that bold and aggressive individuals put their life at stake in order to gain benefits. Why should some individuals be consistently more risk-prone than others, both across contexts and over time, as described by the boldness-aggression syndrome? We develop an evolutionary model that shows how a basic principle from life-history theory – the principle of asset protection – can explain this observation.

Two short essays accompany this chapter in the subsequent I**ntermezzo**. The model developed in **Chapter 3** gives rise to a stable polymorphism. In the first essay we describe two qualitatively different routes through which this polymorphism can be attained in the course of evolution. The second essay provides a first discussion of feedback mechanisms involved in asset protection, examining how such feedbacks affect the emergence and stability of personalities.

In **Chapter 4** we take up this point and investigate the feedback mechanisms involved in asset protection more systematically. We investigate in detail how the feedbacks depend on various features of the behavioural choices, such as the timing of reproductive benefits and survival effects.

In **Chapter 5** we turn to individual differences in responsiveness. We develop a model to address two central questions. First, how can unresponsive strategies persist when more responsive and flexible behaviour should provide a selective advantage? Second, why should individuals differ consistently in their responsiveness rather than adjusting their responsiveness to the needs of the prevailing situation? In this chapter we also provide a novel explanation for behavioural syndromes by showing that individual differences at the level of behavioural organization (namely, the responsiveness to environmental stimuli) can induce correlative associations among all kinds of otherwise unrelated traits.

Chapter 6 focuses on the question of adaptive behavioural consistency. In social interactions, consistency can be favoured since it makes individuals predictable. This explanation hinges on the presence of responsive individuals that adjust their behaviour in response to the behavioural history of their social partners. However, responsiveness is only beneficial in the presence of consistent individual differences. We develop an evolutionary model that investigates this feedback between responsiveness and consistency.

The general discussion in **Chapter 7** provides a summary of the thesis and puts the main results into a broader context.

Chapter 2

The evolution of animal personalities

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ABSTRACT

In many animal species, individuals differ consistently in their behavioural tendencies, and the behaviour in one context is correlated with that in other contexts. From an adaptive perspective, the evolution of such personalities is still not well understood, because in many situations a more flexible structure of behaviour should provide a selective advantage. In this chapter we review several mechanisms that may contribute to an adaptive explanation of animal personalities. We focus on three basic questions. First, which factors favour the evolution of behavioural variation? Second, which factors favour the evolution of time-consistent behaviour? And third, which factors favour behavioural correlations across contexts?

Concerning the causes of variation we discuss the role of frequency-dependent selection and spatiotemporal variation in the environment. Variation can be the outcome of selection when each behavioural type has a fitness advantage when rare; when individuals facing an unpredictable environment play a bet-hedging strategy; or when different behavioural types complement each other in a synergistic way (e.g., division of labour).

Concerning the causes of correlations we address the role of architectural constraints, adaptation to the local habitat, and differences in state among individuals. We argue that behavioural correlations are unavoidable if individual behaviour is governed by a limited number of control variables (e.g., hormones) and then ask the question why the number of control variables is apparently quite small. Correlations are also to be expected when individuals differ in state and the optimal phenotype is state-dependent. Time-consistent behaviour will often result from positive feedbacks (e.g., due to learning) where state and behaviour reinforce each other.

INTRODUCTION

In many animal species, individuals of the same sex, age and size differ consistently in whole suites of correlated behavioural tendencies, comparable to human personalities (Clark & Ehlinger, 1987; Digman, 1990; Gosling, 2001; Sih *et al.*, 2004b). Examples abound. Birds often differ consistently in the way they explore their environment and these differences are associated with, for example, differences in boldness and aggressiveness (Groothuis & Carere, 2005). Rodents as mice and rats differ consistently in the way they deal with environmental challenges and such differences encompass, for example, differences in attack, avoidance and nest-building behaviour (Koolhaas *et al.*, 1999). Interestingly, personality differences are often associated with morphological (Ehlinger & Wilson, 1988), physiological (Korte *et al.*, 2005) and cognitive (Reddon & Hurd, 2009) differences among individuals. In this chapter we focus on the evolutionary causes of animal personalities (Wilson, 1998; Buss & Greiling, 1999; Dall *et al.*, 2004) What are the factors promoting the evolution of personalities? And how do these factors shape the structure (what type of traits are associated with each other?) and ontogenetic stability of personalities?

Understanding the evolution of animal personalities (henceforth personalities) requires a shift in our thinking about animal behaviour (Wilson, 1998). While behavioural ecologists have traditionally “atomized” the organism into single behavioural traits that are studied in isolation (Gould & Lewontin, 1979), the study of personalities requires a more holistic approach for at least two reasons. First, personalities refer to suites of correlated traits that are stable across (at least part of) the ontogeny of individuals (Sih *et al.*, 2004a; Sih *et al.*, 2004b). Consequently, interdependencies between multiple different traits (e.g., how does the boldness of an individual affect its aggressiveness and exploration behaviour) and the same trait expressed at different points during ontogeny (e.g., how does juvenile aggressiveness affect adult aggressiveness) have to be taken into account. Second, on a proximate level, trait correlations are often caused by genetic (Mackay, 2004), hormonal (Ketterson & Nolan, 1999) or cognitive mechanisms (Rolls, 2000) affecting multiple traits at the same time. In order to understand the evolution of such trait correlations we need an approach that integrates mechanisms and adaptation (Tinbergen, 1963; McNamara & Houston, in press).

What we need to understand: taking a closer look

Personalities refer to differences in suites of correlated behavioural traits that are stable across part of the ontogeny of individuals. In some cases, personality differences are associated with differences in the morphological (Ehlinger & Wilson, 1988), physiological (Koolhaas *et al.*, 1999), cognitive (Howard *et al.*, 1992) or environmental (Wilson, 1998) condition that individuals face, that is, with differences in state (McNamara & Houston, 1996). Some state differences are readily observable (e.g., differences in size, sex, position in dominance hierarchy), others are much less conspicuous (e.g., differences in nutrition, stress response system or level of experience with a particular behaviour).

The state of an individual affects the cost and benefits of its actions, and thus its optimal behaviour (McNamara & Houston, 1996; Houston & McNamara, 1999; Clark & Mangel, 2000). Consequently, individuals should adjust their behaviour to their current state, a phenomenon termed state-dependent behaviour (condition-dependent behaviour, phenotypic plasticity). Importantly for personalities, single states often affect the costs and benefits of multiple behavioural traits at the same time (McNamara & Houston, 1996). Differences in states thus provide a potentially powerful explanation for differences in suites of correlated behavioural traits.

Explaining personalities in terms of differences in state, however, requires us to provide answers to two basic questions. First, why do individuals differ in states in the first place? In many cases, the maintenance of such differences seems puzzling. Why, for example, should individuals differ in physiological characteristics as stress responsiveness (Aron & Aron, 1997; Koolhaas *et al.*, 1999) or basal metabolic rate (Careau *et al.*, 2008)? Second, why are such differences stable over time? Many states (e.g., energy reserves, experience with a particular behaviour, future fitness expectation) are affected by many different factors, including an individual's own behaviour. Such states are potentially highly variable over time. Why, then, should differences in states be stable over time and what are the mechanisms that give rise to such stability?

Differences in state thus provide a plausible explanation for personality differences (Dall *et al.*, 2004; Sih & Bell, 2008), but only a partial one. Personality differences can also be observed for individuals that do not seem to differ in state. In fact, many empirical studies that report personality differences aim to control for state differences among individuals.

The observation of personalities among individuals that do not differ in states is particularly puzzling. First, why should individuals differ in their response to the same decision problem (e.g., how to explore an environment) when facing identical costs and benefits associated with behavioural actions? Should we not rather expect that any given decision problem has a unique best behavioural solution which in turn outcompetes all others over evolutionary time? Second, why are the responses to different decision problems associated with each other in a correlative way (Clark & Ehlinger, 1987; Digman, 1990; Gosling, 2001; Sih *et al.*, 2004b)? Why should a bold individual, for example, be more aggressive than its shy conspecific and why should bold individuals tend to be bold throughout ontogeny? Such limited plasticity seems especially surprising since behaviour, in contrast to many morphological features, is often thought to be potentially highly plastic (but see DeWitt *et al.*, 1998). Shouldn't then a more flexible phenotype, that adjusts its behaviour to the current condition be advantageous (Wilson, 1998; Dall *et al.*, 2004)?

These are the type of questions we address in this chapter. To structure our thinking we will group our discussion under the two main themes of variation and correlation, reflecting two main aspects of personalities. We first focus on the causes of variation within populations. In particular, we discuss how random causes, frequency-dependent selection and spatiotemporal variation in the environment can give rise to variation in behaviour and states underlying behaviour. We then focus on the two types of behavioural correlations that are defining for personalities, correlations over time and across contexts. In particular, we will discuss the role of the architecture of behaviour, stable state differences and social conventions in causing stable behavioural correlations.

CAUSES OF VARIATION

Individuals can differ substantially in their behavioural response when confronted with the same decision problem (e.g., how to explore an environment, how to respond to a predator) and such behavioural variation is a key feature of personalities (Clark & Ehlinger, 1987; Digman, 1990; Gosling, 2001; Sih *et al.*, 2004b). Behavioural variation can take various forms. In some cases, variation is best depicted as a broad unimodal distribution (e.g., variation in many human personality traits, (Nettle, 2006)), in other situations, a small number of discrete variants coexist (e.g., variation in mating strategies, (Gross, 1996)). As discussed above, behavioural variation may or may not be associated with variation in states among individuals. Moreover, behavioural variation may or may not be associated with genetic variation (Wilson, 1994b; Bouchard & Loehlin, 2001).

In this section we focus on the on the ultimate causes of behavioural variation. As we have emphasized above, behavioural variation is often caused by variation in states and state-dependent behaviour and we briefly discuss the two main routes to state differences among individuals, evolved vs. random state differences. We then discuss two basic mechanisms that can give rise to adaptive variation in behaviour, frequency-dependent selection and spatiotemporal variation in the environment.

Differences in states

State differences among individuals are ubiquitous: pick any two individuals within a population and you typically find that these individuals differ in some aspects of their morphological, physiological, cognitive or environmental condition. Through their effect on the costs and benefits of behavioural actions such state differences are an important source of adaptive behavioural differences. In many situations aspects of the state of an individual are under the direct control of that individual. Individuals typically have, for example, the choice among different environmental conditions (e.g., habitats, social environments) or the choice how to fine-tune certain aspects of their physiological systems (e.g., stress responsive system, basal metabolic rate). Why should individuals that do initially not differ in states differ in such choices? At first sight, one would perhaps expect that there is one best choice for any choice among different states.

In what follows, we discuss two main routes that give rise to adaptive variation in states, frequency-dependent selection and spatiotemporal variation. State differences among individuals, however, need not always reflect adaptive evolution. In many situations, aspects of the state of an individual are affected by factors that are not under the control of the individual. Differences in states arise whenever these factors differ between individuals. One individual, for example, grows up in a rich environment while another grows up in a poor environment. One individual finds a high-quality food source and thus increases its nutritional condition while another one does not find such a food source. One individual gets infected by a parasite while another one does not. Examples of state differences caused by such random factors abound.

Frequency-dependent selection

In groups of foraging animals, individuals typically have the choice between two different behavioural roles (Giraldeau & Beauchamp, 1999), an individual can either search for food sources on its own (“producer”) or exploit food sources discovered by others (“scrounger”). Producer-scrounger situations (Barnard & Sibly, 1981) are a prototype example in which the benefits associated with a phenotype depend negatively on the frequency of that phenotype in the population: the higher the frequency of scroungers in a group, the less beneficial this role becomes, since more scroungers compete for fewer resources. Such situations give rise to so-called negative frequency-dependent selection (Maynard Smith, 1982), a form of selection that is known to be an important source of variation within populations (Heino *et al.*, 1998; Dugatkin & Reeve, 2000; Sinervo & Calsbeek, 2006).

In situations with negative frequency-dependence selection, selection acts to increase the frequency of rare phenotypes within populations. In its simplest form, as in the producer-scrounger example above (Barnard & Sibly, 1981), this rareness advantage gives rise to two phenotypes that coexist in stable frequencies within a population. Moreover, whenever individuals have the choice between more than two phenotypes, negative frequency dependence can give rise to situations in which any number of phenotypes can coexist in stable frequencies. When negative frequency dependence interacts with positive frequency dependence, as for example in the so-called rock-scissor-paper games (Maynard Smith, 1982), selection can give rise to a dynamic equilibrium in which multiple phenotypes coexist at continuously changing frequencies (Sinervo & Lively, 1996; Sinervo & Calsbeek, 2006).

Negative frequency-dependent selection can, as in the producer-scrounger game above, give rise to adaptive behavioural variation among individuals that do initially not differ in states. The same process can also give rise to adaptive state differences among individuals. The benefits to, for example, a particular physiological or cognitive architecture (e.g., particular level of stress responsiveness, particular learning rule) might depend on how common this architecture is in the population, thus promoting the coexistence of different architectures (Wolf *et al.*, 2008b). Similarly, the benefits of being in a particular environment (e.g., territory, habitat or social position) might depend on the frequency with which other individuals choose this environment, thus promoting the coexistence of individuals in different environmental states (Ens *et al.*, 1995; Wilson, 1998).

Negative frequency-dependent selection is a common phenomenon in social interactions (Maynard Smith, 1982; Svensson & Sheldon, 1998; Dugatkin & Reeve, 2000). It occurs, for example, in direct interactions among individuals if there is an inherent benefit to adopt a different phenotype to that of the interacting partners. Such situations occur in agonistic interactions, as for example hawk-dove like encounters (Maynard Smith, 1982), in which the aggressive hawk strategy is beneficial whenever the opponent plays dove, whereas the non-aggressive dove strategy is beneficial whenever the opponent plays hawk. They also occur in more cooperative interactions, when social partners benefit from diversifying into different behavioural roles that complement each other (Clark & Ehlinger, 1987). The benefits of such behavioural complementation can be caused by various mechanisms. Choosing different behavioural roles may help, for example, to avoid competition among partners, to reap the benefits of behavioural specialization or to reduce the risk associated with a certain strategy.

Negative frequency dependence can also be caused more indirectly (Kokko & Lopez-Sepulcre, 2007) via competition for different types of resources that have density dependent benefits (i.e., the benefits of a resource decrease with the number of individuals that compete for that type of resource). Such density dependence gives rise to negative frequency dependence: the more individuals that compete for a particular type of resource (e.g., territory, habitat, mate) the less beneficial it becomes. Density-dependent resource competition can thus promote the coexistence of individuals that choose for different resources (Wilson, 1998), which in turn gives rise to adaptive differences in states and behaviour among individuals.

Negatively frequency-dependent selection can thus give rise to adaptive variation in states and/or behaviour among individuals. In principle, this variation might or might not be associated with genetic variation (Maynard Smith, 1982; Wilson, 1994b). Consider, for example, a situation in which two phenotypes coexist with frequencies of 30% and 70% (e.g., producer and scroungers, individuals with a low and a high basal metabolic rate or slow and fast learners). This phenotypic variation can arise both in a population of genetically identical individuals that adopt each of the phenotypes randomly but with the same probability (choose one phenotype in 30%, the other in 70% of the cases) or in a genetically polymorphic population in which a fixed proportion of individuals adopts each of the phenotypes (30% of the individuals choose one phenotype, 70% the other).

Individual differences in foraging behaviour in the larval fruitfly (*Drosophila melanogaster*) provide a good example of the latter situation (Fitzpatrick *et al.*, 2007). In natural population, a dimorphism in foraging strategies can be observed ("rover" vs. "sitter" individuals). This dimorphism is based on a single major gene polymorphism that is maintained by negative frequency-dependent selection, both the rover and the sitter allele attain their highest relative fitness when rare in the population.

Spatiotemporal variation in the environment

Evolution shapes the phenotype of individuals to match their environment, and in many natural situations, the environment and, thus, the optimal phenotype, varies in space or in time. What is the expected evolutionary outcome in such a situation? In particular, should we expect that, as it is often thought to be the case (Nettle, 2006; Koolhaas *et al.*, 2007; Penke *et al.*, 2007), environmental variation promotes phenotypic variation within populations? And if so, should we expect that such phenotypic variation is associated with genetic variation?

It turns out that the answers to these questions depend on the details of the situation (Hedrick *et al.*, 1976; Hedrick, 1986; Seger & Brockmann, 1987; Moran, 1992; Leimar, 2005), in particular, on whether the population faces spatial or temporal variation in the environment (for an alternative classification see Frank & Slatkin, 1990; Donaldson-Matasci *et al.*, 2008) and on how well individuals can match their phenotype to their environment.

To see the importance of phenotype-environment matching consider first a situation in which individuals can match their phenotype to their environment in an error and cost-free manner, be it via habitat choice (i.e., the environment is chosen to match the phenotype), phenotypic plasticity (i.e., the phenotype is chosen to match the environment) or a combination of both. In such a situation evolution is expected to result in perfect phenotype-environment matching. No variation is maintained within each environment. This example is certainly extreme and unrealistic (DeWitt *et al.*, 1998), it illustrates, however, that environmental variation can only give rise to phenotypic variation within environments in situations with limited phenotype-environment matching.

Consider now the most basic scenario of spatial variation. A population inhabits an environment with two types of habitats, different phenotypes are favoured within each habitat. As we have just seen, if perfect phenotype-environment matching is possible, no variation within environments can be maintained. This is different in situations with an intermediated degree of phenotype-environment matching, that is in situations where habitat choice or phenotypic plasticity is possible but not perfect. Individuals might, for example, make errors when choosing habitats. In such situations phenotypic variation can be maintained both at a population level and within each habitat (Seger & Brockmann, 1987). The reason for this is as follows. Since some degree of phenotype-environment matching is possible, coexisting genotypes (or phenotypes of a plastic genotype) experience different environments, each genotype will, on average, experience more often that environment in which it is favoured. Variation within environments arises since phenotype-environment matching is not perfect. The resulting phenotypic variation can in principle be due to plasticity, a genetic polymorphism or a combination of both factors.

A good example for adaptive variation caused by spatial variation in the environment is provided by the bluegill sunfish (*Lepomis macrochirus*) that inhabits North American freshwater lakes (Ehlinger & Wilson, 1988). In these populations, consistent individual differences in foraging tactics (e.g., hover duration, pattern of movement) have been described. It turns out that these differences can be associated with differences in habitat use: the most efficient foraging tactic depends on whether an individual is in littoral or open water zones and individuals that employ different tactics are preferentially (but not exclusively, thus phenotype-environment matching is not perfect) found in that habitat that fits their foraging tactic best. Interestingly, differences in foraging tactics are associated with rather subtle morphological differences (e.g., fin size, fin placement) between individuals, which again tend to favour one habitat over the other. We will return to this point below when discussing the causes of consistency.

Spatial variation need not correspond to differences in the abiotic environment, as above, but can also be induced by variation in the biotic environment of individuals. It has been suggested, for example, that variation in neuroticism in humans is maintained by the fact that high levels of neuroticism are beneficial in predatory environments, whereas low levels of neuroticism are favoured in predator-free environments (Nettle, 2006).

In addition to spatial variation, also temporal variation in environmental conditions has often been suggested to contribute to the maintenance of personality differences. However, exactly as for spatial variation, the evolutionary effects of temporal fluctuations depend on population regulation, the scope for phenotype-environment matching, the costs of plasticity, and many other details of the biological system under consideration. To see this, consider a simple scenario of temporal fluctuations. Each generation all individuals within a population face the same environment , but the environment varies across generations, and different environments favour different phenotypes. As we have seen above, whenever individuals can adjust their phenotype to their current environment in an error and cost-free manner, no variation is maintained within environments. However, unlike for spatial variation, genetic variation cannot be maintained in situations with limited phenotype-environment matching, at least as long as generations are non-overlapping (see the discussion of bet-hedging below for how purely phenotypic variation can be maintained in such a scenario). The reason is as follows. All genotypes face exactly the same environment, there is no frequency dependence and among any number of potential genotypes there will typically be exactly one that achieves the highest (geometric mean) fitness (Seger & Brockmann, 1987).

Many animal species, however, are iteroparous and have overlapping generations and if we allow for this, also temporal fluctuations can maintain genetic polymorphisms (Ellner & Hairston, 1994). The intuition is as follows. As the lifetime of individuals increases (and thus the generation overlap), temporal fluctuations tend to average out within the lifetime of a single individual and the model comes closer and closer to a temporal analogue of a spatial model without habitat choice which can maintain genetic polymorphisms in the case of local density dependence (Levene, 1953).

A well-known feature of temporally fluctuating environments, be it with or without overlapping generations, is that so called bet-hedging genotypes are selectively favoured (Seger & Brockmann, 1987), that is genotypes that switch during development stochastically between two or more phenotypes. A bet-hedging genotype thus gives rise to a mixture of phenotypes (e.g., aggressive and non-aggressive individuals, individuals with a low and a high stress responsiveness). This can be seen as a risk-spreading strategy, since no matter how the environment turns out, some of the bet-hedging phenotypes are well adapted. More technically, a diversifying bet-hedger can reduce its variance in fitness in an optimal way and thereby increase its geometric mean fitness.

In summary, in species with non-overlapping generations, temporal fluctuations can only maintain phenotypic variation. In species with overlapping generations, also genetic variation can be maintained, but again, bet-hedging strategies are selectively favoured (Leimar, 2005).

Temporal fluctuations need not be restricted to the abiotic environment of individuals. Dingemanse and colleagues, for example, studied a population of great tits (*Parus major*) for which environmental conditions (masting of beeches) varied across years (Dingemanse *et al.*, 2004). They found that different behavioural types were favoured dependent on the environmental condition (in terms of adult survival and number of offspring surviving to breeding), which in turn might explain the maintenance of variation in this populations.

Temporal fluctuations can also arise through the social environment of individuals. Mouse populations, for example, are known to go through phases of growth and decline. It has been hypothesized that these fluctuations can explain the maintenance of genetic variation in aggressiveness in such populations since the extreme phenotypes have differential fitness at different population densities (Chitty, 1967; Van Oortmerssen & Busser, 1989). Recent research on populations of western bluebirds (*Sialia mexicana*) points in a similar direction (Duckworth & Badyaev, 2007). During range expansions across the north-western United States highly aggressive individuals were selectively favoured when colonizing new populations since those individuals could more easily displace less aggressive mountain bluebirds. Once mountain bluebirds were displaced, however, high levels of aggression were selectively disfavoured, presumably because aggressive individuals provide almost no parental care. Such temporal variation in selection pressures might thus explain the maintenance of variation in aggressiveness within these populations.

CAUSES OF CORRELATIONS

Up to now we focussed on the causes of behavioural differences for particular decision problems (e.g., how to explore an environment, how to respond to a predator). Personalities, however, refer to much more than such behavioural differences (Clark & Ehlinger, 1987; Digman, 1990; Gosling, 2001; Sih *et al.*, 2004b). First, personalities refer to behavioural differences that are stable through part of the ontogeny of individuals (time-consistency of behaviour), that is, individuals that score relatively high (low) in a given behavioural situation often tend to score relatively high (low) in the same situation at later points in time. Second, personalities refer to behavioural differences that extend to whole suites of correlated behaviours, that is, correlated variation in functionally different contexts (e.g., antipredator behaviour is correlated with contest behaviour).

Both types of correlations indicate behavioural inflexibilities (Wilson, 1998; Dall *et al.*, 2004) in the sense that the behaviour that an individual exhibits at one point in time and in one particular context is predictive for the same individual's behaviour at later points in time and in different contexts. Why did evolution give rise to such behavioural inflexibilities? Why should an individual stickleback that is, for example, relatively aggressive at one point in time also be relatively aggressive at later points in time (Bakker, 1986)? And why should aggressive individuals also be bolder than their non-aggressive conspecific (Huntingford, 1976)? It would seem that a flexible structure of behaviour is more advantageous.

To answer these questions, we first explore why, in some cases, evolution gives rise to architectures of behaviour that result in apparently maladaptive behavioural correlations. We then focus on state variables as a cause of behavioural correlations in general and discuss two main sources for the stability of state differences over time, inherently stable state differences and positive feedback mechanisms. Behavioural correlations need not reflect underlying state variables and we conclude this section by discussing how social conventions can give rise to adaptive behavioural correlations.

Architectur of behaviour

On a proximate level, the behavioural phenotype of an individual is affected by its architecture of behaviour, that is, the genetic, physiological, neurobiological and cognitive systems underlying its behaviour. This architecture, in turn, gives rise to behavioural correlations whenever multiple traits are affected by a common underlying mechanism within this architecture. Such common mechanisms are ubiquitous, examples include pleiotropic genes (Mackay, 2004), hormones (Ketterson & Nolan, 1999), neurotransmitters (Bond, 2001), behavioural rules (Todd & Gigerenzer, 2000) and emotions (Rolls, 2000) that affect multiple traits at the same time.

It has been shown, for example, that the positive correlation of aggressiveness through ontogeny in the three-spined stickleback (*Gasterosteus aculeatus*) is caused by pleiotropic genes (Bakker, 1986). Pleiotropic genes are also thought to be responsible (Riechert & Hedrick, 1993; Maupin & Riechert, 2001) for the positive correlation between agonistic behaviour, antipredator behaviour and superfluous killing in the American desert spider (*Agelenopsis aperta*). The negative correlation between mating effort and parental effort in several bird species is caused by the hormone testosterone (McGlothlin *et al.*, 2007). And finally, the fearfulness of an individual affects its reaction to a multitude of potentially threatening situations, including persistent dangers in its ecology, novelty and interactions with conspecifics (Boissy, 1995).

Behavioural correlations can thus be the result of a relatively rigid architecture of behaviour. The resulting behavioural associations appear adaptive in some cases (see below), in others, however, they give rise to apparently maladaptive behaviours (Sih *et al.*, 2004a). It might, for example, be advantageous for a female spider to show high levels of aggression towards territorial intruders, but why should such individuals also kill and consume all potential mates during courtship and as a consequence be left unmated at the time of egg laying (Arnqvist & Henriksson, 1997)? Similarly, it might be advantageous for a salamander larvae to be relatively active in the absence of predatory cues but why should such individuals also be relatively active in the presence of such cues (Sih *et al.*, 2003)? In other words, rigid behavioural architectures can explain behavioural correlations at the proximate level, but from an ultimate perspective, one is tempted to ask why such rigid behavioural architectures persist over evolutionary time. Especially in cases where a rigid architecture gives rise to apparently maladaptive behaviour, one would expect evolution to uncouple unfavourable behavioural associations.

The evolution of a more flexible behavioural architecture might in principle be prevented for two types of reasons. First, a more flexible architecture might be advantageous (i.e., an individual with such an architecture would achieve a higher fitness than an individual with a more rigid architecture) but not attainable by evolution. Such a situation can occur because the evolutionary transition from one complex phenotype (here: rigid architecture) to another complex phenotype (more flexible architecture) is typically not possible in one step but requires many intermediate steps. The architectures associated with these intermediate steps, however, might be disadvantageous to the individual. In other words, the evolution of a more flexible behavioural architecture might be associated with crossing an adaptive valley of the fitness landscape which in turn prevents the evolution of a more flexible behavioural architecture. Such a situation occurs if the current behavioural correlations correspond to a local peak in the fitness landscape, reflecting the fact that the involved traits are to some extent well adapted to each other. Second, a more flexible behavioural architecture might not be advantageous, that is an individual with such an architecture would achieve a lower fitness than an individual with a more rigid architecture. Such a situation can occur if a more flexible architecture is associated with costs (e.g. costs of plasticity, DeWitt *et al.*, 1998) that are not outweighed by the corresponding benefits. In both cases, trait correlations can persist even though they give rise to behavioural traits that, when viewed in isolation from their architectural basis, might appear maladaptive.

Stable state variables

Many aspects of the state of an individual affect the cost and benefits of multiple behavioural traits at the same time (McNamara & Houston, 1996). Consequently, individuals should make these behaviours dependent on their current state. State differences in combination with state-dependent behaviour (condition-dependent behaviour, phenotypic plasticity) thus provide a natural explanations for adaptive behavioural correlations of apparently unrelated behavioural traits. However, state differences do not immediately explain why individuals should be consistent over time. Put differently, why should initial state differences among individuals be relatively stable over time? In this section we discuss two main roads to consistency of states, inherently stable state variables and positive feedback mechanisms between state and behaviour.

INHERENTLY STABLE STATE VARIABLES

As we have discussed above, random causes, frequency-dependent selection and spatiotemporal variation can give rise to populations with variation in states among individuals. Whenever a change of state among these variants is associated with substantial costs, such situations can result in consistent differences in state and, consequently, consistent differences in whole suites of (state-dependent) traits that are affected by this state.

In some situations, differences in states are associated with differences in morphological and physiological characteristics that are costly to change. Consider, for example, sex differences. In many animal species, frequency-dependent selection maintains two sexes at constant proportions within populations. These equilibrium proportions can in principle be maintained in populations in which individuals change their sex over time. Such a sex change, however, is often associated with substantial costs to the individual (caused by the necessary morphological and physiological changes). We thus typically observe stable (life long) sex differences among individuals which are, in turn, associated with whole suites of correlated behavioural traits. In humans (Costa *et al.*, 2001), for example, women typically score higher than males on traits related to the agreeableness axis (e.g., cooperativeness, empathy, trust), in many other animal species, sex differences exist for example in parental care and courtship behaviour (Kelley, 1988).

In some situations, evolution gives rise to populations in which individuals are distributed among a small number of discrete size classes (Brockmann, 2001). A change among these variants is typically associated with substantial costs, which in turn favours consistency in size and thus consistency in behavioural traits that are affected by body size. A common phenomenon, for example, is the use of fighting or sneaking as an alternative mating tactic depending on body size, as observed in dung beetles, bees, and many other species (Gross, 1996).

Morphological and physiological differences, which can only be changed under substantial costs, need not be as conspicuous as in the case of sex or size differences. As discussed above (Ehlinger & Wilson, 1988), within populations of bluegill sunfish (*Lepomis Macrochirus*) individuals differ in morphological characteristics that are functional either in the littoral or open water zone (e.g., fin size, fin placement). Such (stable) differences are associated with consistent differences behavioural traits, as for example foraging tactics. Interestingly, the underlying morphological differences are not obvious to an observer, in fact, sunfish have been studied for many years without recognizing the adaptive nature of these differences (Wilson, 1998).

Inherently stable state differences need not be associated with morphological and physiological characteristics that are costly to change. In some cases stability is caused (in part) by factors external to the individual. Human societies, for example, encompass a large diversity of social positions (e.g., teachers, managers, bureaucrats). While it is in principle possible for an individual to change its position, such changes are typically very costly to the individual (e.g., in terms of required training or education). As a result, individuals typically stick to their position once chosen. Consistent differences in such positions, in turn, are often associated with consistent differences in suites of correlated behavioural traits. Human leaders, for example, are more extrovert and more conscientious than non-leaders (Judge *et al.*, 2002); entrepreneurs are more conscientious and open, but less neurotic and agreeable than managers (Zhao & Seibert, 2006).

SELF-REINFORCING FEEDBACK LOOPS

Many aspects of the state of an individual are much more labile than the ones discussed above. Consider, for example, the energy reserves of an individual, the experience that an individual has with a certain behaviour or the future fitness expectations of an individual. These states are, like many others, labile since they can easily be changed by many different factors, including the individual's own behaviour.

Labile states can, as inherently stable states, affect multiple behavioural traits at the same time thus explaining suites of correlated behavioural traits. But why should labile states be stable over time? Differently asked, why should initial differences in such states among individuals be stable over time?

In some situations the state and behaviour of individuals are coupled by a positive feedback (Sih *et al.*, 2004b; Sih & Bell, 2008): initial state differences give rise to differences in behaviour which act to stabilize or even increase the initial state differences. Such positive feedback mechanism, in turn, can give rise to consistent individual differences in labile states and behavioural traits that are associated with these states.

An important positive feedback is the feedback between behaviour and the experience an individual has with this behaviour. Individuals often get better with increased experience (Rosenzweig & Bennett, 1996), that is, processes like learning, training and skill formation give rise to lower costs or higher benefits for the same action when repeated, which in turn favours consistency in this behaviour (Wolf *et al.*, 2008b).

Positive feedbacks via experience can give rise to consistent individual differences in single behavioural traits. Animals often learn how to recognize predators (Griffin, 2004), for example, which in turn makes it less costly to explore and forage a risky habitat for individuals that did this before. Under such conditions, whenever variation in risk-taking behaviour is maintained within populations (Wilson, 1998; Wolf *et al.*, 2007a), positive feedbacks acts to promote consistent individual differences in risk-taking behaviour.

Positive feedbacks can also give rise to consistent differences in suites of correlated behavioural traits. Experience gained in one context, for example, can affect the cost and benefits of behavioural actions in another context and thus give rise to a cross context association of behavioural traits. Individuals that learn to assess the strength of conspecific competitors might, for example, at the same time get better at assessing the risk associated with predators.

Positive feedback need not act via behaviour directly. The cost and benefits of behavioural traits that are related to resource acquisition (e.g., aggression, boldness), for example, often depend on characteristics of the individual that are affected by the resources available to an individual (e.g., size, strength, resource holding potential) and this interaction can give rise to a positive feedback loop (Sih & Bell, 2008). The strength of individuals positively affects its fighting ability, for example, which in turn gives rise to more resources that positively affect its strength. This feedback favours consistency in all kinds of traits related to the characteristic.

Positive feedbacks can also act via physiological characteristics of the individual. It has been suggested, for example, that in many animal species, deviations from a once chosen growth rate are costly to the individual (Stamps, 2007; Biro & Stamps, 2008). Compensatory growth, for example, often comes at the cost of increased risk of disease, higher mortality rates, or decreased physiological capacity later in life (Mangel & Munch, 2005). Similarly, deviations from a once chosen basic metabolic rate or stress responsiveness might be costly to the individual. In such situations, consistency in such physiological characteristics (growth rate, basic metabolic rate, stress responsiveness) is favoured and thus consistency in suites of traits that are associated with these characteristics. Differences in growth rates, for example, affect the cost and benefits of all kinds of traits that are related to food intake as aggression and boldness (Stamps, 2007).

SOCIAL CONVENTIONS

An adaptive association of different behaviours need not reflect an underlying state variable that affects the costs and benefits of these behaviours, as in the situations discussed above. Rather, behavioural traits (be it the same trait expressed at different points during ontogeny or different traits) can get associated with each other because individuals in a population follow an adaptive behavioural rule (or convention) that favours the association of these traits.

When an individual is confronted with another individual in a social interaction, for example, it might make its behaviour dependent on the behavioural history of the other individual. To be concrete, when A and B interact in a hawk-dove like encounter (Maynard Smith, 1982), individuals might follow the rule "if the opponent played hawk before, choose dove, otherwise choose hawk". Such an eavesdropping strategy (Johnstone, 2001) makes sense whenever there is some consistency in the behaviour of individuals. Consistency thus favours eavesdropping since it allows the eavesdropper to choose the best response to the behaviour of its partner (e.g., choose hawk when confronted with a dove, otherwise choose dove). Conversely, eavesdropping favours consistency whenever it is beneficial for individuals to be predictable. This interaction between consistency and eavesdropping can thus give rise to populations in which individuals follow a behavioural rule that favours consistency and, as a result, individuals show consistent behaviour.

Do such conventions arise in natural situations? The so called winner-loser effect (Chase *et al.*, 1994) might be a good example. It is a well known phenomenon that winners of previous contests are more likely to win again (and losers are more likely to lose again), even against different opponents and in situations in which there are no asymmetries between the opponents. According to a survey across several taxa (Rutte *et al.*, 2006), when there are no other asymmetries between opponents, the probability of winning a subsequent contest is almost doubled for previous winners, but is reduced more than five times for previous losers even against different opponent. Winner-loser effects are currently not well understood but one explanation that is given by several authors is based on the arguments above: the prior success of the opponent might act as a 'random historical asymmetry' that is used to settle the conflict (Parker, 1974; Maynard Smith & Parker, 1976; Hammerstein, 1981; Van Doorn *et al.*, 2003a; Van Doorn *et al.*, 2003b) Social conventions that favour consistency are not limited to aggressive interactions. An influential idea in explaining cooperation is that individuals should make their behaviour dependent on an image score of the other individual (Nowak & Sigmund, 1998; Leimar & Hammerstein, 2001), a measure of how cooperative the other individuals has been in the past. Such image scoring can, in turn, favour consistency in cooperative behaviour.

DISCUSSION

In this chapter, we have focussed on the evolutionary causes of personalities. The existence of personalities, however, should be expected to have consequences for evolutionary process (Wilson, 1998; Dall *et al.*, 2004). In social contexts, for example, the existence of variation in one trait often selects for variation in another trait. Variation in cooperativeness, for example, can select for variation in choosiness which in turn selects for cooperativeness (McNamara *et al.*, 2008). Importantly, variation in cooperativeness can thus trigger a coevolutionary process of cooperativeness and choosiness that give rise to very different evolutionary outcomes (here: high levels of cooperation) when compared to situations without such initial variation.

We aimed to provide on overview about the basic factors and mechanisms that promote the evolution of personalities. We focussed on two basic questions: which factors promote adaptive behavioural variation within populations and which factors promote adaptive correlations among behavioural traits, be it across contexts or over time?

Factors promoting variation and correlations can interact in various ways. Random causes, frequency-dependent selection and spatiotemporal variation can give rise to variation in states among individuals. Whenever such states affect the cost and benefits of behavioural traits, state differences promote state-dependent behaviour and thus adaptive behavioural variation or, whenever the costs and benefits of multiple behavioural traits are affected at the same time, adaptive behavioural variation that is correlated across contexts. In principle, behavioural variation should be expected to be stable as long as the underlying variation in states is stable. Whenever states are very costly to change and thus inherently stable (e.g., sex and size differences) variation is expected to be stable. In the case of labile states (e.g., energetic state, experience with a certain behaviour), variation can be stabilized via positive feedback mechanisms between behaviour and states: variation in states gives rise to variation in behaviour that acts to stabilize or increase initial state differences.

Spatiotemporal variation and frequency-dependent selection can give rise to behavioural variation that is not associated with underlying state differences and state-dependent behaviour (e.g. producers and scroungers, hawks and doves). Such variation can be stabilized over time via positive feedback mechanisms: the initial variation in behaviour gives rise to differences in states that act to stabilize the behavioural differences (e.g., producers gain experience that makes producing more beneficial). Such feedbacks can also extend to multiple behavioural traits, thus giving rise to adaptive behavioural correlations (e.g. experience gained in producer-scrounger context can affect the cost and benefits of behaviour in different contexts). Alternatively, behavioural variation in single or multiple behavioural traits can be stabilized via social conventions which favour consistency in behaviour.

The above summary emphasizes that personalities ask for a holistic approach to behaviour. Rather than "atomizing the organism" (Gould & Lewontin, 1979) into single behavioural traits that are studied in isolation, multiple different traits have to be studied in concert: behaviour in one context (e.g., antipredator, mating, fighting, parental care) can often only be understood when taking the interdependencies with past and future behaviour in the same and other contexts into account. Personalities ask for an integration of mechanism and adaptation (Tinbergen, 1963; McNamara & Houston, in press). As we have emphasized above, behavioural correlations are often caused by the architecture of behaviour, that is by the genetic, physiological, neurobiological and cognitive systems underlying behaviour. In order to understand such correlations we thus have to understand the coevolution behaviour and mechanisms causing behaviour.

Chapter 3

Life-history trade-offs favour the evolution of animal personalities

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ABSTRACT

In recent years evidence has been accumulating that personalities are not only found in humans (Pervin & John, 1999) but also in a wide range of other animal species (Wilson *et al.*, 1994a; Boissy, 1995; Gosling & John, 1999; Koolhaas *et al.*, 1999; Gosling, 2001; Groothuis & Carere, 2005). Individuals differ consistently in their behavioural tendencies and the behaviour in one context is correlated with the behaviour in multiple other contexts. From an adaptive perspective, the evolution of animal personalities is still a mystery, since a more flexible structure of behaviour should provide a selective advantage (Coleman & Wilson, 1998; Wilson, 1998; Dall *et al.*, 2004). Accordingly, many researchers view personalities as resulting from constraints imposed by the architecture of behaviour (Sih *et al.*, 2004b). In contrast, we show here that animal personalities can be given an adaptive explanation. Our argument is based on the insight that the trade-off between current and future reproduction (Roff, 2002) often results in polymorphic populations (Rueffler *et al.*, 2004) where some individuals put more emphasis on future fitness returns than others. Life-history theory predicts that such differences in fitness expectations should result in systematic differences in risk-taking behaviour (Clark, 1994). Individuals with high future expectations (who have much to lose) should be more risk-averse than individuals with low expectations. Since this applies to all kinds of risky situations, individuals should consistently differ in their behaviour. By means of an evolutionary model we demonstrate that this basic principle results in the evolution of animal personalities. It simultaneously explains the coexistence of behavioural types, the consistency of behaviour through time and the structure of behavioural correlations across contexts. Moreover it explains the common finding that explorative behaviour and risk-related traits like boldness and aggressiveness are common characteristics of animal personalities (Wilson *et al.*, 1994a; Boissy, 1995; Gosling & John, 1999; Koolhaas *et al.*, 1999; Gosling, 2001; Groothuis & Carere, 2005).

INTRODUCTION

The phenomenon of animal personalities is one of the most intriguing challenges to the adaptationist programme in behavioural research. Empirical findings in more than 60 species, ranging from primates to ants, suggest that animal behaviour is much less flexible than previously thought (Wilson *et al.*, 1994a; Boissy, 1995; Gosling & John, 1999; Koolhaas *et al.*, 1999; Gosling, 2001; Groothuis & Carere, 2005). Individuals consistently differ in whole suites of correlated behaviours and these differences are often heritable (Bakker, 1986; Dingemanse *et al.*, 2002; Drent *et al.*, 2003; Sinn *et al.*, 2006). At present, the existence of such personalities – also termed behavioural syndromes (Sih *et al.*, 2004a), coping styles (Koolhaas *et al.*, 1999) or temperaments (Reale *et al.*, 2000) – is puzzling in several respects. First, why do different personality types stably coexist? Second, why is behaviour not more flexible but correlated across contexts and through time? And third, why are the same types of traits correlated in very different taxa (Koolhaas *et al.*, 1999; Gosling, 2001; Sih *et al.*, 2004b)? Here we develop an evolutionary model that provides answers to all of these questions.

We start with the observation that some of the most prominent personality traits described in the literature can be categorized in terms of risk-taking behaviour. A good example is the correlation between aggressiveness towards conspecifics and boldness towards predators: individuals that take more risk in intraspecific fights also take more risk when confronted with a predator. This aggression-boldness syndrome has been described for many species (Sih *et al.*, 2004b) including fish (Huntingford, 1976; Bell & Stamps, 2004), birds (Groothuis & Carere, 2005) and rodents (Koolhaas *et al.*, 1999). From life-history theory it is known that individuals should adjust their risk-taking behaviour to their residual reproductive value (Clark, 1994; Roff, 2002), i.e. their expected future fitness. Individuals with relatively high expectations should be relatively risk-averse, since they have to survive in order to realize those expectations. By the same reasoning, individuals with relatively low expectations should be relatively risk-prone since they have little to lose. Consequently, whenever individuals differ in their fitness expectations, we should expect stable individual differences and correlated behavioural traits: some individuals are consistently risk-prone whereas others are consistently risk-averse.

MODEL AND RESULTS

By means of a simple model we now show that these intuitive arguments do indeed provide an evolutionary explanation for animal personalities. We proceed in three steps. First, we show that the trade-off between current and future reproduction can easily give rise to polymorphic populations where some individuals put more emphasis on future reproduction than others. Second, we demonstrate that this variation in life-history strategies selects for systematic differences in risk-aversion. Third, we show that these differences in risk-taking behaviour extend to various risky situations and are stable over time, thereby giving rise to animal personalities.

Consider the following stylized life-history (Figure 3.1A). Individuals live for two years and reproduce at the end of each year. The foraging habitat is heterogeneous with both high- and low-quality resources. Individuals face a trade-off between reproduction in year 1 and reproduction in year 2 that is mediated by exploration behaviour. We characterise the exploration behaviour by the strategic variable x, which ranges from superficial ($x = 0$) to thorough ($x = 1$). Individuals that explore their environment thoroughly have a high probability of obtaining a high-quality resource in year 2. For simplicity, we let this probability correspond to x. Yet, the probability of reproducing in year 1, $g(x)$, decreases with the intensity of exploration. Here we take $g(x) = (1 - x)^{\beta}$, where $\beta > 1$.

The payoff from feeding on high- or low-quality resources declines with the density of individuals (N_{high} or N_{low}, respectively) competing for such resources. It is given by:

$$F_i = \frac{f_i}{1 + \alpha N_i} \qquad i = high, low \tag{1}$$

where α represents the strength of competition and f_{high} and f_{low} ($f_{high} > f_{low}$) denote the intrinsic benefit of obtaining a high- and a low-quality resource, respectively. At the end of each year, individuals produce a number of offspring that is proportional to the payoff they obtained in that year. To summarise, an individual with exploration intensity x produces $g(x) \cdot F_{low}$ offspring at the end of its first year; at the end of its second year it produces F_{high} offspring with probability x and F_{low} offspring with probability $1 - x$.

For this basic life cycle, natural selection gives rise to the stable coexistence of two extreme exploration strategies (Figure 3.1B): some individuals explore the environment thoroughly, thereby investing in future reproductive success, whereas others explore superficially, putting more emphasis on current reproduction. This dimorphism is a stable evolutionary outcome whenever $2f_{low} > f_{high} > 1$ (see Appendix).

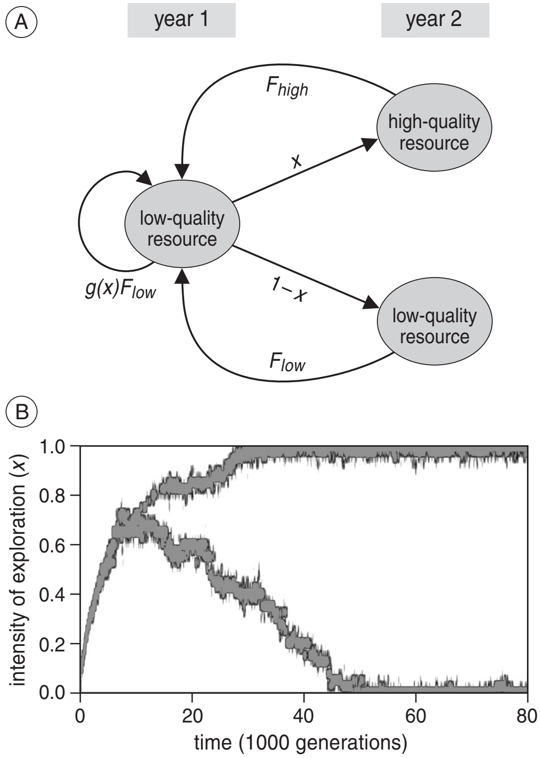

Figure 3.1 Stable coexistence of exploration strategies due to a life-history trade-off. A, Structure of the life-history model illustrating the trade-off between current and future reproduction. Natural selection acts on the exploration intensity x that corresponds to the probability of finding a high-quality resource in the future. While having a positive effect on reproduction in year 2 (future fitness), a high value of x decreases the probability $g(x)$ of obtaining reproductive resources in year 1. F_{low} and F_{high} denote the reproductive output in case of a low- and high-quality resource, respectively. B, The trade-off in A induces disruptive selection on exploration intensity and gives rise to the stable coexistence of superficial ($x = 0$) and thorough ($x = 1$) explorers.

We now extend the above life history by assuming that each individual is confronted with a number of risky contexts (Sih *et al.*, 2004a) throughout its lifetime (see Methods). Between year 1 and year 2, each individual may face one or more foraging decisions under predation risk (anti-predator games) and one or more aggressive encounters with randomly chosen conspecifics. In each of the anti-predator games an individual can either behave in a bold or a shy manner. Only bold individuals receive a payoff (in terms of higher fecundity) but they also incur some risk of dying. Aggressive encounters are modelled as hawk-dove games (Maynard Smith, 1982), where hawks receive a higher payoff than doves but do not always survive hawk-hawk interactions.

Let us first consider the two most basic cases where all individuals either play one anti-predator game or one hawk-dove game. Our individual-based simulations (Figure 3.2) confirm the general principle (Clark, 1994) that individuals with higher future expectations (in our case: thorough explorers) should behave in a more cautious way. Superficial explorers evolve to behave boldly (resp. aggressively) whereas thorough explorers evolve low levels of boldness (resp. aggressiveness). This outcome is consistent across replicate simulations and holds for a broad range of parameter conditions (see Appendix).

To show that this principle gives rise to personalities we now consider scenarios where individuals play several risky games between year 1 and year 2. We stress that in all of our simulations, in principle fully flexible behaviour could evolve. For example, an individual that behaves aggressively in a first hawk-dove game could behave shyly in an anti-predator game and show any level of aggression in a subsequent hawk-dove game. Yet, we find that selection gives rise to stable individual differences within the same game and correlated behavioural traits across different games (Figure 3.3). Figure 3.3A considers the scenario where individuals play two hawk-dove games sequentially. Here superficial explorers evolve high levels of aggression in both games whereas thorough explorers evolve to be consistently non-aggressive. Figure 3.3B depicts the scenario where individuals face one anti-predator and one hawk-dove game sequentially. Here evolution

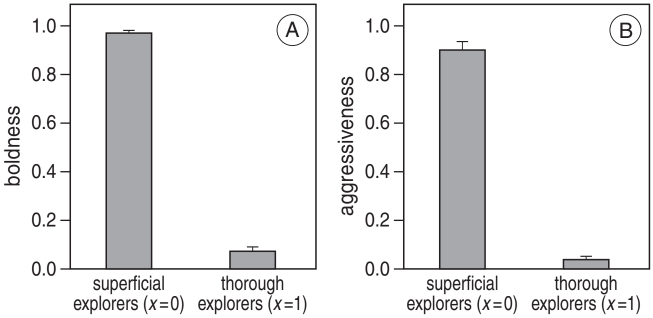

Figure 3.2 Evolution of variation in risk-taking behaviour. The outcome of evolution after $3 \cdot 10^5$ generations of selection where individuals following the life-cycle depicted in Figure 3.1 play a single risky game between year 1 and year 2. A, In case of an anti-predator game superficial explorers evolve high levels of boldness whereas thorough explorers show low levels of boldness. B, In case of a hawk-dove game superficial explorers are aggressive whereas thorough explorers are non-aggressive. The bars correspond to mean trait values averaged over ten replicate simulations (error bars indicate standard errors).

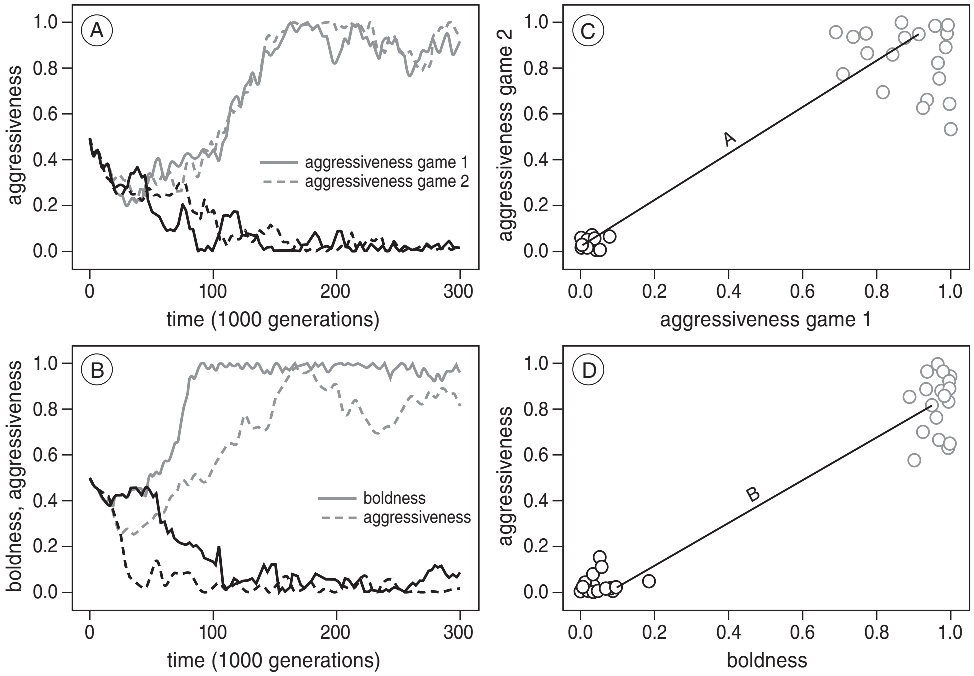

Figure 3.3 Evolution of personalities. Simulations illustrating the evolution of consistent individual differences between superficial explorers (grey) and thorough explorers (black). A, When individuals face two hawk-dove games superficial explorers evolve high levels of aggressiveness in both games whereas thorough explorers are consistently non-aggressive. B, Confronted with both an anti-predator and a hawk-dove game a behavioural syndrome evolves: superficial explorers are bold and aggressive whereas thorough explorers are shy and non-aggressive. These outcomes are robust across replicate simulations. C and D summarise the outcome of 20 replicate simulations for the scenarios in A and B, respectively. Each simulation is represented by two circles corresponding to the evolved trait combinations of superficial and thorough explorers. Straight black lines indicate the trait combinations for the simulations depicted in A and B.

gives rise to the coexistence of superficial explorers that are both bold and aggressive and thorough explorers that are shy and non-aggressive. These results are consistent across replicate simulations (Figure 3.3C,D), they hold for a broad range of parameter conditions (see Appendix) and they extend to more complex situations where individuals play more than two games (not shown). In other words, we robustly observe the well-known behavioural syndrome linking explorative behaviour, aggression and boldness, which has been reported for numerous species in a diversity of taxa (Koolhaas *et al.*, 1999; Gosling, 2001; Groothuis & Carere, 2005).

Up to now we have assumed, for simplicity, that individuals reproduce asexually. We obtain qualitatively the same results for scenarios that allow for recombination and diploid genetics, as long as individual alleles have a large phenotypic effect. Under this condition disruptive selection gives rise to a small number of discrete phenotypes (Rueffler *et al.*, 2006; Van Doorn & Dieckmann, 2006), each

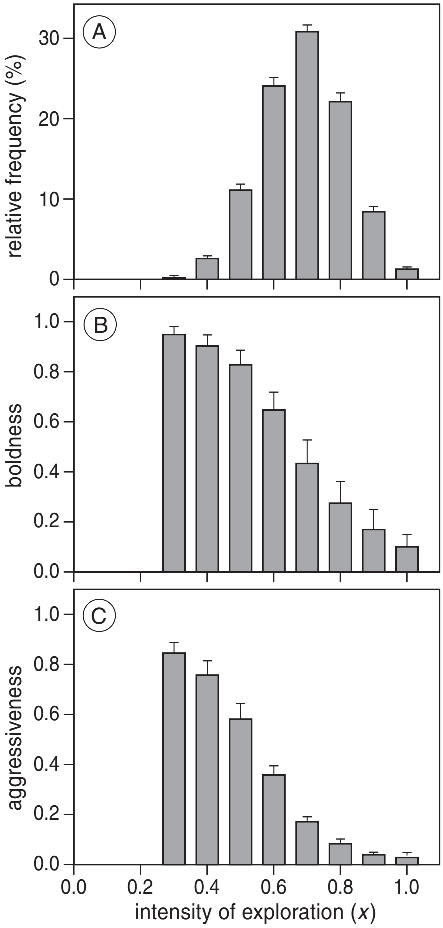

Figure 3.4 Evolution of continuous variation in personalities. If all traits are encoded by multiple loci with small effects, disruptive selection on the exploration intensity x does not result in two discrete phenotype classes but in a broad distribution of exploration strategies (A). The graphs depict the average level of boldness (B) and aggressiveness (C) that evolved as a function of x within $2 \cdot 10^5$ generations (mean of ten replicate simulations; error bars indicate standard errors). The evolved levels of boldness and aggressiveness are strongly correlated, corresponding to a boldness-aggressiveness syndrome (correlation coefficients in the ten simulations ranged from 0.40 to 0.81, with a mean value of 0.65).

corresponding to a distinct personality type. A more realistic approach, however, would be to consider quantitative traits, which are often thought to be influenced by many loci with small effects. We now incorporate such quantitative genetics into our model (see methods).

Consider a scenario where individuals face one anti-predator and one hawk-dove game sequentially. As shown in Figure 3.4A, disruptive selection does now not result in two extreme exploration strategies but in the stable coexistence of a broad range of explorative behaviours. Similarly, with respect to both boldness and aggressiveness, we find a gradation of behavioural traits ranging from low to high levels (Figure 3.4B,C). A clear pattern emerges: the more superficially an individual explores its environment (Figure 3.4A), the more boldly it behaves in the anti-predator game (Figure 3.4B) and the more aggressive it is in the hawk-dove game (Figure 3.4C). In other words, in the case of quantitative genetic variation we find a whole spectrum of personality types, which is in line with many empirical studies (Dingemanse *et al.*, 2004; Bell, 2005).

CONCLUSIONS

To sum up, our model offers a plausible explanation for individual differences within a population, the evolution of behavioural correlations within and across contexts and the fact that particular traits like explorative behaviour, boldness and aggressiveness tend to be associated. Our theory is well testable by predicting (1) under what circumstances behavioural correlations should occur, (2) what particular traits should be correlated and (3) what sign the correlations should take. Behavioural correlations are to be expected whenever individual differences in residual reproductive value (i.e., expected future fitness) occur. One might think of the difference between high- and low-ranking individuals in a dominance hierarchy, between dispersers and philopatric individuals in a metapopulation or between residents and floaters in a territorial system. In any such situation we would expect correlations between those behavioural traits that involve risks which might prevent individuals from reaping the returns from reproductive investments. In addition to intraspecific aggression and boldness one might also think of behaviours such as brood defence, nest guarding or conspicuous displays to attract mates. All other things being equal, we would expect such traits to be positively correlated.

Our model certainly does not explain all aspects of animal personalities (e.g., cooperativeness, McNamara *et al.*, 2004) and alternative evolutionary mechanisms may also play an important role (Wilson, 1998; Hedrick, 2000; Rands *et al.*, 2003; Dall *et al.*, 2004). Yet, as argued above, we believe that our line of argument applies to a broad class of ecological situations. In all these situations the same basic principle will give rise to the evolution of animal personalities: the more an individual has to lose, the more risk-averse it should be, across contexts and through time.

METHODS

Methods summary

Our conclusions are based on general arguments that are supported by individual-based simulations (main text) and analytical results based on evolutionary invasion considerations (Appendix). We consider a population where individuals follow the basic life-cycle illustrated by Figure 3.1A. Moreover, between year 1 and year 2, each individual plays one or more anti-predator games and/or one or more hawk-dove games. Individuals are characterised by a suite of heritable traits corresponding to (1) their life-history strategy x, (2) for each anti-predator game the tendency to be bold, and (3) for each hawk-dove game the tendency to be aggressive. Individuals could in principle evolve fully flexible behaviour. For example, an individual that behaves aggressively in a first hawk-dove game could exhibit low levels of aggressions in a subsequent hawk-dove game. The reproductive success of individuals is frequency- and density-dependent and reflects the fecundity associated with the life-history strategy, the mortality risks associated with bold and aggressive behaviour, and the payoff accumulated in the games. The resulting fitness function is analysed in the Appendix by means of an invasion analysis. In the main text, the assumptions are implemented in individual-based simulations where trait frequencies change over time under the influence of natural selection. The simulations were run until evolutionary equilibrium was reached. The resulting population was analysed focussing on three key questions. First, does evolution give rise to the coexistence of life-history strategies? Second, does evolution result in stable differences between individuals if the same game is played repeatedly? And third, does evolution lead to behavioural correlations between boldness and aggressiveness?

Basic model

We first consider an asexual population of haploid individuals. Each individual is characterised by the allelic values at $k + 1$ loci, where one locus determines the exploration behaviour and the other loci determine the behaviour in the k games played between year 1 and year 2. Allelic values range between 0 and 1 and correspond to the exploration intensity x or the strategy in a particular game (probability to be bold or aggressive).

In the first year, an individual with exploration intensity x produces $g(x) \cdot F_{low}$ offspring, where $g(x) = (1 - x)^{\beta}$. All figures are based on $\beta = 1.25$, but similar results are obtained for all $\beta > 1$. Between years 1 and 2, an individual accumulates payoffs in the games it participates in, but it also runs the risk of dying (see below). In case an individual survives its reproductive output in year 2 is increased by the payoff it accumulated in these games. All figures shown are based on $f_{high} = 3.5$, $f_{low} = 3.0$ and $\alpha = 0.005$, but similar results are obtained as long as $2 f_{low} > f_{high} > 1$.

During reproduction mutations occur with a small probability ($\mu = 2 \cdot 10^{-3}$). Mutations have a small effect: they change the allelic value by a value that is drawn from a normal distribution with mean zero and standard deviation , with the constraint that allelic values remain in the interval from 0 to 1. All results are independent of the specific parameter values for the mutational process and the initial conditions.

Anti-predator games and aggressive encounters

In each of the anti-predator (hawk-dove) games, an individual behaves boldly (aggressively) with a probability determined by its genotype. In an anti-predator game, a bold individual obtains a payoff b but dies with probability γ whereas a shy individual obtains no payoff and always survives. Aggressive encounters are modified hawk-dove games where individuals fight for a resource of value V. In such an encounter, individuals are paired at random. Payoffs are obtained as in the standard hawk-dove game (Maynard Smith, 1982) with one exception: if two aggressive ("hawk") individuals meet, one gets V while the opponent gets 0 and moreover dies with probability δ . All figures are based on $b = 0.1$, $\gamma = 0.1$ for each of the anti-predator games and $V = 0.1$, $\delta = 0.5$ for each of the hawk-dove games.

Quantitative genetics

In the model underlying Figure 3.4, we consider a sexual population of diploid individuals where each behaviour is governed by multiple loci with small effects. We consider a scenario with one anti-predator and one hawk-dove game. In total there are five different traits (see below), each of which is governed by a set of five unlinked diallelic loci. There is additive interaction within and across loci implying that there are in total 11 equidistant phenotypic values for each trait. The first trait corresponds to the exploration strategy, where the different genotypes correspond to 11 exploration tendencies ranging from 0 to 1 in steps of 0.1. The strategy in the anti-predator (hawk-dove) game is modelled as a norm of reaction (Roff, 2002). The shape of the reaction norm is characterised by two genetically determined parameters a and b such that an individual with exploration intensity x behaves boldly (aggressively) with a probability given by the logistic function $1/(1 + \exp(-b(x - a)))$. The value of a corresponds to the exploration intensity at which both behavioural options (bold-shy and hawk-dove, respectively) are chosen with equal probability while b determines the slope of the reaction norm at $x = a$. As described above, a and b are each encoded by a set of 5 loci with range restrictions $0 \leq a \leq 1$ and $-25 \leq b \leq 25$.

Payoffs are obtained as described above, individuals mate at random, and the number of offspring produced per individual at the end of each year is proportional to the total payoff obtained in that year. With a small probability ($\mu = 2 \cdot 10^{-5}$) a mutation occurs at a randomly chosen locus. When this happens, the affected allele changes into the alternative allele.

ACKNOWLEDGEMENTS

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Appendix

The conclusions in the main text are based on general arguments that are supported by individual-based simulations. We show here that the corresponding simulation results are robust and apply to a broad range of parameter regimes. Throughout we assume that individuals follow the basic life cycle that is illustrated by Figure 3.1A in the main text. In our model, a prerequisite for the evolution of animal personalities is a stable polymorphism of the exploration trait x. We therefore start by demonstrating that the coexistence of superficial and thorough explorers is a stable evolutionary outcome whenever the trade-off between current and future reproduction is convex. We then study the consequences of this dimorphism in exploration traits on the evolution of behavioural strategies in a single anti-predator game and a single hawk-dove game. Here, as in the subsequent sections, we allow individuals to condition their behaviour in these games on their explorative behaviour. For both games the result is that in evolutionary equilibrium superficial explorers will always be at least as risk-prone as thorough explorers and strictly more risk-prone for a broad range of parameter combinations. Finally, we study the evolution of behavioural correlations across games (i.e., one anti-predator and one hawk-dove game) and stable individual differences within games (i.e., two hawk-dove games). We demonstrate that personalities are stable evolutionary outcomes for a broad range of parameter settings.

COEXISTENCE OF EXPLORATION STRATEGIES

As in the main text, we first focus on the situation where individuals play no games. In the simulations, we observed the emergence of a dimorphism in exploration strategies: the investment in exploration is high (even maximal) for part of the population (thorough explorers; $x_h = 1$) while it is low (even minimal) for the rest (superficial explorers; $x_l = 0$). We here show that this is a robust outcome.

Result 1

The dimorphism ($x_h = 1$, $x_l = 0$) is a stable evolutionary equilibrium whenever $\beta > 1$ and $2f_l > f_h > 1$, i.e. whenever the trade-off between current and future reproduction is convex and the intrinsic benefit f_h of obtaining a high-quality resource is high enough to prevent extinction of the population but not high enough to make thorough exploration the dominant strategy.

PROOF

Let n_h and n_l denote the density of age 1 individuals with exploration trait $x_h = 1$ and $x_l = 0$, respectively. Let F_h and F_l be the number of offspring produced by individuals feeding on a high- and a low-quality resource, respectively. The population dynamics of the dimorphic population is then governed by the equations

$$\begin{aligned} n_h(t+1) &= n_h(t-1)F_h(t) \\ n_l(t+1) &= n_l(t)F_l(t) + n_l(t-1)F_l(t) \end{aligned} \tag{1}$$

with $F_h(t) = \dfrac{f_h}{1+\alpha n_h(t-1)}$ and $F_l(t) = \dfrac{f_l}{1+\alpha\left(n_l(t)+n_h(t)+(n_l(t-1)\right)}$.

It is obvious from (1) that in any population dynamical equilibrium $\hat{F}_h = 1$ and $\hat{F}_l = \frac{1}{2}$. The unique population dynamical equilibrium with positive densities for both exploration types is therefore given by

$$\hat{n}_h = \frac{f_h - 1}{\alpha}, \quad \hat{n}_l = \frac{2f_l - f_h}{2\alpha}. \tag{2}$$

For $2f_l > f_h > 1$ a positive equilibrium exists, which is always asymptotically stable. Let us therefore assume that the dimorphic population (x_h, x_l) has settled on its population dynamical equilibrium (2). We now show that this dimorphism is globally invasion stable, as long as $\beta > 1$. In other words, no rare mutant with an exploration intensity $0 < x < 1$ can grow in the population. The population dynamics of a rare mutant with strategy x is given by

$$n(t+1) = n(t)(1-x)^{\beta}\hat{F}_l + n(t-1)\left((1-x)\hat{F}_l + x\hat{F}_h\right). \tag{3}$$

The growth rate $\lambda(x)$ of this mutant is given by the dominant solution of the corresponding characteristic equation, which in view of $\hat{F}_h = 1$ and $\hat{F}_l = \frac{1}{2}$ is given by

$$\lambda^2 - (1-x)^{\beta}\hat{F}_l\lambda - \left((1-x)\hat{F}_l + x\hat{F}_h\right) = \lambda^2 - \tfrac{1}{2}(1-x)^{\beta}\lambda - \tfrac{1}{2}(1-x) = 0. \tag{4}$$

The resident equilibrium is immune against invasion by x if $\lambda(x)$ is smaller than one, the growth rate of the two resident strategies. It is well known (Edelstein-Keshet, 2005) that the dominant solution of the quadratic equation $\lambda^2 + \alpha_1\lambda + \alpha_0 = 0$

is smaller than one in absolute value whenever $|\alpha_1| < 1 + \alpha_0 < 2$. When applied to equation (4), this yields $\frac{1}{2}(1-x)^\beta < \frac{1}{2}(1-x) < 2$ or, equivalently, $\beta > 1$. Hence no mutant strategy $0 < x < 1$ can invade the resident dimorphism if $\beta > 1$. This establishes Result 1.

RISK-AVERSION IN A SINGLE ANTI-PREDATOR GAME

In view of Result 1, from now on we make the simplifying assumption that the population is dimorphic with respect to exploration intensity, with $x_h = 1$ and $x_l = 0$. In this section we study a situation were each individual plays one anti-predator game between year 1 and year 2. In this game, individuals can either be bold or shy. A bold individual receives a payoff b but dies with probability γ whereas a shy individual receives no payoff and always survives. Since the anti-predator game is embedded in a life-history context we imagine b to be relatively small when compared to the life-history payoff (i.e., $b < \hat{F}_l = \frac{1}{2}$).

Individuals can condition their behaviour on their exploration intensity x. The strategy of an individual is therefore a pair $y = (y_h, y_l)$, where y_h (resp. y_l) is the probability of behaving boldly given that the individual has explored its environment with intensity x_h (resp. x_l). We now derive

Result 2
The unique invasion proof equilibrium strategy $y^* = (y_h^*, y_l^*)$ has the following properties:

(a) Superficially exploring individuals are at least as risk-prone as thoroughly exploring individuals, i.e. $y_l^* \geq y_h^*$.

(b) For $\frac{1}{2}\Gamma < b < \Gamma$ superficial explorers are always bold whereas thorough explorers are always shy:

$$\tfrac{1}{2}\Gamma < b < \Gamma \quad \Leftrightarrow \quad (y_h^*, y_l^*) = (0, 1) \tag{5}$$

where $\Gamma = \dfrac{\gamma}{1-\gamma}$ is a measure for the mortality-risk in the anti-predator game.

PROOF
Consider a resident population playing $\hat{y} = (\hat{y}_h, \hat{y}_l)$ at its population dynamical equilibrium, with corresponding payoffs $(\hat{F}_h, \hat{F}_l)$. Let us first consider a mutant with $y = (y_h, \hat{y}_l)$, i.e. a mutant only differing from the resident in its probability of being bold after having explored the environment thoroughly. Since the mutation has no effect in case of superficial exploration we can, without loss of generality,

focus on mutants that are thorough explorers. The population dynamics of such a mutant is characterised by

$$n(t+1) = n(t-1)\left((1-y_h)\hat{F}_h + y_h(1-\gamma)(\hat{F}_h + b)\right) . \tag{6}$$

The growth rate $\lambda = (y, \hat{y})$ of this mutant is therefore

$$\lambda = (y, \hat{y}) = \sqrt{y_h\left((1-\gamma)\,b - \gamma\hat{F}_h\right) + \hat{F}_h} . \tag{7}$$

Note that λ is a strictly monotonic function in the mutant trait y_h.

Using $\hat{F}_h = \dfrac{1-\hat{y}_h(1-\gamma)\,b}{1-\gamma\hat{y}_h}$ it is easy to see that the coefficient of y_h in (7) is positive for $b > \Gamma$ and negative for $b < \Gamma$, where $\Gamma = \dfrac{\gamma}{1-\gamma}$.

Hence $y_h = 1$ is the best response to $\hat{y}$ for $b > \Gamma$ (i.e., the strategy y maximising $\lambda(y, \hat{y})$, while $y_h = 0$ is the best response to $\hat{y}$ for $b < \Gamma$. As a consequence, $y_h^* = 1$ is the unique invasion proof behaviour for $b > \Gamma$ whereas $y_h^* = 0$ is the unique invasion proof behaviour for $b < \Gamma$.

Let us now consider a mutant of the form $y = (\hat{y}_h, y_l)$. In this case we can assume, without loss of generality, that the mutant is a superficial explorer. The population dynamics of such a rare mutant is now governed by

$$n(t+1) = n(t)\,\hat{F}_l + n(t-1)\left((1-y_l)\hat{F}_l + y_l(1-\gamma)(\hat{F}_l + b)\right) . \tag{8}$$

Using $\hat{F}_l = \dfrac{1-\hat{y}_l(1-\gamma)\,b}{2-\gamma\hat{y}_l}$, analogous considerations as above show that $y_l^* = 1$ is the unique invasion proof behaviour for $b > \frac{1}{2}\Gamma$ whereas $y_l^* = 0$ is the unique invasion proof behaviour for $b < \frac{1}{2}\Gamma$. Taken together, these considerations establish Result 2.

RISK-AVERSION IN A SINGLE HAWK-DOVE GAME

In this section we study a situation where each individual plays one hawk-dove game with a randomly chosen partner between year 1 and year 2. If two doves are matched, both get a payoff $V/2$. If a hawk meets a dove, the hawk gets V while the opponent gets 0. If two hawks are matched, one gets V while the opponent gets 0 and moreover dies with probability δ. Now we imagine V to be relatively small compared to the life-history payoffs (i.e., $V < \hat{F}_l = \frac{1}{2}$).

As in the case of an anti-predator game, the strategy of an individual is a pair $z = (z_h, z_l)$, where and are the conditional probabilities with which an individual plays hawk. We now show

Result 3
Any invasion proof equilibrium strategy $z^* = (z_h^*, z_l^*)$ has the following properties:
(a) Superficial explorers are at least as risk-prone as thorough explorers, i.e. $z_l^* \geq z_h^*$.
(b) If the payoff V is sufficiently small, superficial explorers will play hawk with a strictly higher probability than thorough explorers:

$$V < \delta \quad \Rightarrow \quad z_l^* > z_h^* \tag{9}$$

PROOF
Consider a resident population playing $\hat{z} = (\hat{z}_h, \hat{z}_l)$ at its population dynamical equilibrium $(\hat{F}_h, \hat{F}_l, \hat{\pi})$, where $\hat{\pi}$ is the frequency of hawks in the resident population. Again we consider two types of rare mutants in turn. First consider a mutant strategy of the form $z = (z_h, \hat{z}_l)$. As in the previous section we may assume that the mutant is a thorough explorer. This implies that the population dynamics of the rare mutant is given by

$$n(t+1) = n(t-1)\,(z_h \hat{E}_{hawk} + (1 - z_h)\,\hat{E}_{dove}) \ . \tag{10}$$

where $\hat{E}_{hawk}$ and $\hat{E}_{dove}$ is the expected reproductive success of a thoroughly exploring individual given that it plays hawk or dove, respectively. These expectations are given by

$$\hat{E}_{hawk} = (1 - \tfrac{1}{2}\delta\,\hat{\pi})\,\hat{F}_h + (1 - \hat{\pi})V + \hat{\pi}\tfrac{1}{2}V = \hat{F}_h + V - \hat{\pi}\tfrac{1}{2}\,(V + \delta\,\hat{F}_h)$$

$$\hat{E}_{dove} = \hat{F}_h + (1 - \hat{\pi})\tfrac{1}{2}V \ . \tag{11}$$

The growth rate of the mutant is of the form

$$\lambda(z, \hat{z}) = \sqrt{z_h \hat{E}_{hawk} + (1 - z_h)\,\hat{E}_{dove}} = \sqrt{\hat{E}_{dove} + z_h\,(\hat{E}_{hawk} - \hat{E}_{dove})} \ . \tag{12}$$

Note that λ is a strictly monotonic function in the mutant trait z_h, implying that $z_h = 1$ is the best response to $\hat{z}$ if $\hat{E}_{hawk} > \hat{E}_{dove}$, while $z_h = 0$ is the best response if $\hat{E}_{hawk} < \hat{E}_{dove}$. The difference $\hat{E}_{hawk} - \hat{E}_{dove}$ is proportional to $V - \hat{\pi}\delta\,\hat{F}_h$. Using the fact that in population dynamical equilibrium $\hat{F}_h = (1 - \tfrac{1}{2}V(1 + \hat{z}_h - \hat{\pi}))/(1 - \tfrac{1}{2}\delta\,\hat{\pi}\,\hat{z}_h)$, a straightforward calculation yields that $\hat{E}_{hawk} > \hat{E}_{dove}$ whenever $\hat{\pi}^2 + 2C\hat{\pi} - 2/\delta < 0$, where $C = 1/V - \frac{1}{2}$. From this we can conclude:

$$\hat{E}_{hawk} - \hat{E}_{dove} > 0 \quad \Leftrightarrow \quad \hat{\pi} < T_h(V, \delta) = -C + \sqrt{C^2 + 2/\delta}\ . \tag{13}$$

Hence $z_h = 1$ is the best response to the resident strategy if $\hat{\pi}$, the frequency of hawks in the resident population is below the threshold value T_h, and $z_h = 0$ is the best response if $\hat{\pi}$ is above that value.

Next consider a rare mutant strategy of the form $z = (\hat{z}_h, z_l)$. In this case we may assume that the mutant is a superficial explorer. As a consequence, the population dynamics of the mutant is given by

$$n(t+1) = n(t)\,\hat{F}_l + n(t-1)\,(z_h \hat{E}_{hawk} + (1 - z_h)\,\hat{E}_{dove}) \tag{14}$$

with

$$\hat{E}_{hawk} = \hat{F}_l + V - \hat{\pi}\tfrac{1}{2}(V + \delta\,\hat{F}_l)$$

$$\hat{E}_{dove} = \hat{F}_l + (1 - \hat{\pi})\,\tfrac{1}{2}V \tag{15}$$

Using the fact that $\hat{F}_l = (1 - \frac{1}{2}V(1 + \hat{z}_l - \hat{\pi}))/(2 - \frac{1}{2}\delta\,\hat{\pi}\,\hat{z}_l)$, we now get $\hat{E}_{hawk} > \hat{E}_{dove}$ whenever $\hat{\pi}^2 + 2C\hat{\pi} - 4/\delta < 0$, where again C is given by $C = 1/V - \frac{1}{2}$. This yields:

$$\hat{E}_{hawk} - \hat{E}_{dove} > 0 \quad \Leftrightarrow \quad \hat{\pi} < T_l(V, \delta) = -C + \sqrt{C^2 + 4/\delta}\ . \tag{16}$$

Hence $z_l = 1$ is the best response to the resident strategy if $\hat{\pi}$ is below the threshold value T_l, and $z_l = 0$ is the best response if $\hat{\pi}$ is above that value.

Using (13) and (16) we can now characterise the equilibrium structure of the hawk-dove game. Note that $0 < T_h < T_l$ since $\delta > 0$. If $V > \delta$, both thresholds are larger than one and (13) and (16) imply that hawk is the dominant strategy, irrespective of the exploration behaviour. Hence $(z_h^*, z_l^*) = (1,1)$ is the only invasion proof equilibrium strategy.

Let us therefore from now on assume $0 < V < \delta$, which implies $T_h < 1$. Now $z^* = (1,1)$ is no longer an invasion proof equilibrium, since $z_h^* = z_l^* = 1$ implies $\hat{\pi} = 1 > T_h$, which in view of (13) implies that a mutant with $z_h = 0$ could invade the population. $z^* = (0,0)$ is also not invasion proof, since $\hat{\pi} = 0 < T_h < T_l$ implies that the hawk strategy could invade irrespective of the exploration strategy. Any mixed strategy with $0 < z_h^* = z_l^* < 1$ can also not be an invasion proof equilibrium, since equality would have to hold in both (13) and (16) (i.e., $\hat{\pi} = T_h = T_l$), which is impossible in view of $T_h < T_l$. We can conclude that z_h^* and z_l^* differ at equilibrium.

In view of (13) and (16), superficial explorers have a higher tendency to play hawk than thorough explorers. Hence, we can conclude that $z_l^* > z_h^*$. Summarising, we have shown that

$$\begin{aligned} V > \delta \quad &\Rightarrow \quad z_l^* = z_h^* = 1 \\ V < \delta \quad &\Rightarrow \quad z_l^* > z_h^* \end{aligned} \tag{17}$$

which establishes Result 3.

With similar arguments as those given in the proof above one can furthermore show that there exist two thresholds $0 < S_1(V,\delta) < S_2(V,\delta) < \delta$ with the following properties:

$$\begin{aligned} S_2 < V < \delta \quad &\Rightarrow \quad z_l^* = 1,\ z_h^* < 1 \\ S_1 < V < S_2 \quad &\Rightarrow \quad z_l^* = 1,\ z_h^* = 0 \\ 0 < V < S_1 \quad &\Rightarrow \quad z_l^* > 0,\ z_h^* = 0\ . \end{aligned} \tag{18}$$

The explicit characterisation of these thresholds is rather intricate, but they are readily calculated numerically. This is illustrated by Figure 3.A1, where the equilibrium structure of the hawk-dove game is represented as a function of V.

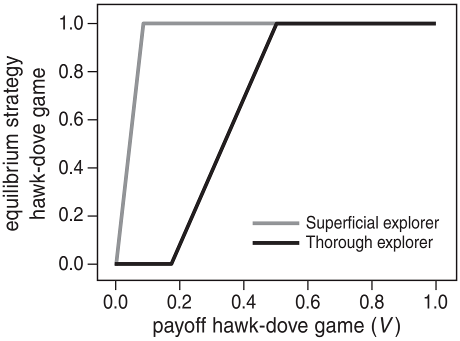

Figure 3.A1 Equilibrium strategies in the hawk-dove game as a function of V, for $f_h = 3.5$, $f_l = 3.0$ and $\delta = 0.5$. Superficial explorers (grey line) are always at least as risk-prone as thorough explorers (black line). For $V < \delta$ superficial explorers play hawk with a strictly higher probability than thorough explorers, for $V > \delta$ playing the pure strategy hawk is a dominant strategy.

EVOLUTION OF BEHAVIOURAL CORRELATIONS

Up to now our analysis has confirmed the life-history principle that individuals with higher fitness expectations (in our case: thorough explorers) should behave in a more cautious way. We here show that the same principle gives rise to the evolution of behavioural syndromes, i.e. correlated behavioural traits across two different games.

Consider the scenario where each individual sequentially plays one anti-predator game and one hawk-dove game between years 1 and 2. Individuals can condition their behaviour on their exploration intensity and a strategy is now a quadruple of the form $s = (y_h, y_l, z_h, z_l)$. We here only sketch how to derive the invasion proof equilibrium strategies of the model. To this end, we consider a resident population with strategy $\hat{s} = (\hat{y}_h, \hat{y}_l, \hat{z}_h, \hat{z}_h)$ at its population dynamical equilibrium $(\hat{F}_h, \hat{F}_l, \hat{\pi})$, where $\hat{\pi}$ is the frequency of hawks in the population. Then we consider four types of rare mutants, each differing in only one component from the resident strategy $\hat{s}$. Take, for example, a mutant of the form $s = (y_h, \hat{y}_l, \hat{z}_h, \hat{z}_h)$. As above, we may assume without loss of generality that the mutant is a thorough explorer. The population dynamics of this mutant is then given by

$$n(t+1) = n(t-1)\,(y_h \hat{E}_{bold} + (1-y_h)\,\hat{E}_{shy}) \tag{19}$$

where $\hat{E}_{bold}$ and $\hat{E}_{shy}$ is the expected reproductive success of a thoroughly exploring individual given that it plays bold or shy, respectively. The expected payoff from the hawk-dove game is $\hat{z}_h = (1 - \frac{1}{2}\hat{\pi})V + (1 - \hat{z}_h)(1 - \hat{\pi})\,\frac{1}{2}\,V = (1 + \hat{z}_h - \hat{\pi})\frac{1}{2}\,V$. Therefore these expectations are given by

$$\begin{aligned} \hat{E}_{bold} &= (1-\gamma)\big((1 - \tfrac{1}{2}\delta\,\hat{\pi}\,\hat{z}_h)(\hat{F}_h + b) + (1 + \hat{z}_h - \hat{\pi})\tfrac{1}{2}V\big) \\ \hat{E}_{shy} &= (1 - \tfrac{1}{2}\delta\,\hat{\pi}\,\hat{z}_h)\,\hat{F}_h + (1 + \hat{z}_h - \hat{\pi})\tfrac{1}{2}V\ . \end{aligned} \tag{20}$$

The growth rate of the mutant

$$\lambda(s, \hat{s}) = \sqrt{y_h \hat{E}_{bold} + (1-y_h)\,\hat{E}_{shy}} = \sqrt{\hat{E}_{shy} + y_h\,(\hat{E}_{bold} - \hat{E}_{shy})} \tag{21}$$

is again a strictly monotonic function in the mutant trait y_h. If $\hat{E}_{bold} > \hat{E}_{shy}$, $y_h = 1$ is the best response to $\hat{s}$, while $y_h = 0$ is the best response if $\hat{E}_{bold} < \hat{E}_{shy}$. Analogous considerations characterise the best responses with respect to the other three traits.

Having derived the best response structure, all invasion proof equilibrium strategies can be calculated. Each such equilibrium s^* has to be a best response to itself, i.e. each of the four strategy components of s^* has to be a best response to the resident environment $\hat{s} = s^*$.

Based on these conditions we numerically calculated the evolutionary equilibria $s^* = (y_h^*, y_l^*, z_h^*, z_l^*)$ as a function of the payoff in the hawk-dove game V and the payoff in the anti-predator game b (Figure 3.A2). First note that behavioural correlations across the two games are only possible if there is behavioural variation in both games. We know from Results 2 and 3 that variation in a single anti-predator game occurs for $\frac{1}{2}\Gamma < b < \Gamma$ and in single hawk-dove game for $V < \delta$. The corresponding area in parameter space is bordered by black lines in the figure. The grey area indicates the parameter combinations for which we find behavioural syndromes, i.e. behavioural correlations across the two games. The white area in the figure corresponds to payoff configurations where all individuals play the same pure strategy in at least one of the two games, irrespective of their exploration behaviour.

We stress that these results are in perfect agreement with the individual-based simulations that we performed.

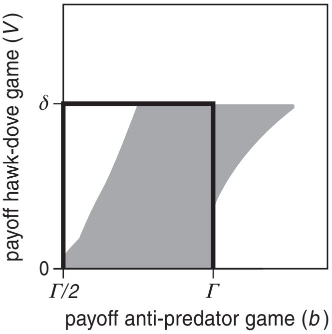

Figure 3.A2 The combinations of payoffs in the anti-predator and the hawk-dove game that result in the evolution of behavioural syndromes, i.e. positive behavioural correlations across two different games (grey area). For payoff combinations where we did not find positive correlations, at least one of the games had a dominant pure strategy, precluding behavioural variation in relation to exploration behaviour. Evolutionary equilibria were calculated numerically for $f_h = 3.5$, $f_l = 3.0$ and $\gamma = 0.1$ and $\delta = 1/2$, where $\Gamma = \gamma/(1-\gamma)$. The black lines border those payoff combinations for which thorough and superficial explorers differ in equilibrium behaviour in both of the individual games.

EVOLUTION OF TIME-CONSISTENT BEHAVIOUR

Our approach for analysing the evolution of stable behavioural differences within the same game follows the approach described in the preceding section. We here consider the scenario where each individual plays two hawk-dove games between years 1 and 2. A strategy is now a quadruple of the form s = $(z_{h,1}, z_{l,1}, z_{h,2}, z_{l,2})$. The resident population at its population dynamical equilibrium is now characterised by $(\hat{F}_h, \hat{F}_l, \hat{\pi}_1, \hat{\pi}_2)$ where $\hat{\pi}_1$ $(\hat{\pi}_2)$ is the population frequency of hawks in the first (second) hawk-dove game. As above, we derive the best response structure by considering four types of rare mutants. Based on these conditions we numerically calculated the evolutionary equilibria $s^* = (z^*_{h,1}, z^*_{l,1}, z^*_{h,2}, z^*_{l,2})$ as a function of the payoff V_2 in the first hawk-dove game and the payoff in the second hawk-dove game (Figure 3.A3).

First note that, analogously to the results in Section 4, stable behavioural differences are only possible if there is behavioural variation in each of the hawk-dove games. We know from Result 3 that variation in a single hawk-dove game occurs for $V < \delta$. The corresponding area in parameter space is bordered by black lines. The grey area indicates the parameter combinations for which we find stable behavioural differences, i.e. positive behavioural correlations across the two hawk-dove games. The white area in the figure corresponds to payoff configurations where all individuals play the same pure strategy in at least one of the two games, irrespective of their exploration behaviour. Again, these results are in perfect agreement with the individual-based simulations that we performed.

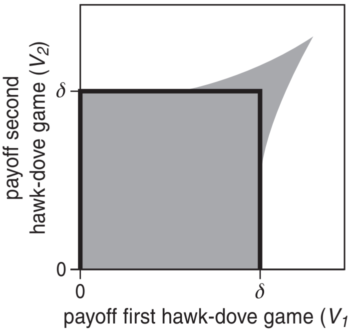

Figure 3.A3 The combinations of payoffs that give rise to stable behavioural differences within contexts, i.e. positive correlations in two subsequently played hawk-dove games (grey area). For payoff combinations where we did not find positive correlations, at least one of the games had a dominant pure strategy, precluding behavioural variation in relation to exploration behaviour. Evolutionary equilibria were calculated numerically for $f_h = 3.5$, $f_l = 3.0$ and $\delta = 1/2$. The black lines border those payoff combinations for which thorough and superficial explorers differ in equilibrium behaviour in both of the individual hawk-dove games.

Intermezzo

1. Do animal personalities emerge?

Max Wolf
G. Sander van Doorn
Olof Leimar
Franz J. Weissing

Nature 451: E9–E10, 2008

2. Evolution of animal personalities

Max Wolf
G. Sander van Doorn
Olof Leimar
Franz J. Weissing

Nature 450: E5–E6, 2007

The publication of the previous Chapter 3 (Wolf *et al.*, 2007a) led to some scientific discussion among researchers including the publication of two 'Brief communications arising' in Nature from colleagues of us, each of which followed up by a brief reply from ourselves. I chose to reproduce both the original responses to our paper and our replies to these responses. The chronologically second response (Massol & Crochet, 2008; Wolf *et al.*, 2008a) addresses an interesting technical point concerning the emergence of polymorphisms. The chronologically first response (McElreath *et al.*, 2007; Wolf *et al.*, 2007b) addresses the feedbacks between risky action and future fitness expectations, an issue that we will be investigated in depth in Chapter 4 of this thesis.

DO ANIMAL PERSONALITIES EMERGE?

F. Massol & P. Crochet *Nature* 451: E8–E9 (2008)

The evolution of animal personalities is a topic of primary importance in behavioural ecology. An intriguing empirical fact is the consistency of animal responses to repeated stresses or threats. Wolf *et al.* propose an evolutionary model to explain the emergence of consistent personalities (Wolf *et al.*, 2007a). They show that a population dimorphism for an exploration trait implies the existence of behavioural syndromes, such as decreased aggressiveness and the boldness of 'thorough explorers'. This finding helps explain how animal responses can be consistent, despite the seeming advantages of flexible responses. However, we contend that the emergence of a dimorphism depends critically on the intensity of the trade-off between exploration investment and first-year fecundity.

Wolf *et al.* (2007a) introduced a model of temporal allocation to fecundity to answer questions related to animal personalities. Their model is based on four ingredients: individuals reproduce twice during their lives; two habitats are available (bad and good) and influence the fecundity of individuals (individuals in bad habitats produce fewer offspring); all individuals first reproduce in a bad habitat; individuals can trade off some of their fecundity during their first reproduction event to find a better habitat to reproduce in the second year. Thus, 'thorough explorers' bet on their second reproduction event, while 'superficial explorers' reproduce equally well at all opportunities. The authors prove that a population dimorphism of the exploration trait influences the evolution of behavioural responses in hawk–dove and predator–prey games. Without introducing any constraints on responses to these games, they predict the emergence of two extreme syndromes, with superficial explorers being consistently bold and aggres-

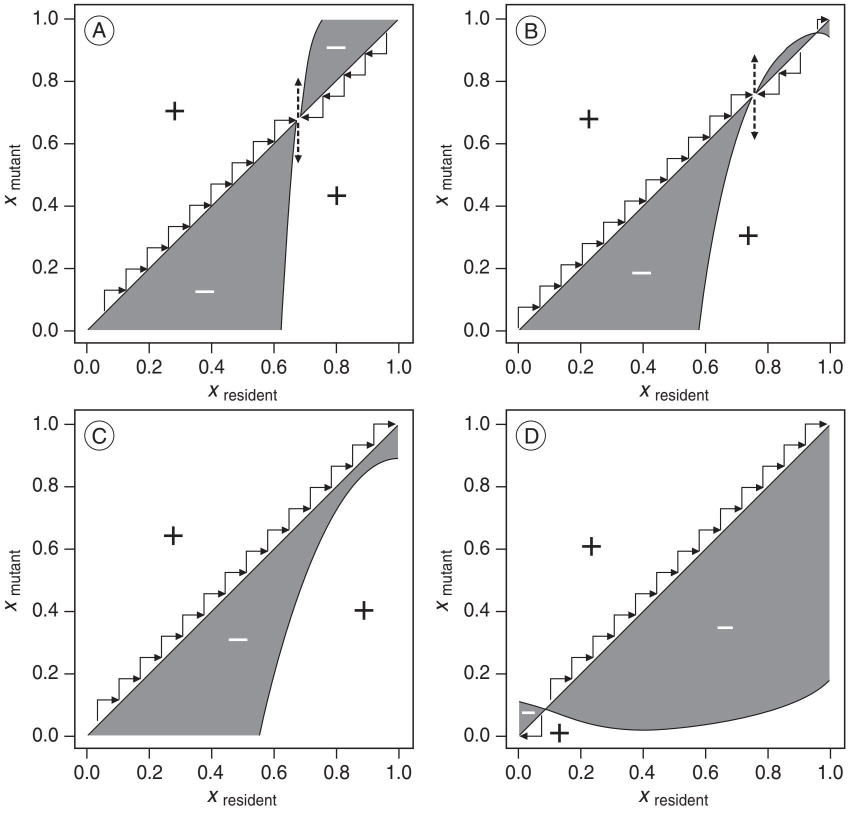

Figure I.1 Pairwise invasibility plots. These diagrams show which mutant strategies can invade in an initially monomorphic situation. The x axis represents the initial exploring strategy (x_{resident}), and the y axis, the mutant strategy (x_{mutant}). White regions indicate cases where the mutant can invade (+), while black regions (–) represent cases where an initially rare mutant never invades. The solid arrows suggest possible evolutionary trajectories under the assumption of small mutation effects. Dashed arrows indicate evolutionary branching after monomorphic evolution. Parameter values: in all panels $\alpha = 0.005$, $f_h = 3.5$ and $f_l = 3.0$; in (A) $\beta = 1.25$ (as in Wolf *et al.*, 2007a); in (B) $\beta = 1.6$; in (C) $\beta = 1.8$; and in (D) $\beta = 10$.

sive and thorough explorers, shy and non-aggressive. These results encompass the predictions of Bishop–Cannings' theorem (Bishop & Cannings, 1976), which states that strategies yielding stochastic responses cannot be evolutionarily stable. The authors take a step further by showing the consistency of responses across different games.

Despite its interesting conclusions, this model has a weak point. The conclusions of Wolf *et al.* are based on the existence of a population dimorphism of the exploration strategy. Although the authors do prove that a dimorphic population is protected from further invasions, they leave unaddressed the issue of its emergence. We looked at the fitness of a rare mutant in an initially monomorphic population, as is classically done in adaptive dynamics studies (Hofbauer & Sigmund, 1990; Nowak & Sigmund, 1990; Dieckmann & Law, 1996; Geritz *et al.*, 1998; Geritz *et al.*, 1999; Waxman & Gavrilets, 2005). A pairwise invasibility plot (Geritz *et al.*, 1998; Geritz *et al.*, 1999; Waxman & Gavrilets, 2005) confirms that the parameter set investigated by the authors ($\alpha = 0.005$, $f_h = 3.5$, $f_l = 3.0$, $\beta = 1.25$) leads to a dimorphism through a branching point (Figure I.1A). However, this result depends critically on parameter β, which controls the trade-off between exploration investment and first-year fecundity: for higher β, pairwise invasibility plots display a branching point, an evolutionary repellor and an evolutionarily stable strategy ($\beta = 1.6$, Figure I.1B), two evolutionarily stable strategies and an evolutionary repellor ($\beta = 10$, Figure I.1D) or only one evolutionarily stable strategy ($\beta = 1.8$, Figure I.1C). These situations do not generically lead to a stable dimorphism.

Proving that a dimorphic coalition is protected from invasions or that it emerges through evolutionary branching are different tasks (Slatkin, 1980; Maynard Smith, 1989; Dieckmann & Law, 1996). Wolf and colleagues' proof deals only with the former. We have shown that the emergence of a dimorphism happens only under restricted conditions. The emergence of animal personalities might thus be limited by extrinsic constraints, for example, the difficulty of both rearing offspring and looking for a better habitat. Finally, branching points in haploid models cannot be literally translated as the emergence of dimorphism in diploid sexually reproducing organisms because recombination and the absence of assortment or dominance can prevent the evolution of genotypic bimodality (Waxman & Gavrilets, 2005).

DO ANIMAL PERSONALITIES EMERGE? – REPLY

M. Wolf, G. S.van Doorn, O. Leimar & F. J. Weissing *Nature* 451: E9–E10 (2008)

The more an individual stands to lose, the more cautious it should be. In a recent contribution (Wolf *et al.*, 2007a) we have shown that this basic principle gives rise to consistent individual differences in risk related behaviour whenever individuals differ in future fitness expectations. To illustrate this, we considered a model where differences in fitness expectations result from a trade-off between current and future reproduction. Massol and Crochet argue (Massol & Crochet, 2008) that the emergence of such differences depends on the shape of this trade-off. This claim is based on the technical argument that our model has a 'branching point' only for a limited range of the trade-off parameter β . In contrast, we show here that the emergence of individual differences is a robust phenomenon that does not depend on such details. Our analysis illustrates the important insight that a branching point is not needed for the emergence of polymorphism.

In the Supplementary Information (Wolf *et al.*, 2007a) to our paper we prove that a dimorphic population consisting of the two extreme exploration strategies $x = 0$ and $x = 1$ is stable. This is reflected by the fact that in all pairwise invasibility plots for $\beta > 1$ (e.g., those shown in Massol & Crochet, 2008)a mutant with strategy $x_m = 0$ can invade in an $x = 1$ resident population, and vice versa. Yet it is not self-evident that such a stable dimorphism is attainable from a monomorphic ancestral state. According to adaptive dynamics theory (Geritz *et al.*, 1998) a stable polymorphism will evolve in the presence of a branching point. Massol and Crochet (2008)correctly argue that our model only has a branching point if the trade-off is moderate (e.g., $\beta = 1.25$, Figure I.2A) but not if it is very strong (e.g., $\beta = 2.0$, Figure I.2C). Nevertheless, our individual-based simulations (Wolf *et al.*, 2007a) led us to conclude that a dimorphism emerges for all $\beta > 1$. In other words, a dimorphism can evolve in the presence (Figure I.2B, $\beta = 1.25$) but also in the absence of a branching point (Figure I.2D, $\beta = 2.0$).

To substantiate this result we ran more than 1000 additional individual-based simulations with varying initial conditions and varying β-values. To be specific, 100 β-values were randomly drawn from the uniform distribution on the interval $1 < \beta < 10$. For each of these β-values we ran 11 simulations with initial x-values between 0.0 and 1.0 in steps of 0.1. The mutation rate was $\mu = 1\times10^{-5}$, and the mutational step sizes were drawn from a normal distribution with mean zero and standard deviation 0.3. The outcome was unambiguous: the stable dimorphism of the two extreme strategies $x = 0$ and $x = 1$ emerged in *all* these simulations, irrespective of the initial conditions and the value of β .

How can this seeming discrepancy with the adaptive dynamics approach be explained? Adaptive dynamics analysis often makes two important assumptions (Geritz *et al.*, 1998), which may be considered a worst-case scenario for the emergence of polymorphism. First, populations have a low level of diversity since the resident population is only rarely challenged by mutants. Second, mutations have small phenotypic effect. The scope of these assumptions has been debated (Barton & Polechova, 2005; Dieckmann & Doebeli, 2005; Waxman & Gavrilets, 2005) and neither of them is strictly satisfied in our individual-based simulations. First, several mutants are typically present simultaneously, since new mutations often occur before old ones are ousted from the population. Second, mutational effect sizes are drawn from a normal distribution implying that mutations of large effect are rare but sometimes occur. The consequence of these differences in assumptions can be illustrated by the pairwise invasibility plot in Figure I.2C. When mutations are very rare and have small effects one would predict (as Massol and Crochet do) that evolution gives rise to the monomorphic population $x = 1$, which can be considered an evolutionary trap. Yet, as can also be seen in this figure, a mutant with a sufficiently deviant phenotype ($x_m < 0.83$) can invade the population and trigger the evolution to the stable dimorphism.

We think that the assumptions used in our individual-based simulations are quite realistic. It is well known that natural populations tend to contain considerable amounts of standing genetic variation, and widely accepted approaches like quantitative genetics (Lynch & Walsh, 1998) are based on this fact. At present, the distribution of mutational effect sizes is only known for a small number of empirical examples (Barton & Keightley, 2002; Eyre-Walker & Keightley, 2007). The limited evidence available indicates that such distributions seem to have 'fat tails,' suggesting that mutations with larger effect sometimes occur. In fact, this is not implausible. The Evo-Devo revolution (Carroll, 2005) has provided plenty of examples where single mutations (e.g. in a regulatory pathway) have a huge phenotypic effect. Traditionally it is assumed that such mutations can be neglected since they generally result in disintegrated phenotypes with low fitness (Fisher, 1930). But this is not necessarily the case. Consider, for example, a switching device that switches between two well integrated phenotypes (in our model: superficial and thorough exploration). It is easily conceivable that a mutation that has a large effect on the position of the switch (e.g., one that knocks out one of the two phenotypes, thereby leading to the unconditional expression of the alternative phenotype) gives rise to a high-fitness individual.

The issues raised by Massol and Crochet (2008) are interesting and important, but they should be put into the proper perspective. Their critique does not touch upon the main thrust of our theory, which is that individual differences in future

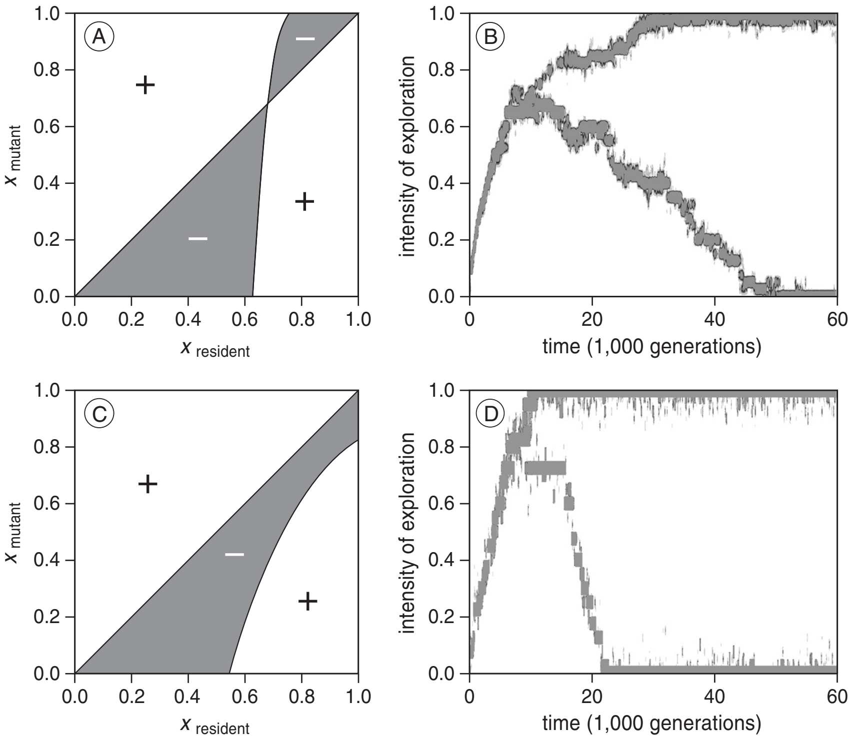

Figure I.2 Emergence of a polymorphism in the presence and in the absence of a branching point. Pairwise invisibility plots are shown together with corresponding individual-based simulation results for two values of the trade-off parameter β. In (A) and (B), $\beta = 1.25$, the standard parameter setting used in (Wolf *et al.*, 2007a); in (C) and (D), $\beta = 2.0$. The white regions (+) in the pairwise invasibility plots correspond to mutant strategies that can invade a given resident population, while dark grey regions (–) indicate mutants that cannot invade. According to adaptive dynamics theory (Geritz *et al.*, 1998), configuration (A) is a branching point leading to the emergence of a polymorphism. In (C), there is a single evolutionary attractor at $x = 1$, and a branching point does not exist. Despite of these differences, a dimorphism evolves in the individual-based simulations for both scenarios. In scenarios without a branching point (such as C) this happens whenever mutational step sizes are not too small. Here the mutation rate was $\mu = 3\mathrm{x}10^{-4}$ and mutational step sizes were drawn from a normal distribution with mean zero and standard deviation.

reproductive value give rise to consistent individual differences in risk-related behaviour. We worked out (Wolf *et al.*, 2007a) one (potentially important) model for the emergence of differences in future reproductive value, but we stressed that there are more mechanisms and processes leading to such differences. In all these cases, our theory predicts the emergence of personalities.

EVOLUTION OF ANIMAL PERSONALITIES?

R. McElreath, B. Luttbeg, S.P. Fogarty, T. Brodin & A. Sih *Nature* 450: E5 (2007)

Wolf *et al.* (2007a) propose a model to explain the existence of animal personalities, consistent with behavioural differences among individuals in various contexts (Gosling, 2001; Sih *et al.*, 2004a; Sih *et al.*, 2004b) —their explanation is counter-intuitive and cogent. However, all models have their limits, and the particular life-history requirements of this one may be unclear. Here we analyse their model and clarify its organismal scope.

Under some conditions, Wolf *et al.* (2007a) find consistent behavioural differences between individuals that reproduce early in life and those that delay reproduction to explore their habitats instead to enhance future reproduction. Non-explorers that reproduce early in life later become bold and aggressive, whereas exploratory individuals with greater future reproductive potential are shy and unaggressive. These differences are caused by asset protection (Clark, 1994) where individuals with greater future fitness take fewer risks that would jeopardize that fitness.

Asset protection, however, is a negative feedback process that, given time, makes individuals more alike, not less. In Clark's original asset protection paper (Clark, 1994), many decisions are made over an animal's lifespan. Over time, individuals tend towards similar behaviour, despite any initial differences in assets, because those with assets take few risks and acquire little new fitness. Those without high assets take more risks and (unless they die trying) acquire new fitness assets that become worth protecting.

If, in the model of Wolf *et al.*, individuals experience many hawk-dove encounters, successful hawks would eventually accumulate enough fitness for playing dove to become their optimal behaviour. Given time to accrue new assets, behavioural types would converge. Two particular conditions that could prevent this convergence are: animals with very short lives might not have time to change their assets sufficiently to cause changes in behaviour; and early life-history choices can have such large fitness consequences that subsequent bold and aggressive behaviour has relatively little influence on assets. Notably, these conditions do not seem to fit the maintenance of stable personalities in long-lived organisms such as humans.

The model of Wolf *et al.* requires bold/aggressive contexts not to dominate one another in fitness consequences, otherwise the negative feedback of asset protection will apply at this smaller scale (Supplementary Fig. A2 of Wolf *et al.*, 2007a: in the square in which behavioural correlations could evolve, there is a wedge-shaped region without correlation between the hawk–dove and predator games).

We reproduced their model and found that, in this region, thorough explorers are less aggressive than non-explorers, but no one is bold. Without the hawk-dove game, explorers would be shy and non-explorers bold, but when the hawk-dove game has sufficiently higher fitness consequences than the boldness game, all individuals are shy to eliminate the risk of dying before the fitness windfall from the hawk-dove game. This is the asset-protection principle, working on the scale of the low-fitness behavioural contexts, producing behavioural inconsistency, unless the contexts do not dominate one another.

An alternative way of explaining behavioural consistency and correlations is through positive (not negative) feedback. For example, if thorough explorers gain assets (energy, size, knowledge) that improve their abilities to escape predators or to win fights, then we might find positive correlations between exploration, boldness and aggressiveness. Additional behaviour would positively feed back on state, maintaining differences in assets and behavioural types. What is needed next is a unified modelling framework in which both negative and positive state feedback, as well as other mechanisms, can be compared.

EVOLUTION OF ANIMAL PERSONALITIES? – REPLY

M. Wolf, G. S.van Doorn, O. Leimar & F. J. Weissing *Nature* 450: E5–E6 (2007)

The evolution of animal personalities is still poorly understood. The emergence of consistent individual differences is relatively easy to envisage when initial differences in behaviour are reinforced by positive feedback mechanisms. Such reinforcement might act through learning or training, or through behaviour-induced changes in an individual's condition (Rands *et al.*, 2003) or environment (Hemelrijk & Wantia, 2005). However, positive feedback is not required. We showed that, even without such feedback, differences in fitness expectations result in consistent differences in risk-taking behaviour (Wolf *et al.*, 2007a). This was illustrated by a model that, for simplicity, considers a short life history. McElreath *et al.* (2007) argue that our results extend to long-lived organisms only under specific conditions. Although we agree that the full scope and limitations of our model still have to be mapped out, we believe that our arguments are also relevant to long-lived organisms.

Our theory is based on the principle of asset protection (Clark, 1994): the more an individual stands to lose, the more cautiously it should behave. McElreath *et al.* (2007) argue that asset protection entails a negative feedback that tends to erode individual differences. This may indeed be the case if large assets can be accumulated by risky behaviour: risk-proneness while accumulating assets would then be followed by risk-aversion while protecting the acquired assets. However, the analysis of McElreath *et al.* is incomplete for at least two reasons.

First, not all payoffs should be considered as assets. Payoffs can be either spent immediately in current reproduction or invested into future reproductive potential. Only the latter, resulting in an increase in future reproductive value (Williams, 1966), corresponds to assets. Consequently, when the payoffs of risky games only affect immediate reproduction, no asset accumulation takes place and there is no negative feedback eroding individual differences. There might even be positive feedbacks, enhancing individual differences, if risky payoffs tend to be immediate whereas non-risky payoffs tend to increase the future reproductive value.

Second, McElreath *et al.* extrapolate our model to long-lived organisms in a one-sided manner. They assume that differences in assets due to life-history decisions only occur once in an individual's lifetime whereas the number and importance of risky games increases with life expectancy. There are certainly examples where an individual's fate is governed by a single life-history switch. Yet, such 'career decisions' (Ens *et al.*, 1995) are typically associated with long-lasting fitness consequences that are not eroded by everyday risky behaviour. More commonly, however, life-history decisions (such as thorough or superficial exploration) have to be taken repeatedly throughout an individual's life. As a consequence, assets are not only eroded but can also be built up.

In conclusion, the potential of negative feedback to erode individual differences is substantially smaller than McElreath *et al.* suggest. We therefore maintain that asset protection furthers the understanding of animal personalities in both short-and long-lived organisms. Yet, there are certainly situations in which negative feedbacks as described by McElreath *et al.* are important. In such situations, a switch might occur from a risk-prone to a risk-averse personality. Indeed, personalities are not always stable from the cradle to the grave. Take our own species, where young individuals with a risky lifestyle become more cautious later in life (when assets are at stake). Similarly, hover wasps switch from risk-prone to risk-averse behaviour once they are close enough to the breeding position (Field *et al.*, 2006). Our theory accounts for such switches associated with asset accumulation and it produces testable predictions for their occurrence. Hence, even in the presence of negative feedbacks, the principle of asset protection is crucial for understanding animal personalities.

Chapter 4

Animal personalities
and the divergence of life histories

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Unpublished manuscript

ABSTRACT

Several prominent personality traits that are described in the literature are related to risk-taking behaviour. Individuals that are willing to take risks in one context tend be risk-prone in different contexts and such differences tend to be consistent for some period of time. In a previous paper we showed that such differences can be understood in terms of asset-protection: individuals with low future fitness expectations have little to lose and should therefore be consistently more risk-prone than individuals with higher expectations. Our previous analysis focussed on how differences in fitness expectations select for consistent differences in suites of correlated behaviours. Risky actions, however, affect the fecundity and mortality profile of individuals and thus feed back on the fitness expectations of individuals. Such feedbacks become important whenever initial differences in fitness expectations are small. We here provide a general analysis investigating the effects of such feedbacks on the emergence and stability of personalities. Our results show that, dependent on the timing of the cost and the benefits of the risky actions, two qualitatively different scenarios are possible. First, risky choices are associated with mortality and fecundity effects that act to decrease prior differences in the willingness to take risks (negative feedback). Risk-averse individuals get more risk-prone and vice-versa. Second, risky choices are associated with mortality and fecundity effects that that act to increase prior differences in the willingness to take risks (positive feedback). Interestingly, in the presence of positive feedbacks, selection can result in the coexistence of consistently risk-prone and risk-averse behavioural types even in the absence of initial differences in fitness expectations.

INTRODUCTION

The evolution of animal personalities is a topic of primary importance in behavioural ecology, yet poorly understood (Wilson, 1998; Dall *et al.*, 2004; Sih & Bell, 2008). Many personality traits are related to risk-taking behaviour. A good example for this is the so called boldness-aggressiveness syndrome which has been described for many animal species (Sih *et al.*, 2004b) including fish (Huntingford, 1976; Bell & Stamps, 2004), birds (Groothuis & Carere, 2005) and rodents (Koolhaas *et al.*, 1999). Individuals differ consistently in their aggressiveness towards conspecifics and these differences are positively correlated with differences in the boldness in response to a predator and activity levels in unfamiliar environments. Many other cases of consistent individual differences in risk-taking behaviour have been described, including differences in risky helping behaviour in cooperatively breeding species (Cant & Field, 2001; Cant & Field, 2005), differences in risky defensive behaviour (Cronin & Field, 2007), differences in risky parental care (Ghalambor & Martin, 2001) and the observation that many risky traits (e.g., risky drinking, smoking and driving) tend to be positively correlated in humans (Petridou *et al.*, 1997). Why did evolution give rise to such differences, that is, why are some individuals consistently more risk-prone than others, across contexts and over time?

In a previous paper (Wolf *et al.*, 2007a) we have shown that consistent differences in suites of risky behavioural traits can be explained by the asset-protection principle (Houston & McNamara, 1989; Clark, 1994). The basic argument is as follows. According to life-history theory individuals should adjust their risk-taking behaviour to their residual reproductive value, i.e. their expected future fitness. Individuals with relatively high expectations should be relatively risk-averse, since they have to survive in order to realize those expectations. By the same reasoning, individuals with relatively low expectations should be relatively risk-prone since they have little to lose. Since this applies to all kinds of risky behaviours, consistent differences in fitness expectations should give rise to consistent differences in suites of risky behaviours.

Our previous paper focussed on the question how differences in fitness expectations shape differences in suites of correlated behavioural traits. Risky actions, however, affect the fecundity and mortality profile of individuals and thus feed back on the fitness expectations of individuals. The present paper provides a more general analysis of asset protection and animal personalities that takes these feedbacks into account.

To see the importance of such feedbacks consider first a scenario where risky actions act to increase the future fecundity of risk-prone individuals (McElreath *et* *al.*, 2007; Sih & Bell, 2008). Since individuals with relatively low fitness expectations should be more willing to take risky actions than individuals with relatively high expectations, the former will accumulate benefits in terms of future fecundity relative to the latter, which, in turn increase their future fitness expectations. In other words, individual differences in fitness expectations give rise to behavioural differences that act to decrease the initial differences in fitness expectations. Importantly, whenever the initial differences in fitness expectations are small, such negative feedbacks should tend to erode the basis of behavioural differences among individuals over time.

Consider next a situation with a trade-off between the immediacy of benefits associated with behavioural actions and their risk. To put it simple, risky actions act to increase current fecundity while less risky actions act to increase future fecundity. Individuals that avoid risks in such a situation will increase their future fecundity and thus their future fitness expectation, relative to individuals that are more risk-prone. In other words individual differences in fitness expectations give rise to behavioural differences that act to increase initial differences in fitness expectations. Importantly, such positive feedbacks act to stabilize behavioural differences among individuals over time, even more, such feedbacks should give rise to consistent differences even when differences in fitness expectations are initially absent.

The above examples illustrate that feedbacks from risky actions on the fitness expectations of individuals can play an important role for the emergence and stability of animal personalities. They also illustrate that the timing of costs and benefits associated with risky choices will affect whether feedbacks act to stabilize or erode behavioural differences over time (Wolf *et al.*, 2007b).

The present paper aims to investigate these verbal arguments in detail. Our analysis provides a quantitative understanding of the feedbacks involved in asset-protection and the conditions under which negative and positive feedbacks are to be expected. In Section 2, we present a simple toy model that illustrates how the presence of positive feedbacks selects for cross context consistency in risk-taking behaviour, even in the absence of initial differences in fitness expectation. In Section 3, the main part of the paper, we investigate the feedbacks involved in risk-taking behaviour in a general age-structured population context.

A SIMPLE MODEL

Risk can be defined as the willingness of individuals to put their life in danger in order to gain benefits. Although this definition is intuitive, it is difficult to apply in a life history context; it is not immediately clear how benefit and danger should be weighed relative to one another. We therefore adhere to a somewhat broader definition, and consider a decision risky if it increases the variance of lifetime reproductive success. In the example model that follows, we consider two life-history decisions that are risky by this definition, and ask whether selection favours consistency in risk-taking. In other words, we will attempt to evaluate the fitness of individuals that consistently choose the safe or the risky option, relative to that of individuals that combine the safe option for one of the decisions with the risky option for the other.

The two life-history decisions that have to be made early in life. The first decision involves a choice between two foraging strategies. Individuals can choose to forage in a predator-rich environment or avoid predation by adopting a cautious strategy, for example, by shunning open areas and foraging in dense vegetation. We assume that the mortality rate due to predation is size dependent; predators are more successful in attacking small individuals. As a consequence, foraging under predation risk is associated with high mortality early in life. Avoiding predation by foraging in dense vegetation, on the other hand, is associated with a higher probability of attack by parasites. We assume that parasites induce mortality at a rate that does not vary with an individual's age. As a result of the difference between these mortality profiles, foraging under predation risk is associated with a higher variance of life-time reproductive success than avoiding predation, and should therefore be qualified as risky. The second decision involves a choice between queuing for a high-quality breeding territory or settling immediately at an inferior breeding site. Individuals that choose to settle at a low-quality site can start to reproduce as soon as they are mature. Individuals that queue for a high-quality breeding territory have to wait until a high-quality site becomes available, once they obtain a territory, however, they produce more offspring per breeding season than individuals that chose not to queue. Accordingly, queuing is associated with increased reproductive success later in life. Whether a queuing individual will realize a high reproductive success is conditional on survival. Hence, queuing is associated with a higher variance of reproductive success, and it can therefore be classified as a risky choice.

In many cases, particular life-history choices are associated with initial investments that are at least partly when an individual switches between alternative options. Examples of such investments include the cost of establishing a position in a dominance hierarchy in queues for high-quality breeding sites (Ens *et al.*, 1995), the costs of building a nest and finding a mate once a territory has been occupied (Wootton, 1984), or the initial reduction in foraging efficiency of an individual that adopts a new strategy to find food, which only improves as the individual gains experience (Rosenzweig & Bennett, 1996). Without explicitly modelling these initial investments, we assume that they are large enough to prevent individuals from switching once they have made their life-history decisions. This allows us to model the decisions as once-in-a-life-time events. Switching costs can be incorporated in the general analysis that is developed in Section 3, and the analytical results presented there can be extended to examine interactions between arbitrarily complex (repeated) life-history decisions.

A necessary condition for the presence of a behavioural correlation between two life-history decisions is that there exists behavioural variation for each decision. Negative frequency-dependent selection is a likely mechanism to support such behavioural variation. Under the influence of frequency-dependent selection, one expects a population to evolve to an equilibrium state where the different actions for each decision have the same fitness expectation. Whether, in such an equilibrium, also every possible combination of choices for the two life-history decisions gives the same payoff depends on the presence of interactions between the two life-history decisions. The nature of such interactions is not immediately obvious, since the two decisions in our example act primarily on different fitness components that combine in a complicated way to determine life-time reproductive success. Moreover, if fitness interactions are present, it is not immediately obvious whether it is beneficial to combine queuing with foraging under predation risk or with predator avoidance. To address this question, we ran individual-based computer simulations of the life-histories of a population of individuals with genetically encoded strategies for the foraging and queuing decisions.

Resource consumption and growth

All individuals are born with initial size $s_0 = 0.05$ and grow during their lifetime until they reach their maturation size s_m. The rate of growth dependents on the amount of resources that an individual consumes. We assume that the two different foraging strategies are associated with different habitats with independently regulated resources, that is, individuals compete for resources only with other individuals that use the same foraging strategy. We follow the common assumption that individual resource intake scales with body size to the second power, and that maintenance costs scale with body size to the third power. The net-intake of resources per time step, c_i, of an individual i with body size s_i is thus given by

$$c_i = \frac{s_i^2}{1 + \alpha \sum_j s_j^2} - \beta s_i^3 \tag{1}$$

where the parameters α and β are set by the rates of resource renewal and decay, the maximum intake rate of individuals and the cost of maintenance per unit of body mass. Together, these parameters determine the rate of growth and the number of individuals that can be supported in each habitat. The sum in the denominator of the first term on the right hand side of equation (1) is over all individuals that forage in the same habitat as individual i . In our simulations we used $\beta = 1$ and we choose α such that the total population size equilibrated at around 24,000 individuals.

Individuals that are below their maturation size invest all of their surplus energy into growth, such that the size of the individual at the next time step increases by c_{i} . The individual stops growing when it reaches maturation size, and from that point onwards invests all surplus energy into reproduction.

Reproduction

The fecundity of a mature individual $F_i = b_i\, c_i$ is proportional to its net resource intake, but the proportionality constant b_i depends on whether the individual has settled on a low-quality territory ($b_i = b_L$), has obtained a high-quality breeding site ($b_i = b_H$), or is still queuing for a high-quality site ($b_i = b_Q$). Individuals reproduce sexually. The number of offspring that an individual female produces per time step is Poisson distributed with expectation $2F_i$. The father of every offspring individual is drawn randomly from the males in the population in such a way that the probability that an individual male is selected is proportional to his fecundity. The sex ratio at birth was taken to be 1:1.

Mortality and the occupation of territories

Generations are overlapping. The probability that an individual survives to the next time step, P_i , is given by $P_i = \exp(-\, m_i)$, where m_i is the mortality rate per time step for individual i . For individuals that adopt the cautious foraging strategy the mortality rate remains constant with age at $m_i = m_C$. Individuals that forage in the predator-rich environment experience a low baseline mortality rate m_P but a high size-dependent mortality early in life. The total mortality rate in the predator-rich environment is given by $m_i = m_P + m_S \exp(-(s_i - s_0)/\sigma)$. The mortality rate is at its maximum value at birth (newborn individuals are attacked at rate $m_P + m_S$ per timestep) and the size-dependent component has decreased to 37% of its maximum value m_S by the time the individual has grown σ length units. We took $\sigma = 0.2$.

When the owner of a high-quality territory dies, the territory is assigned to a random individual from the queue. If there are no individuals in the queue, a random individual on a low-quality territory is allowed to occupy the high-quality territory. Once an individual obtains a high-quality breeding site, it occupies that site until the end of its life. The total number of high-quality breeding sites was set to 3,000 in our simulations: only one eighth of the individuals could occupy a high-quality site at any point in time.

Genetics

The life-history decisions of an individual are determined by three multilocus genetic traits. The first two traits, z_Q and z_P, range from 0 to 1 and encode the marginal probabilities to queue and to forage under predation risk, respectively. The third trait, ρ, ranges from -1 to 1 and determines whether or not the two life-history decisions are taken independently of one another. When $\rho \neq 0$, the probability of taking a life-history decision is conditional on choices that were made earlier. The sign and magnitude of ρ correspond to the behavioural correlation between queuing and foraging under risk that can be observed at the population level. Precise definitions of the choice probabilities for the life-history decisions are

Each one of the genetic traits z_Q, z_P and ρ was encoded by eight unlinked, bi-allelic, diploid loci with additive effects on the phenotype. Individuals also carried eight diploid loci that determined the size at maturation. For the parameter values used in our simulations, maturation size converged within 20 generations to an evolutionarily stable value of 0.52 ± 0.03 (mean ± s.d.). Mutations between alleles occurred with probability $1 \cdot 10^{-5}$ per allele per generation.

Table 4.1 Probabilities of behavioural choices

Combination of life-history decisions		Probability
Queuing	Foraging under predation risk	
Yes	Yes	$z_Q z_P + C_{PQ}$[1]
Yes	No	$z_Q (1 - z_P) - C_{PQ}$
No	Yes	$(1 - z_Q) z_P - C_{PQ}$
No	No	$(1 - z_Q)(1 - z_P) + C_{PQ}$

[1] The covariance between life-history decisions, C_{PQ}, is encoded by the genetic trait ρ. Specifically, $C_{PQ} = \rho \sqrt{z_Q (1 - z_P)} \sqrt{z_P (1 - z_P)}$.

RESULTS

A typical simulation is presented in Figure 4.1. The simulation started with a monomorphic population with initial values $z_P = 0.375$, $z_Q = 0.25$ and $\rho = 0$. For the first 60,000 timesteps (corresponding to approximately 900 generations) we did not allow the behavioural correlation ρ to evolve. During this time, the values of z_P and z_Q converged to an evolutionary equilibrium at which individuals utilize a mixed strategy. At this equilibrium, negative frequency-dependent selection has equalized the payoffs associated with the alternative choices for each decision, and behavioural variation continues to exist within the population. After 60,000 timesteps, we allowed the correlation between the two life history decisions to evolve. As illustrated in Figure 4.1, the value of ρ increased slowly over the course of 4000 generations, approaching its maximal value +1. At the end of the simulation, the population still exhibited behavioural variation in queuing and foraging

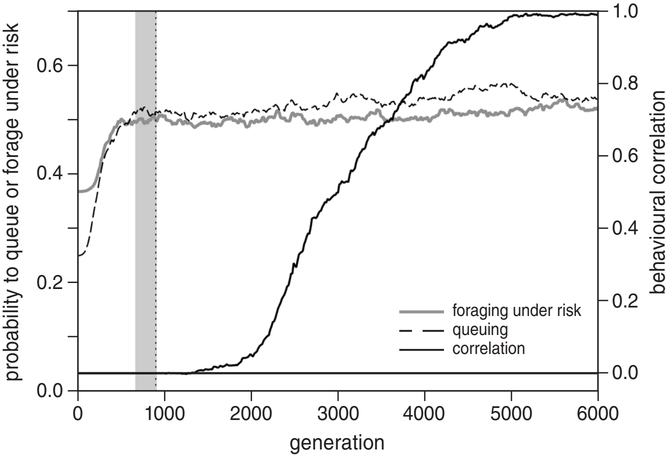

Figure 4.1 Evolution of decision probabilities and behavioural correlation. If the decisions to queue and to forage under risk are taken independently of from each other, the choice probabilities for both decisions rapidly converge on an evolutionary equilibrium. This equilibrium, however, is not evolutionary stable with respect to pleiotropic mutations with pleiotropic effects that induce a behavioural correlation between the two decisions (such mutations were allowed after about 900 generations; indicated by the dashed line). Mutations that increase the behavioural correlation are selectively favoured and, at the new evolutionary equilibrium, the decision to queue is almost always taken together with the decision to forage in the predator-rich environment. Mortality and fecundity parameters were set at: $m_C = 0.04$, $m_P = 0.02$, $m_S = 0.06$, $b_H = 4.0$, $b_L = 2.0$, $b_Q = 0.0$. The grey area indicates a period of 15,000 timesteps (corresponding to about 200 generations) during which the data shown in Figure 4.2 were collected.

behaviour, and life-history decisions were strongly correlated: individuals that chose to queue, also foraged in the predator-rich environment.

In order to understand the selective forces that drive the evolution of a positive correlation between queuing and foraging under risk, we measured population characteristics and fitness components at the evolutionary equilibrium before a behavioural correlation evolved (Figure 4.2). The panels on the left hand side in Figure 4.2 show baseline values that represent an average over all behavioural phenotypes, the panels on the right hand side show the additive effects of queuing and foraging under risk, as well as their interaction on the frequency distribution (Fig. 4.2B), growth trajectory (Fig. 4.2D), fecundity (Fig. 4.2F) and cumulative mortality (Fig. 4.2H).

Size-dependent mortality gives rise to an age-distribution that decays slightly faster than exponentially (Fig. 4.2A) and the growth trajectory is typical for a species with determinate growth (Fig. 4.2C), i.e., individuals grow until they reach maturation size (the dashed line indicates the average age-at-maturation), and then invest all surplus energy into the production of offspring (Fig. 4.2E). The average fecundity increases with age due to the fact that an older individual is more likely to have obtained a high-quality territory if it decided to queue for one. Mortality is highest early in life, when small individuals in the predator rich environment suffer a high attack rate, decreases while the individual grows, and reaches a constant rate after maturation, when individuals have stopped growing.

Young individuals are underrepresented among those that forage in the predator-rich environment, whereas older individuals are slightly overrepresented (Fig. 4.2B). This is a consequence of size-dependent predation. As illustrated by Figure 4.2H, the decision to forage under predation risk entails a trade-off between mortality early and late in life. Other than that, individuals that forage under predation risk show a somewhat faster growth, due to the slightly reduced competition in the predator-rich environment (Fig. 4.2D). The main effect of the decision to queue is that it lowers fecundity early in life, when individuals still wait for a high-quality territory, whereas it increases fecundity later in life (Fig. 4.2F) when individuals have actually obtained a high-quality site.

The decision to queue primarily affects fecundity, whereas the decision to forage in the predator-rich environment primarily affects mortality. As a consequence, direct interactions between the two decisions are weak (Fig. 4.2B, D, F, H; dark grey bars). The two life history decisions do, however, show a strong interaction effect on fitness (Fig. 4.3A). Since the probability to queue and forage under risk are at an evolutionary equilibrium during the period over which measurements were taken, it is no surprise to find that the additive effects of both decisions on fitness are negligible (left and middle column in Fig. 4.3A). Nevertheless,

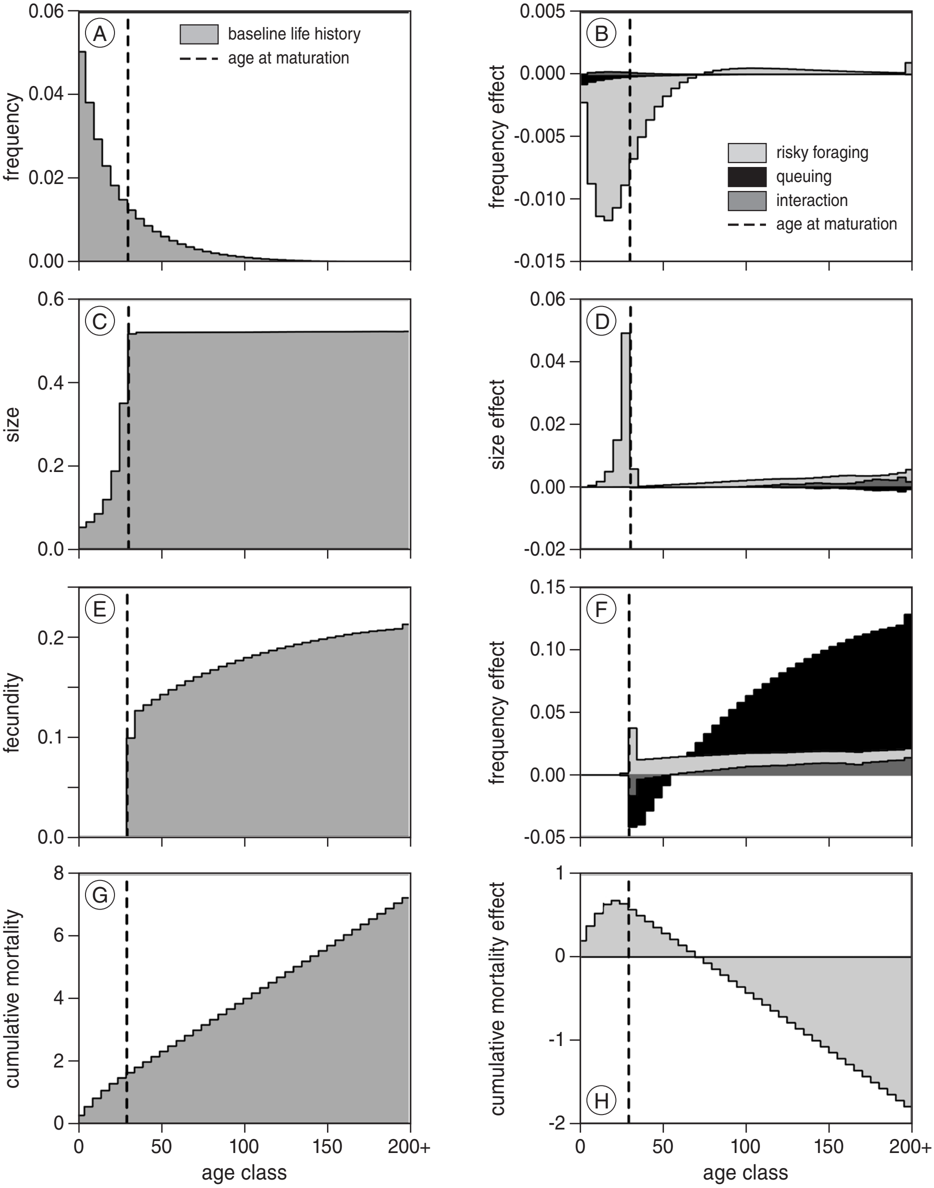

Figure 4.2 Age distribution and fitness components. The simulation shown in Figure 4.1 provides data on the life histories of individuals that chose different combinations of actions. From these, we extracted the population average frequency (A) and size distribution (C), as well as the fecundity (E) and mortality rates (G). Individual life history decisions as well as certain combinations of decisions may cause a deviation from the baseline values. These deviations are shown in the panels on the right hand side (B, D, F, H). For each panel, the deviations are decomposed into an additive (expected) effect of each individual decision and an interaction effect.

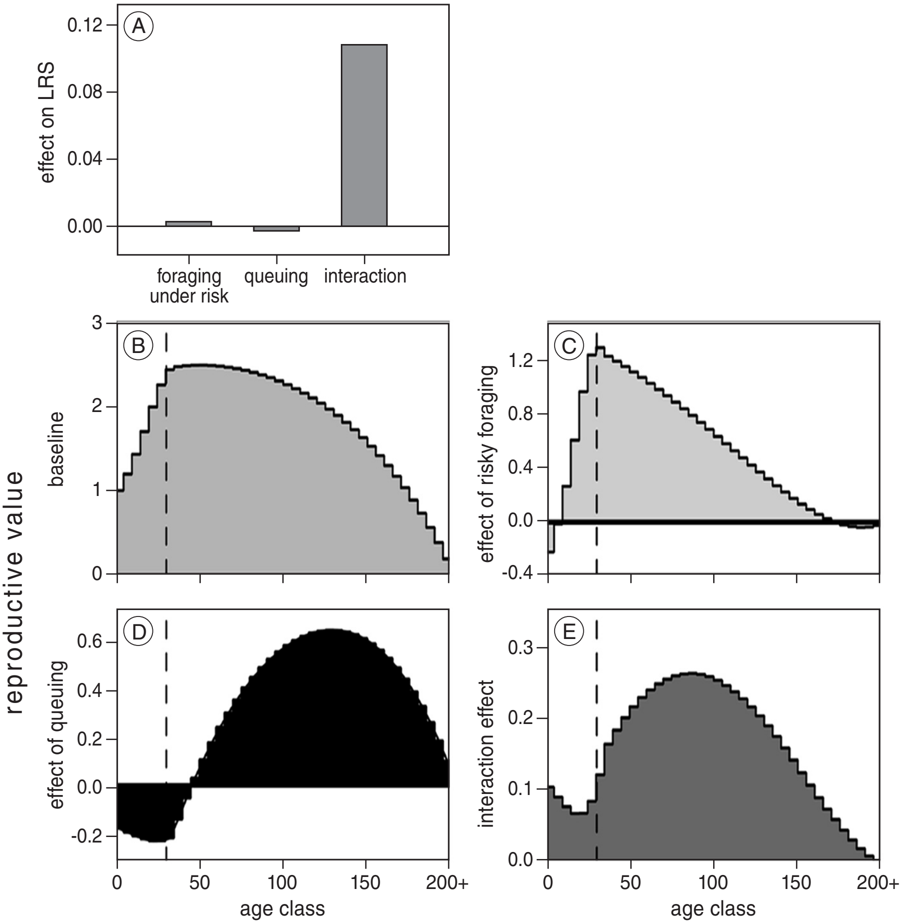

Figure 4.3 Combining decisions provides a fitness benefit. Even though direct interaction effects of queuing and foraging under risk on individual fitness components are weak (Fig. 4.2), there is a strong interaction effect of the two decisions on fitness (A). Combining queuing with foraging under risk gives a roughly 5% increase in lifetime reproductive success, relative to an individual that combines queuing with the cautious foraging strategy. Distributions of the baseline values and effect sizes of decisions on reproductive values (B-E) explain this interaction. Both queuing and foraging under risk can be seen as investments in future reproductive value at the cost of immediate reproductive value (C, D). Combining both decisions in the right manner allows individuals to maximize the benefits of either early or late reproduction (represented by the two maxima in panel (E)).

individuals that queue and forage under risk, or those that do not queue and adopt the cautious foraging strategy do markedly better than individuals that combine queuing with predator avoidance or those that do not queue and forage under risk. The reason is that queuing and foraging under risk can both be seen as an investment into the future: both increase reproductive value late in life, at the cost of reproductive value early in life (Fig. 4.3C, D). Combining queuing and foraging under risk yields a high fitness, because individuals that survived the dangers of size-dependent mortality early in life have a high life expectancy, which allows them to maximally capitalize on the benefits of a high-quality territory. Individuals that avoid predation risk and do not choose to queue, on the other hand, have also chosen a beneficial combination of actions, which makes the best of the opportunities for reproduction early in life. These two favourable combinations of actions consistently favour either early or late reproduction, which explains why the distribution of interaction effects on reproductive value has two maxima (Fig. 4.3E).

RISK IN A LIFE-HISTORY CONTEXT

Building on the intuition that was developed in the previous section, we now examine selection on multiple life-history decisions in a general age-structured population context. The aim of the following analysis is to quantify how life-history decisions that have already been made affect the costs and benefits of decisions that still have to be taken, and whether positive feedbacks between risky decisions and the expected payoffs of such decisions can select for a divergence of life histories associated with risk-prone and risk-avoiding personalities.

We start of by considering a population in which such personalities have not yet evolved, and where population-level behavioural correlations between life-history decisions are absent. Such a situation arises, for example, when the population consists of genetically similar individuals that all play a mixed strategy. The mixed strategy is a vector $\mathbf{y} = (y_1, y_2, \mathbf{K}, y_N)$ that specifies for each one of N life-history decisions the probability y that a given individual takes life-history decision i , independent of which other life-history decisions the individual has taken. Albeit that individuals play a mixed strategy, the behavioural phenotype of any particular individual is given by a combination of actions $\mathbf{x} = (x_1, x_2, \mathbf{K}, x_N)$, where the elements x_i take discrete values $x_i \in \{0, 1\}$that reflect whether or not the individuals took life-history decision i . The frequency of phenotype $\mathbf{x}$ in the population is given by $p(\mathbf{x}, \mathbf{y})$, where

$$p(\mathbf{x}, \mathbf{y}) = \prod_{i=1}^{N} (x_i\, y_i + (1 - x_i)(1 - y_i)) \tag{2}$$

Decisions are characterized by their effects on future fecundities and survival probabilities. For each phenotype, these life-history effects can be summarized by the population projection matrix $\mathbf{L}(\mathbf{x})$,

$$\mathbf{L}(\mathbf{x}) = \begin{pmatrix} \dots & F_a(\mathbf{x}) & \dots & \dots \\ \ddots & & & \\ & P_a(\mathbf{x}) & & \\ & & \ddots & \end{pmatrix}, \quad \text{with age } a \in \mathrm{N}\text{:}\ \ 0 \le \alpha \le \mathrm{A} \tag{3}$$

The matrix elements $F_a(\mathbf{x})$ and $P_a(\mathbf{x})$ represent, respectively, the age-specific fecundities and survival probabilities of an individual with phenotype $\mathbf{x}$.

Lifetime reproductive success

After the population has reached a stable size and age distribution, fitness is determined by the net reproductive rate. This quantity is given by

$$R_0(\mathbf{y}) = \sum_{\mathbf{x}} \sum_{a=0}^{A} p(\mathbf{x}, \mathbf{y})\, r_a(\mathbf{x})\,, \tag{4}$$

where $r_a\,(\mathbf{x})$ is the average number of offspring that a newborn individual with phenotype $\mathbf{x}$ can expect to produce at age a. At this point, it is convenient to define S_a, the survival probability from age 0 to age a, and M_a, the cumulative mortality rate over that age interval. These quantities are related to the survival probabilities P_a by

$$S_a(\mathbf{x}) = \prod_{0 \le \alpha' < \alpha} P_a(\mathbf{x}) = \mathrm{e}^{\sum\limits_{0 \le \alpha' < \alpha} \ln(p_{\alpha'}(\mathbf{x}))} = \mathrm{e}^{-M_a(\mathbf{x})}\,. \tag{5}$$

Using this definition, we find that

$$r_a(\mathbf{x}) = F_a(\mathbf{x})\, \mathrm{e}^{-M_a(\mathbf{x})}\,. \tag{6}$$

The effects of the life-history decisions on the fecundities can be decomposed into additive and interaction components, and we write

$$F_a(\mathbf{x}) = \overline{F}_a + (\mathbf{x} - \mathbf{y}) \cdot \mathbf{f}_a + \tfrac{1}{2}(\mathbf{x} - \mathbf{y})\, \mathbf{F}_a (\mathbf{x} - \mathbf{y})^{\mathrm{T}}\,, \tag{7}$$

where $\overline{F}_a$ is the baseline fecundity and $\mathbf{f}_a$ is a vector that contains the additive effects of the life-history decisions on the fecundity at age a. The last term of expansion (7) represents the contribution of direct interactions between life-history decisions. The off-diagonal elements of matrix $\mathbf{F}_a$ capture the strength of such interactions; the diagonal elements of $\mathbf{F}_a$ are zero. The Appendix provides details on how the baseline fecundity and the elements of $\mathbf{f}_a$ and $\mathbf{F}_a$ can be calculated from the phenotype specific fecundities $F_a(\mathbf{x})$.

After defining a similar decomposition of the cumulative mortality rates,

$$M_a(\mathbf{x}) = \bar{M}_a + (\mathbf{x}-\mathbf{y})\cdot \mathbf{m}_a + \tfrac{1}{2}(\mathbf{x}-\mathbf{y})\,\mathbf{M}_a(\mathbf{x}-\mathbf{y})^{\mathrm{T}}\ , \tag{8}$$

we make two simplifying assumptions. First, we assume that the effects of individual life-history decisions are small, such that selection is weak. In other words, $\max\left(\|\mathbf{f}_a\|,\|\mathbf{m}_a\|\right) = \varepsilon \ll 1$. Second, we assume that the life-history decisions have approximately additive effects at the scale of the fecundities and mortality rates such that the direct interaction component is typically much smaller than the additive component, i.e., $\|\mathbf{F}_a\|,\|\mathbf{M}_a\| = \|\mathbf{f}_a\|,\|\mathbf{m}_a\|$. The latter is not a severe restriction in the context of the present study, as we are primarily interested in explaining correlations between traits that do not obviously have direct epistatic effects on fitness components.

The average number of offspring that a newborn individual with phenotype $\mathbf{x}$ can expect to produce at age a can now be approximated as

$$r_a(\mathbf{x}) = \bar{r}_a + (\mathbf{x}-\mathbf{y})\cdot(\bar{S}_a\,\mathbf{f}_a - \bar{r}_a\,\mathbf{m}_a) + \tfrac{1}{2}(\mathbf{x}-\mathbf{y})\,(\bar{S}_a\,\mathbf{F}_a - \bar{r}_a\,\mathbf{M}_a + \mathbf{K}_a)(\mathbf{x}-\mathbf{y})^{\mathrm{T}} \tag{9}$$

where $\bar{r}_a = \bar{F}_a\bar{S}_a = \bar{F}_a \exp(-\bar{M}_a)$. This approximation includes the terms that are of the same order of magnitude as the interaction components. Note that the interaction term contains an extra symmetric matrix $\mathbf{K}_a$ in addition to the matrices of direct interaction coefficients $\mathbf{F}_a$ and $\mathbf{M}_a$. This matrix captures the combined life-history effects of decisions that originate from the interaction between different fitness components. The matrix $\mathbf{K}_a$ is given by

$$\mathbf{K}_a = \bar{r}_a\,\mathbf{m}_a^{\mathrm{T}}\,\mathbf{m}_a - \bar{S}_a\,(\mathbf{f}_a^{\mathrm{T}}\,\mathbf{m}_a + \mathbf{m}_a^{\mathrm{T}}\,\mathbf{f}_a) \tag{10}$$

Fitness gradients and curvature of the fitness landscape

The selection gradient on the i-th component of the mixed strategy $\mathbf{y}$ is given by the difference of the net-reproductive rates of two populations that play alternative pure strategies for decision i (see Appendix). From this result, it follows that up to leading order

$$\frac{\partial R_0(\mathbf{y})}{\partial y_i} = \mathbf{e}_i \cdot \sum_{a=0}^{A} \left(\bar{S}_a \mathbf{f}_a - \bar{r}_a \mathbf{m}_a \right) \tag{11}$$

If there is a dominant strategy for decision *i*, then y_i will evolve to zero or one and behavioural variation for that decision will be lost. For the purpose of the present study, we can ignore such cases, and instead focus on the subset of life-history decisions for which selection pushes the strategy component y_i to a stable intermediate value $0 < y_i < 1$. This requires that selection be negatively frequency-dependent such that whichever behaviour is rare enjoys a selective advantage.

Once the population has attained a singular strategy $\mathbf{y} = \mathbf{z}$ at which the selection gradient vanishes, i.e.,

$$\left.\frac{\partial R_0(\mathbf{y})}{\partial y}\right|_{y=z} = \mathbf{0}\ , \tag{12}$$

mutations that affect a single strategy component y_i can no longer invade. In general, there will however still be selection on mutations with pleiotropic effects on multiple life-history decisions. Such mutations create behavioural correlations between different life-history decisions.

The strength of selection on mutations with pleiotropic effects is determined by the mixed second derivatives of R_0. These evaluate to

$$\frac{\partial^2 R_0(\mathbf{y})}{\partial y_i \partial y_j} = \mathbf{e}_i \cdot \sum_{a=0}^{A} \left(\bar{S}_a \mathbf{F}_a - \bar{r}_a \mathbf{M}_a + \mathbf{K}_a \right) \mathbf{e}_j^{\mathrm{T}}\ . \tag{13}$$

If the mixed second derivative for two decisions *i* and *j* is positive, a positive behavioural correlation between the two decisions is favoured. Negative correlations are favoured when the mixed second derivative is negative. Note that behavioural correlations are under selection even without any direct epistatic effects ($\mathbf{F}_a = \mathbf{M}_a = 0$) of life-history decisions on individual fitness components.

A probabilistic interpretation

At the singular strategy, where the selection gradient vanishes, the positive effects of life-history decisions on certain age-specific fecundity or mortality rates must be compensated by negative effects elsewhere in the lifecycle. The exact condition is given by the right hand side of equation (11), which, by definition, evaluates to zero at the singular strategy. There are many ways in which fitness components can be traded off against each other. Here, we will focus on an illustrative example concerning the interaction between two life-history decisions (*i* and *j*) that each involve a trade-off between fecundity and mortality (guidelines for analyzing scenarios involving other types of trade-offs are provided in the Appendix). We define the decisions such that they increase fecundity, at the cost of increased mortality (i.e., all $\mathbf{f}_a \geq 0$ and $\mathbf{m}_a \geq 0$ for both decisions).

We develop a probabilistic interpretation of the main result (13) for this special case, which gives a clear and general insight into the life-history interactions between risky decisions. To start with, $\overline{r}_a$ is interpreted as a probability to produce offspring at age a. In a stationary population, these probabilities sum to 1, such that a newborn individual on average can expect to produce a single offspring during its lifetime. Let A_r denote the age at reproduction as determined by the baseline fecundity and mortality rates. Then, A_r is a random variable with probability density function

$$\Pr\,[A_r = a] = \overline{r}_a \ , \tag{14}$$

This expression is accurate up to second order in ε (i.e., the small parameter that quantifies the strength of selection) at the singular strategy. The survival probabilities determine the distribution of the age of death A_d in a population that follows the baseline life history. In other words,

$$\overline{S}_a = \Pr\,[a \leq A_d] \ . \tag{15}$$

A similar probabilistic interpretation can be developed for the reproductive benefits associated with the life-history decisions i and j. To see this, let

$$b_i = \sum_{a=0}^{A} \mathbf{f}_a^{(i)} \ , \tag{16}$$

denote the cumulative additive effect of decision i on fecundity (measured in additional offspring above the baseline expectation) for an individual that survives until the last age class. Then,

$$\Pr\,[A_r^{(i)} = a] = \frac{\mathbf{f}_a^{(i)}}{b_i} \ , \tag{17}$$

defines the distribution of fecundity effects over the lifetime of an individual. The random variable $A_r^{(i)}$ represents the age at which individuals enjoy the reproductive benefits of decision i. It follows from this definition that

$$\mathbf{f}_a^{(i)} = b_i \Pr\,[A_r^{(i)} = a] \ , \tag{18}$$

By assumption, decision i trades off higher fecundity against a higher mortality rate. An analogous interpretation of mortality effects as stochastic events allows us to write

$$\mathbf{m}_a^{(i)} = c_i \,\mathrm{Pr}\,[A_d^{(i)} < a]\,, \tag{19}$$

where is the total mortality risk associated with decision *i*, and $[A_d^{(i)} < a]$ specifies how that risk is distributed over the life of an individual. The random variable $A_d^{(i)}$ represents the age at death among those individuals that die as a direct consequence of decision *i*.

With these definitions, we can rewrite the selection gradient at the singular strategy as

$$\left.\frac{\partial R_0\,(\mathbf{y})}{\partial y_i}\right|_{y=z} = b_i \,\mathrm{Pr}\,[A_r^{(i)} \leq A_d\,] - c_i \,\mathrm{Pr}\,[A_d^{(i)} < A_r\,] = 0 \ . \tag{20}$$

The first term on the right hand side of this expression represents the number of offspring gained as a result of the fecundity effects of decision *i*. This reproductive benefit is quantified by the probability that the decision results in the production of offspring before death occurs according to the baseline life history. The second term on the right hand side quantifies the risk of the decision as the number of offspring that are lost if decision *i* leads to death before the baseline age at reproduction.

With similar definitions for decision *j*, also the mixed second derivative (equation (13)) can be expressed in terms of probabilities,

$$\begin{aligned}\frac{\partial^2 R_0\,(\mathbf{y})}{\partial y_i\,\partial y_j} &= I + c_i\,c_j \,\mathrm{Pr}\,[A_d^{(i)} < A_r \cap A_d^{(j)} < A_r\,] \ . \\ &\qquad - b_i\,c_j \,\mathrm{Pr}\,[A_d^{(j)} < A_r^{(i)} \leq A_d\,] - b_j\,c_i \,\mathrm{Pr}\,[A_d^{(i)} < A_r^{(j)} \leq A_d\,]\end{aligned} \tag{21}$$

where

$$I = \sum_{a=0}^{A} \left(\bar{S}_a\,\mathbf{F}_a^{(i,j)} - \bar{r}_a\,\mathbf{M}_a^{(i,j)} \right) \tag{22}$$

quantifies the strength of direct epistatic interactions between the two life-history decisions.

Using equation (20) the previous result can be rewritten as

$$\begin{aligned}&\left.\frac{\partial^2 R_0\,(\mathbf{y})}{\partial y_i\,\partial y_j}\right|_{y=z} - I = \\ &\quad c_i\,c_j \,\mathrm{Pr}[A_d^{(i)} < A_r]\,\{\mathrm{Pr}[A_d^{(j)} < A_d^{(i)} \mid A_d^{(i)} < A_r] - \mathrm{Pr}[A_d^{(j)} < A_r^{(i)} \mid A_r^{(i)} \leq A_d]\} + \\ &\quad c_i\,c_j \,\mathrm{Pr}[A_d^{(j)} < A_r]\,\{\mathrm{Pr}[A_d^{(i)} \leq A_d^{(j)} \mid A_d^{(j)} < A_r] - \mathrm{Pr}[A_d^{(i)} < A_r^{(j)} \mid A_r^{(j)} \leq A_d]\} \ .\end{aligned} \tag{23}$$

The first line on the right-hand side of this equation quantifies the effect of decision j on the cost-benefit balance of decision i. This effect scales with $c_i\ c_j\ \Pr[A_d^{(i)} < A_r]$, the mortality risk associated with decision i, and c_j. The sign of the interaction effect depends on the probability of occurrence of the potential positive and negative outcomes of the interaction between the two life-history decisions. On the one hand, decision j could mask the negative consequences of decision i by inducing death before decision i does. Such an event discounts the costs of life history decision i, if decision i would have otherwise caused death before reproduction. Hence, the discounting of costs is quantified by the conditional probability $\Pr[A_d^{(j)} < A_d^{(i)} \mid A_d^{(i)} < A_r]$. On the other hand, decision j could interfere with the positive consequences of decision i by causing death before decision i has paid off with a reproductive benefit. This effect is quantified by the conditional probability $\Pr[A_d^{(j)} < A_r^{(i)} \mid A_r^{(i)} \leq A_d]$, which takes into consideration that a cost is realized only when the benefit associated with decision i materializes before death occurs in the baseline life history. The second line on the right hand side of equation (23) can be interpreted in an analogous way but with the roles of the two life-history decisions reversed.

Ignoring the direct interaction term (I), the sign of the right hand side of (23) determines whether selection favours a positive or negative behavioural correlation between the two life-history decisions. This points to the importance of the two terms between curly brackets. The sign of each of these reflects a balance between two principles that shape life histories. Counteracting coordination of risky decisions is the 'asset protection principle', i.e., individuals that have more to lose in terms of assets that have accumulated from previous risky decisions, should avoid risks to ensure that benefits that lie in the future will actually materialize. Favouring positive correlations in risk-taking behaviour is the 'nothing-to-lose principle', i.e., individuals that have accumulated risks, will tend to devaluate investments into the future, since it is unlikely that they will live much longer. As a result, such individuals are wiling to take additional risks if this allows them to gain immediate reproductive benefits.

Two conclusions follow from these considerations. First, the asset-protection principle does indeed counteract the evolution of risk-averse and risk-prone personalities, but is not the only source of selection. Of equal importance is the accumulation of mortality risk, a factor that so far has not been prominent in the discussion on animal personality. Second, our result highlights the importance of the timing of costs and benefits of risky decisions. If risky decisions pay off quickly, and part of the mortality risk lies in the future, then selection is expected to coordinate behavioural variation in many of such decisions. Even when each individual decision has only a small effect on life-history, such coordination will give rise to risk-averse and risk-prone personalities with large differences between the corresponding life histories. Risk-averse individuals concentrate on survival and future reproductive success; risk-prone individuals adhere to a live-fast-die-young lifestyle, with many immediate benefits, but accumulate mortality risk later in life.

CONCLUSIONS

We investigated situations in which individuals are repeatedly confronted with risky choices. In a previous paper (Wolf *et al.*, 2007a) we had shown that whenever individuals differ in their fitness expectations such situations give rise to risk-prone and risk-averse personality types. The present paper focused on scenarios without such initial differences in fitness expectations. This set-up allowed us to focus attention on (1) the feedbacks from risky actions on the mortality and fecundity profile of individuals and thus on their future fitness expectations and (2) on the effect of these feedbacks on the emergence and stability of personalities.

Risky actions affect the fecundity and mortality profile of individuals. Our analysis shows that the timing of these effects has a decisive role for the type of feedback that should be expected. Two qualitatively different scenarios can be distinguished.

First, risky choices are associated with mortality and fecundity effects that act to decrease prior differences in the willingness to take risks (negative feedback). Such situations occur whenever risk-prone action tend to accumulate future fecundity benefits or decrease increase future survival relative to risk-averse actions. Importantly, whenever the initial differences in fitness expectations are small, such negative feedbacks should tend to erode the basis of behavioural differences among individuals over time.

Second, risky choices are associated with mortality and fecundity effects that reinforce differences risk-taking behaviour. Such situations occur whenever risk-averse actions tend to accumulate future fecundity benefits or decrease increase future survival relative to risk-prone actions. Interestingly, in the presence of positive feedbacks, selection can result in the coexistence of consistently risk-prone and risk-averse behavioural types even in the absence of initial differences in fitness expectations.

Appendix

Here we provide technical details to a number of steps in our mathematical analysis.

DECOMPOSITION OF FECUNDITY AND MORTALITY RATES

In our analyses, we decompose the age-specific fecundities into an average (baseline) value ($\bar{F}_a$) vector of additive effects of individual life history decisions ($\mathbf{f}_a$, with elements for decision i), and a matrix of interaction coefficient ($\mathbf{F}_a$ with elements $\mathbf{F}_a^{(i,j)}$ for the interaction between decisions i and j). In the simplest case, with only two life-history decisions, these values can be calculated from the fecundities associated with a specific combination of behavioural choices, $\mathbf{F}_a(\mathbf{x})$ (where $\mathbf{x} = (0,0),\ (1,0), (0,1)$ or $(1,1)$) as follows,

$$\begin{aligned}
&\bar{F}_a = y_1 y_2\, F_a\big((1,1)\big) + y_1(1-y_2)F_a\big((1,0)\big) + (1-y_1)y_2\, F_a\big((0,1)\big) + (1-y_1)(1-y_2)F_a\big((0,0)\big),\\
&\mathbf{f}_a^{(1)} = y_2\,\big(F_a((1,1)) - F_a((0,1))\big) + (1-y_2)\big(F_a((1,0)) - F_a((0,0))\big),\\
&\mathbf{f}_a^{(2)} = y_1\,\big(F_a((1,1)) - F_a((1,0))\big) + (1-y_1)\big(F_a((0,1)) - F_a((0,0))\big),\\
&\mathbf{F}_a^{(1,2)} = F_a\big((1,1)\big) - F_a\big((1,0)\big) - F_a\big((0,1)\big) + F_a\big((0,0)\big). \qquad (1)
\end{aligned}$$

In general, the expressions are

$$\begin{aligned}
&\bar{F}_a = \sum_{x} p\,(\mathbf{x},\mathbf{y})\, F_a(\mathbf{x})\,,\\
&\mathbf{f}_a^{(i)} = \sum_{x:x_i=0} p\,(\mathbf{x},\mathbf{y} - y_i\mathbf{e}_i)\big(F_a(\mathbf{x} + \mathbf{e}_i) - F_a(\mathbf{x})\big),\\
&\mathbf{F}_a^{(i,j)} = \sum_{\substack{x:x_i=x_j=0\\ i\neq j}} p\,(\mathbf{x},\mathbf{y} - y_i\mathbf{e}_i - y_j\mathbf{e}_j)\big(F_a(\mathbf{x} + \mathbf{e}_i + \mathbf{e}_j) - F_a(\mathbf{x} + \mathbf{e}_i) - F_a(\mathbf{x} + \mathbf{e}_j) + F_a(\mathbf{x})\big)\,, \qquad (2)
\end{aligned}$$

where $\mathbf{e}_i$ is the i -th unit base vector. To simplify the equations in the main text, we have made use of the fact that the matrix $\mathbf{F}_a$ is symmetric. Analogous results hold for the decomposition of the mortality rates.

DERIVATIVES OF THE FITNESS FUNCTION

The fitness gradient, i.e., the derivative of the fitness function (equation) provides information about the strength and direction of directional selection. It is calculated as

$$\begin{aligned}\frac{\partial R_0\,(\mathbf{y})}{\partial y_i} &= \sum_x (2x_i - 1) \sum_{a=0}^{A} \prod_{j \neq i} x_j\, y_j + (1 - x_j)(1 - y_j)\, r_a(\mathbf{x}) \\ &= R_0\big(\mathbf{y} + (1 - x_i)\,\mathbf{e}_i\big) - R_0\,(\mathbf{y} - y_j\mathbf{e}_i) \\ &= \sum_{x:x_i=0} p\,(\mathbf{x}, \mathbf{y} - y_i\mathbf{e}_i) \sum_{a=0}^{A} r_a(\mathbf{x} + \mathbf{e}_i) - r_a(\mathbf{x})\ . \qquad (3)\end{aligned}$$

The end result signifies that the fitness gradient is equal to the difference of the net-reproductive rates of two populations that play alternative pure strategies for decision .

Following a similar procedure, we obtain an expression for the mixed second derivatives of the net reproductive rate,

$$\begin{aligned}\frac{\partial^2 R_0\,(\mathbf{y})}{\partial y_i\, \partial y_j} &= \sum_{x:x_i=x_j=0} p\,(\mathbf{x}, \mathbf{y} - y_i\mathbf{e}_i - y_j\mathbf{e}_j) \times \\ &\qquad \sum_{a=0}^{A} r_a(\mathbf{x} + \mathbf{e}_i + \mathbf{e}_j) + r_a(\mathbf{x}) - r_a(\mathbf{x} + \mathbf{e}_i) - r_a(\mathbf{x} + \mathbf{e}_j)\ . \qquad (4)\end{aligned}$$

where $i \neq j$. Note that the pure second derivatives $R_0^{(\mathrm{i,i})}$ evaluate to zero, since $\mathrm{p}(\mathbf{x}, \mathbf{y})$ is linear in y_i .

TRADE-OFFS BETWEEN FITNESS COMPONENTS

When behavioural variation for a risky decision exists at the singular strategy, that decision must trade-off one fitness component against another. In the main text, we have analyzed a scenario where two decisions trade off fecundity against mortality, i.e., $\mathbf{f}_a^{(i)} > 0$ and $\mathbf{m}_a^{(i)} > 0$ for all age classes $0 \leq a \leq A$. The example model, for which we showed individual-based simulations, featured other simple types of trade-offs: the decision to queue entails a trade-off between fecundity in some age classes and fecundity during the rest of the life cycle, without strong effects on mortality (e.g., $\mathbf{f}_a^{(i)} > 0$ for $0 \leq a \leq A'$ and $\mathbf{f}_a^{(i)} < 0$ for $A' < a \leq A$), whereas the decision to forage under risk involves a trade-off between mortality in some age classes and mortality during the rest of the life cycle, without strong effects on fecundity (e.g., $\mathbf{m}_a^{(i)} < 0$ for $0 \leq a \leq A''$ and $\mathbf{m}_a^{(i)} > 0$ for $A'' < a \leq A$).

These three simple types of trade-off are important, since they can be combined to give rise to any arbitrarily complex trade-off pattern. Conversely, arbitrary trade-offs can be decomposed into simpler components, and interactions between pairs of components can then be understood within the same probabilistic framework as the one developed in the main text. The preparatory decomposition step consists of separating the positive and negative effects of a life history decision on both fecundity and mortality. The distribution of the costs and benefits over the lifetime of an individual can then be considered separately, usually giving rise to additional terms in the probabilistic expressions for the selection gradient and mixed second derivative of the fitness function.

For example, to deal with a life-history decision that trades off mortality rates at different life stages, we separate out the positive and negative effects on mortality. A straightforward way to do this, is to write the cumulative mortality effect of the decision as a sum of age-specific effects $\mu_{a'}^{(i)}$

$$\mathbf{m}_a^{(i)} = \sum_{0 \le a' < a} \mu_{a'}^{(i)} \tag{5}$$

and to separate the positive and negative contributions, by defining

$$\mathbf{m}_a^{(i+)} = \sum_{0 \le a' < a} H\left(+\mu_{a'}^{(i)}\right) \mu_{a'}^{(i)} \ . \tag{6}$$

$$\mathbf{m}_a^{(i-)} = -\sum_{0 \le a' < a} H\left(-\mu_{a'}^{(i)}\right) \mu_{a'}^{(i)} \ .$$

Here, $H(x)$ is the Heaviside step function, which takes the value 1 for all $x > 0$ and 0 otherwise. It follows that $\mathbf{m}_a^{(i)} = \mathbf{m}_a^{(i+)} - \mathbf{m}_a^{(i-)}$. We can then define cost and benefit coefficients c_i and b_i that quantify total mortality risk associated with, respectively, taking ($x_i = 1$) or not taking ($x_i = 0$) decision i, and two random variables $A_d^{(i+)}$ and $A_d^{(i-)}$ that specify how cost and benefit are distributed over the life of an individual. The rest of the analysis then follows the outline presented in the main text.

Chapter 5

Evolutionary emergence of responsive and unresponsive personalities

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ABSTRACT

In many animal species individuals differ consistently in suites of correlated behaviours, comparable to human personalities. Increasing evidence suggests that one of the fundamental factors structuring personality differences is the responsiveness of individuals to environmental stimuli. While some individuals tend to be highly responsive to such stimuli others are unresponsive and show routine-like behaviours. Much research has focused on the proximate causes of these differences but little is known about their evolutionary origin. Here we provide a first evolutionary explanation. We develop a simple but general evolutionary model that is based on two key ingredients. First, the benefits of responsiveness are frequency-dependent; that is, being responsive is advantageous when rare but disadvantageous when common. This explains why responsive and unresponsive individuals can coexist within a population. Second, positive feedback mechanisms reduce the costs of responsiveness; that is, responsiveness is less costly for individuals that have been responsive before. This explains why individuals differ consistently in their responsiveness, across contexts and over time. As a result, natural selection gives rise to stable individual differences in responsiveness. While some individuals respond to environmental stimuli in all kinds of contexts, others consistently neglect such stimuli. Interestingly, such differences induce correlations among all kinds of other traits (e.g., boldness and aggressiveness), thus providing a novel explanation for environment-specific behavioural syndromes.

INTRODUCTION

Empirical findings in more than 100 species, ranging from insects to mammals, suggest that personalities are a widespread phenomenon in the animal kingdom (Clark & Ehlinger, 1987; Wilson, 1998; Gosling & John, 1999; Koolhaas et al., 1999; Gosling, 2001; Sih *et al.*, 2004b; Groothuis & Carere, 2005; Korte *et al.*, 2005; Nettle, 2006). Individuals differ profoundly from each other in their behaviour, and these differences are often consistent over time and extend to various contexts. In birds, fish and rodents, for example, some individuals are consistently more aggressive than others, and aggressive individuals differ from non-aggressive individuals in many other respects like foraging behaviour or the exploration of novel environments (Sih *et al.*, 2004b). From an adaptive point of view both the coexistence of behavioural types and the consistency of individuals are poorly understood (Reale *et al.*, 2007; Bell, 2007a).

Many researchers believe that a fundamental factor structuring personality differences is the degree to which individual behaviour is guided by environmental stimuli (Benus *et al.*, 1987; Hessing *et al.*, 1994; Verbeek *et al.*, 1994; Aron & Aron, 1997; Koolhaas *et al.*, 1999; Groothuis & Carere, 2005; Korte *et al.*, 2005; Belsky *et al.*, 2007; Frost *et al.*, 2007; Schjolden & Winberg, 2007). While some individuals pay attention to environmental stimuli and quickly adapt their behaviour to the prevailing conditions, others show more rigid, routine like behaviour. Such differences in responsiveness (also termed coping-style, reactivity, flexibility, plasticity) have been documented in many organisms including birds – for example great tits (Verbeek *et al.*, 1994), spice finches (Mottley & Giraldeau, 2000) and zebra finches (Beauchamp, 2001) and mammals – for example rats and mice (Koolhaas *et al.*, 1999), pigs (Hessing *et al.*, 1994) and humans (Belsky *et al.*, 2007).

Both in mice and rats (Benus *et al.*, 1987) individuals differ substantially in their responsiveness to environmental changes in a maze task. Some individuals quickly form a routine, are not influenced by minor environmental changes and perform relatively badly when confronted with a changing maze configuration. Others omit forming a routine, are strongly influenced by minor changes and perform relatively well when confronted with changing maze configurations. Similarly, some great tits readily adjust their foraging behaviour to a change in the feeding situation while others stick to formerly successful habits (Verbeek *et al.*, 1994). The finding that humans and other primates differ in their susceptibility to environmental influences (Aron & Aron, 1997; Belsky *et al.*, 2007) might also be interpreted along these lines.

These observations raise two important questions. First, why do responsive and unresponsive individuals coexist within a population? Should we not expect a single "optimal" phenotype? And second, why are differences in responsiveness consistent across contexts and over time? Should we not expect that individuals adjust their responsiveness to the needs of the prevailing situation? In this paper we develop a simple but general evolutionary model to address these questions.

First, we address the coexistence problem. Our crucial insight is that for many realistic scenarios the benefits of responsiveness are negatively frequency dependent. As a consequence responsiveness spreads when rare but is selected against when common. This explains coexistence. Second, we address consistency. We show that stable individual differences in responsiveness arise whenever the costs of responsiveness are lower for those individuals that have been responsive before. We argue that many processes like learning or training give rise to such positive feedbacks thus explaining consistency. Interestingly, our results illustrate that individual differences at the level of behavioural organization (here, the responsiveness to environmental stimuli) can induce correlative associations among all kinds of otherwise unrelated traits.

COEXISTENCE OF RESPONSIVE AND UNRESPONSIVE INDIVIDUALS

Basic scenario

We consider a population of individuals that face environmental uncertainty. By assessing the prevailing environmental state and adequately responding to it, individuals can typically increase their payoff. Yet such a responsive strategy involves costs (DeWitt *et al.*, 1998) as, for example, the time and energy costs of sampling the environment, the mortality cost induced by collecting information or the costs of building and maintaining the required sensory machinery.

Figure 5.1 shows the structure of a simple model that captures the key ingredients of this scenario. Individuals have a choice between the two options L ("left") and R ("right"). The payoffs from these options depend on the environment, which can be in either of two states that occur with probability s_i ($i = 0$ or 1). Accordingly, we denote the payoffs from choosing L and R as a_i and b_i, respectively. Before choosing between L and R, individuals choose whether or not to adopt a responsive strategy. Responsive individuals get to know the current state and can therefore make their behaviour dependent on this information; that is, choose L with probability l_0 or l_1, depending on the state of the environment. Yet, responsiveness is costly and reduces the payoff by C. In contrast, unresponsive individuals cannot distinguish between the two states and have to use the same probability $\overline{l}$ in both states.

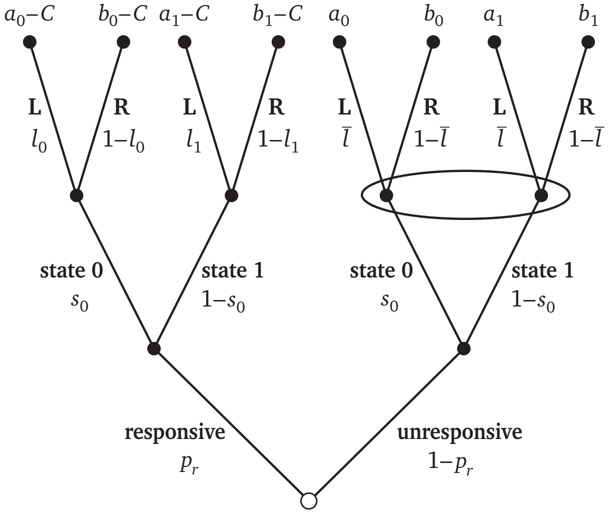


Figure 5.1 Setup of the one-stage model. We consider a scenario where individuals can find themselves in either of two states, where state i occurs with probability s_i. Individuals have the choice between two options L and R. The payoffs associated with these options, a_i and b_i, depend on the state of the environment $i = 0{,}1$ and, in addition, on the strategy established in the population. An individual follows the responsive strategy with probability p_r. Responsive individuals can distinguish between the two states and make their behaviour dependent on the current state. Accordingly, the probability l_i with which a responsive individual chooses option L depends on the state i. In contrast, unresponsive individuals cannot distinguish between the two states and have to use the same probability $\bar{l}$ in both states. While responsiveness allows more flexible behaviour it is costly and reduces the payoff by C.

Benefits of responsiveness

In view of the cost of responsiveness C, the responsive strategy can only spread if the benefits of responsiveness exceed these costs. The benefits of responsiveness are given by the excess payoff E of a responsive over an unresponsive individual. What determines this excess payoff? In state i, a responsive individual plays strategy l_i and thus obtains the payoff $l_i \cdot a_i + (1 - l_i) \cdot b_i$. This payoff will typically exceed the payoff of an unresponsive individual, $\bar{l} \cdot a_i + (1 - \bar{l}) \cdot b_i$, that has to use the general-purpose strategy $\bar{l}$. The payoff difference in state i is therefore $(l_i - \bar{l}) \cdot (a_i - b_i)$ and the benefits of responsiveness are thus given by $E = \sum_i s_i \cdot (l_i - \bar{l}) \cdot (a_i - b_i)$. Hence, the responsive strategy spreads whenever $E > C$ and the unresponsive strategy spreads whenever $E < C$.

Frequency dependence

From now on we make the crucial assumption that the payoffs a_i and b_i are negatively frequency-dependent, that is, the excess payoff of choosing L over R in state i, $a_i - b_i$, decreases with the frequency f_i of individuals that choose option L in state i ($f_i = p_r \cdot l_i + (1 - p_r) \cdot \overline{l}$). This is a realistic assumption and it is now generally agreed on that such frequency dependence is a common phenomenon in all kinds of competitive interactions (see discussion below). In the Appendix we demonstrate that frequency dependence at the level of the choices between L and R gives rise to benefits of responsiveness that are negatively frequency dependent, that is

$$\frac{dE}{dp_r} < 0 \tag{1}$$

The intuition for this result is as follows. Consider a situation where in state i it is advantageous to choose option L ($a_i > b_i$). Hence responsive individuals choose L ($l_i = 1$) while unresponsive individuals have to stick to the general purpose strategy $\overline{l}$. However, the payoff difference between L and R decreases with the frequency of individuals that choose option L. As a consequence the benefits of responsiveness in state i decrease with the frequency of responsive individuals.

Coexistence

Since the benefits of responsiveness $E(p_r)$ are negatively frequency dependent, they will be highest in a population of unresponsive individuals ($p_r = 0$) and lowest in a population of responsive individuals ($p_r = 1$). We have seen that responsive individuals can invade a population of unresponsive individuals whenever $E(0) > C$, while unresponsive individuals can invade a population of responsive individuals whenever $C > E(1)$. Accordingly, both strategies can spread when rare whenever

$$E(0) > C > E(1) \tag{2}$$

leading to the coexistence of responsive and unresponsive individuals. In the Appendix we show that $E(0)$ and $E(1)$ can readily be calculated. $E(0)$ is given by $E(0) = s_0 \cdot s_1 \cdot \Delta$, where $\Delta = \sum_i |a_i - b_i|$ measures for the payoff differences in a population of unresponsive individuals. Note that $E(1)$ is equal to zero whenever, in a population of responsive individuals ($p_s = 1$), a mixed evolutionarily stable strategy (ESS) is played in any of the environmental states.

Example I: Coexistence in a patch choice game

We now illustrate this result and its consequences for a situation where the options L and R correspond to the alternatives in a patch choice game, where each individual has the choice between two patches. The payoff an individual obtains in any of the two patches is given by

$a_i = \frac{A_i}{f_i}$ and $b_i = \frac{B_i}{1-f_i}$, where A_i and B_i are state dependent baseline values of the two patches and f_i is the frequency of individuals that choose patch L in state i.

Figure 5.2A illustrates that negative-frequency dependence on the level of the patch choice game gives rise to benefits of responsiveness that are negatively frequency dependent. Responsive individuals (black line) always obtain a payoff that is as least as high as that of unresponsive individuals (grey line) since they can choose the better patch in each environment. However, as predicted by our analysis above (equation (1)), the payoff difference between responsive and unresponsive individuals (black line), that is, the benefits of responsiveness, decreases with the frequency of responsive individuals. Whether decreasing benefits of responsiveness give rise to the coexistence of responsive and unresponsive individuals depends on the strength of this decrease and on the cost of responsiveness (see equation (2)). For the chosen parameter values of A_i and B_i we expect coexistence whenever the cost of responsiveness C is between $E(1) = 0$ and $E(0) = 0.5$ (right axis). For any of these equilibria, one can readily calculate the corresponding ESS behaviour of responsive and unresponsive individuals in the patch choice game. This is illustrated in Figure 5.2C that shows how these strategies change with the cost of responsiveness.

To test these predictions we implemented our assumptions in individual-based computer simulations in which trait frequencies change over time under the influence of natural selection (see Appendix). The simulation results are in perfect agreement with our analytical predictions. For any value of $C < 0.5$ the population converges to the predicted mixture of responsive and unresponsive individuals; Figure 5.2B shows two simulations for the scenario depicted in Figure 5.2A (C = 0.2), one starting from an ancestral population of responsive individuals and the other from an ancestral population of unresponsive individuals. Figure 5.2D illustrates that also the behaviour of responsive and unresponsive individuals in the patch choice game is in perfect agreement with our analytical predictions. Unresponsive individuals (grey line) evolve an intermediate tendency to choose between the two patches ($\bar{l}^* = 0.58$), while responsive individuals flexibly employ the two extreme strategies "always choose patch A" ($l_0^* = 1$) and "always choose patch B" ($l_1^* = 0$), depending on the state of the environment.

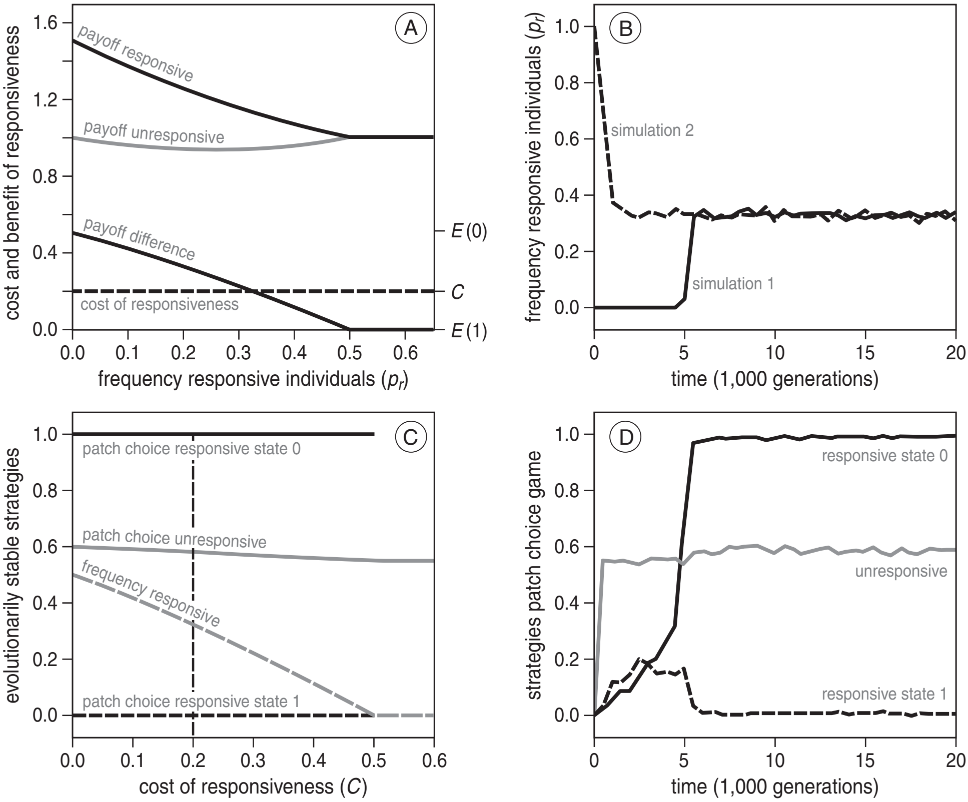


Figure 5.2 Coexistence of responsive and unresponsive individuals due to frequency-dependent selection, illustrated for a situation where the options L and R correspond to the alternatives in a patch choice game. (A) Dependence of payoffs on the proportion of responsive individuals in the population. Responsive individuals always obtain a payoff that is at least as high as the payoff to unresponsive individuals. The benefits of responsiveness (i.e., the excess payoff of responsive individuals, black line) decreases from a value $E(0) = 0.5$ in a population of unresponsive individuals to $E(1) = 0$ in populations with a high proportion of responsive individuals. The benefits of responsiveness exactly balance the cost of responsiveness at $p_r = 0.32$. (B) Two individual-based simulations illustrating that, independent of the initial conditions, natural selection gives rise to the stable mixture of responsive and unresponsive individuals predicted by A. (C) Dependence of the evolutionarily stable strategies on the cost of responsiveness. The dashed black line corresponds to the configuration in A and B. (D) Individual-based simulation showing the evolution of behaviour in the patch choice game. At equilibrium, responsive individuals exhibit a state-dependent pure strategy: "always choose patch L state 0" and "always choose patch R in state 1". Unresponsive individuals employ a mixed strategy.

CONSISTENT INDIVIDUAL DIFFERENCES IN RESPONSIVENESS

Positive feedbacks and consistency

Empirical evidence suggests that individuals that are responsive to environmental stimuli at one point in time and in one context tend to be responsive at later points in time and in different contexts as well (Koolhaas *et al.*, 1999; Groothuis & Carere, 2005). Why should natural selection give rise to such consistency? Consider first the extreme case were being responsive once reduces the cost of further responsiveness to zero. In this case it is obvious that previously responsive individuals should be responsive anew, since they can reap the benefits of responsive behaviour without incurring additional cost. Hence, responsiveness is consistent within and across contexts. This is an extreme scenario because early responsiveness has a very strong feedback on the cost of later responsiveness. However we now show that even the tiniest feedback is sufficient to induce consistent individual differences in responsiveness.

To investigate the effect of such feedbacks we now consider a two stage scenario. In each of the stages, individuals face the choice between adopting a responsive or an unresponsive strategy. The two stages might either represent the same context at different points in time (e.g., patch choice early and late in the season) or different contexts (e.g., a patch choice and aggressive encounters). In both stages individuals face a choice between two options (say L and R in stage 1 and L' and R' in stage 2) where the payoffs are again negative frequency-dependent and dependent on the state of the environment. For simplicity we assume that the environmental states in both stages are uncorrelated. Individuals that are responsive in any of the two stages get to known the environmental state in that stage and can fine tune their behaviour accordingly. The fitness of an individual is given by the sum of payoffs obtained in both stages reduced by the cost of responsiveness. As above, the cost of responsiveness in the first stage is given by C . We assume that the cost of responsiveness in second stage is smaller for individuals that are responsive in the first stage (C_r) than for those individuals that are unresponsive in the first stage (C_{ur}). In the Appendix we show that even the smallest cost reduction gives rise to consistency in responsiveness: at the ESS, individuals that are responsive in the first stage have a higher tendency to be responsive in the second stage ($p_r\big|_r$) than individuals that are unresponsive in the first stage ($p_r\big|_{ur}$), that is

$$p_r^*\big|_r > p_r^*\big|_{ur} \tag{3}$$

In fact, as we presently show, even a very small feedback gives rise to strong consistency in responsiveness across stages.

Example II: Consistency and behavioural syndromes

We now illustrate this result and its consequences for a situation where individuals have to choose a patch in the first stage (as above) and are involved in aggressive encounters in the second stage. Aggressive encounters are modelled as a hawk-dove (Maynard Smith, 1982) game (L' = "hawk" and R' = "dove"): individuals fight for a resource of value V and aggressive hawks risk injury, reducing their payoff by D. Now we assume that the resource value is either V_0 or V_1, depending on the state of the environment.

Figure 5.3A depicts how the ESS level of responsiveness depends on the strength of the feedback. For any degree of cost reduction, first stage responsiveness is represented by the black line while second stage responsiveness of previously responsive and unresponsive individuals is depicted by the dashed and solid grey line, respectively. Note that for strong feedbacks all individuals play a pure strategy in the second stage: previously responsive individuals are always responsive while previously unresponsive individuals are never responsive. Remarkably a dichotomy of similar strength already occurs at very weak feedbacks. In other words, the smallest cost reduction gives rise to consistent individual differences. Our individual-based simulations (Figure 5.3B) are in perfect agreement with these analytical predictions.

Behavioural syndromes

As in the one-stage game considered above, at the ESS, unresponsive individuals play a general-purpose mixed strategy in both stages whereas responsive individuals adapt their behaviour to the prevailing conditions and choose a pure strategy (Fig. 5.3C, 5.3D). Notice that, for a given combination of environmental states, all responsive individuals play the same combination of pure strategies in both stages. At the population level this induces a correlation between the behavioural choices in stage 1 and stage 2. In other words, consistent individual differences in responsiveness induce behavioural correlations that might be interpreted as behavioural syndromes (Clark & Ehlinger, 1987; Sih *et al.*, 2004a). Note that this cross-context correlation is derived in the sense that it reflects consistency rather than an intrinsic link between the two contexts. This is also reflected by the fact that the sign and the strength of these correlations depend on the environment (Fig. 5.3E).

DISCUSSION

Frequency dependence

Our explanation for the coexistence of responsive and unresponsive individuals is

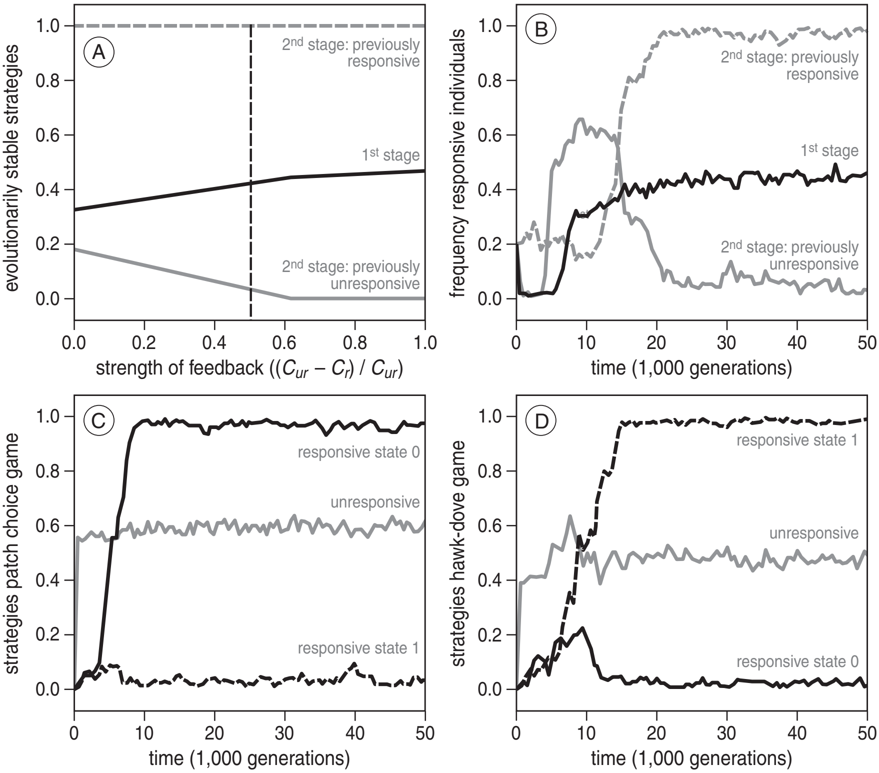
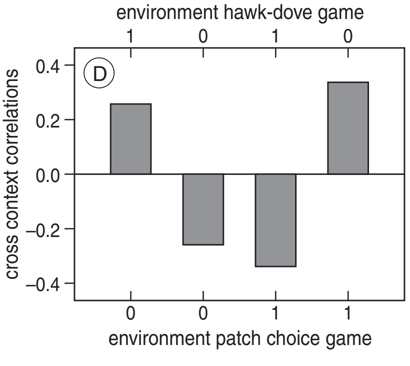


Figure 5.3 Evolution of consistent individual differences in responsiveness due to positive feedbacks. (A) Evolutionarily stable responsiveness illustrating that, independent of the strength of feedback, individuals that are responsive in the first stage (here patch choice game) show high levels of responsiveness in the second stage (here a hawk-dove game) while previously unresponsive individuals show low levels of responsiveness in the second stage. The dashed black line corresponds to the configuration in the individual based simulations B-E. (B) Typical simulation illustrating the evolution of consistent individual differences in responsiveness. Both in the patch choice context (C) and in the hawk-dove context (D) unresponsive individuals evolve a mixed strategy while responsive individuals evolve the pure strategies that are employed dependent on the state of the environment. (E) For each combination of environmental states in the two stages, a correlation results between the behavioural choices (patch choice and hawk-dove game), induced by the fact that individuals differ consistently in their responsiveness and that responsive individuals play a pure strategy in either state. The sign and the strength of these correlations depend on the combination of states in both contexts.



based on the insight that the benefits of responsiveness are negatively frequency dependent. The crucial assumption for this result is that the payoffs at the level of the behavioural choices (e.g. patch choice, aggressive encounters) are negatively frequency dependent. This is a realistic assumption. For example, behaviour in social interactions (e.g., aggressive or cooperative behaviour) has frequency-dependent payoffs almost by definition, since the outcome depends on the behaviour of all participants (Maynard Smith, 1982; Svensson & Sheldon, 1998; Dugatkin & Reeve, 2000). Other forms of frequency dependence arise whenever individuals compete for limiting resources as, for example, in a foraging context. In these situations individual behaviour impacts on the environment which in turn feeds back on the individuals (Kokko & Lopez-Sepulcre, 2007). Next to such ecological mechanisms a variety of other mechanisms can also lead to frequency dependence (Sinervo & Calsbeek, 2006).

Emergence of polymorphism

In our model frequency dependent selection gives rise to a polymorphism. This may, however, reflect the assumption that individuals face a binary choice between adopting a responsive or an unresponsive tactic. Such an 'all or nothing' decision is a reasonable assumption in some situations, in others, responsiveness is better viewed as a continuous trait. We give two examples. First, individuals may vary their degree of sampling on a scale from superficial to thorough. Second, individuals may vary their rate of sampling as, for example, when individuals have a certain tendency to interrupt the adopted behaviour in order to sample.

When responsiveness can vary continuously, negative frequency dependence may either result in a monomorphism with an intermediate degree of responsiveness or a polymorphism where individuals differ in their responsiveness. The evolutionary outcome will reflect the shape of the trade-off individuals face. Intuitively, when the costs and benefits associated with responsiveness give rise to convex trade-offs polymorphism is favoured, concave trade-offs favour monomorphism (Rueffler *et al.*, 2004). Interestingly, the coexistence of responsive and unresponsive phenotypes has been suggested in other contexts as, for example, the coexistence of plastic and canalized developmental strategies (Plaistow *et al.*, 2004) or the coexistence of generalists and specialists (Wilson & Yoshimura, 1994c).

Positive feedbacks

Our model explains consistency in responsiveness by a positive feedback mechanism. Previously responsive individuals have a higher tendency to be responsive again because they face lower costs (or higher benefits) than previously unresponsive individuals. Remarkably, the smallest such asymmetry translates in a strong positive association of responsiveness across stages.

It is highly plausible that positive feedbacks act within contexts as, for example, in the case when responsive individuals get better in being responsive (e.g., assessing cues) with repeated experience (Rosenzweig & Bennett, 1996). Cross-context feedbacks might seem less likely, however, they can be caused by various mechanisms and we give three examples. First, the cost of responsiveness may consist of a context-independent part (e.g., screening the environment) and a context-specific part (e.g., screening for specific cues). With respect to a second context, the context-independent part represents fixed costs that do not have to be paid again. Second, individuals that are responsive in one context may build up knowledge and skills that can be used in a different context. If, for example, individuals get better in interpreting environmental cues the costs are lower for experienced than for inexperienced individuals. Third, information gathered in one context may prove useful for assessing the state of the environment in a different context, that is, information acquired in one context may spill over to a different context.

Responsiveness and behavioural flexibility

In the empirical literature differences in responsiveness are also referred to as differences in flexibility, plasticity and reactivity. These categories are often used synonymously (e.g., Koolhaas *et al.*, 1999; Korte *et al.*, 2005). However, this is not always adequate. While responsiveness refers to the propensity of an individual to adjust its behaviour to the prevailing environmental conditions, behavioural flexibility refers to the tendency of an individual to show varying behaviour when confronted with the same context repeatedly. One might think that responsive individuals are flexible (i.e., show varying behaviour) and unresponsive individuals are rigid (i.e., show the same behaviour). Our analysis shows, however, that this relation is more ambiguous.

Consider a situation where individuals are repeatedly confronted with the same context under uncertainty. Both responsive and unresponsive individuals will appear flexible to an observer. Responsive individual are flexible since they play a state dependent pure strategy and thus change their behaviour with the environmental state. Yet, also unresponsive individuals are flexible since they play a mixed strategy and hence change their behaviour due to randomization. There is, however, a crucial difference between the two strategies: only responsive individuals vary their behaviour systematically in response to the environmental conditions.

The relation between responsiveness and flexibility is not always as ambiguous. We give two examples. First, consider the above scenario where individuals are repeatedly confronted with the same context but now assume that there is a cost associated with changing behaviour (e.g., switching patches might be costly). Such a cost has a differential effect on responsive and unresponsive individuals. While responsive individuals change their behaviour only when it pays to, unresponsive individuals do not improve their payoff by changing behaviour. Consequently, whenever there is a cost associated with changing behaviour, unresponsive individuals should rigidly stick to the behaviour once chosen while responsive individuals should keep changing their behaviour flexibly whenever the environmental state changes. Note that in such a case unresponsive individuals still mix between both alternatives on a population level: some choose consistently option *L* while others choose option *R*.

Second, consider a situation where individuals, instead of choosing between two discrete alternative *L* and *R*, face a choice between a continuum of alternatives. For example, instead of choosing between an aggressive hawk and a non-aggressive dove strategy, individuals might choose an intensity of aggression that varies continuously between a minimum level *L* and a maximum level *R*. In this case, the mixed strategy of unresponsive individuals does not correspond to a randomization but to an intermediate intensity of aggression. Thus, when confronted with such a context repeatedly, unresponsive individuals rigidly show the same intermediate level of aggression while responsive individuals flexibly exhibit maximal and minimal levels of aggression, dependent on the state of the environment.

Implications for understanding animal personalities

The defining feature of animal personalities is that individual behaviour is correlated over time and across contexts. Such correlations, or behavioural syndromes (Clark & Ehlinger, 1987; Sih *et al.*, 2004b) seem puzzling since a more flexible structure of behaviour should be advantageous. Current explanations fall into two classes. According to the 'constraint view', trait correlations result from constraints on the architecture of behaviour (Sih *et al.*, 2004b). This view emphasizes seemingly non-adaptive aspects of behaviour and limited plasticity. However, it remains unclear why the underlying constraints are not removed by natural selection. Interestingly, our model exemplifies that individuals with a flexible architecture may invade the constraint one, but not necessarily go to fixation.

According to the 'adaptive view', trait correlations are the result of natural selection. Particular combinations of traits appear together because they work well together (Wilson, 1998; Rands *et al.*, 2003; Dall *et al.*, 2004; McElreath & Strimling, 2006; Stamps, 2007; Wolf *et al.*, 2007a). For example, the boldness-aggressiveness syndrome has been explained in terms of differences in energy reserves (Rands *et al.*, 2003), differences in future fitness expectations (Wolf *et al.*, 2007a) and differences in growth rates (Stamps, 2007). While being in the realm of the adaptive view, our results provide a different type of explanation. Individual differences at the level of the behavioural organization can give rise to correlative associations of all kinds of otherwise unrelated behaviours.

Consider the above scenario where evolution gives rise to a correlation between the patch choice behaviour of individuals and their aggressiveness (Fig. 5.3E). Suppose that the patches differ in their riskiness (e.g., presence of a predator) such that patch choice might be interpreted as a choice between being bold and being shy. In this case the correlation pattern in Figure 5.3E resembles an environment-specific boldness-aggressiveness syndrome that has been found in natural populations of sticklebacks (Bell & Stamps, 2004; Dingemanse *et al.*, 2007). Notice, however, that this correlation is not caused by an intrinsic link between boldness and aggressiveness. Rather it is caused by the fact that the coexisting responsive and unresponsive individuals employ different decision rules to choose between the behavioural alternatives (L vs. R). While responsive individuals use a fine-tuned rule that conditions the behaviour on the prevailing environmental circumstances ("show tendency l_i in state i"), unresponsive individuals employ a general-purpose rule that does not distinguish between particular environmental conditions ("always show tendency $\overline{l}$"). As a result, responsive individuals play the same combination of pure strategies in the two choice situations, which induces the behavioural correlations at the population level. Trait correlations do therefore not necessarily reflect an inherent connection between the associated traits but can be a by-product of stable individual differences at the level of behavioural organization.

METHODS

Here we give the set-up of the individual-based simulations. The analytical results are derived in the Appendix.

We simulated a spatially heterogeneous metapopulation with many "islands" (i.e., local patches). The islands differ in their environmental conditions for the choice situations (L vs. R): for the patch choice (hawk-dove) context in stage 1 (stage 2) a fraction s_0 (s'_0) of the islands is in state 0, the remaining islands are in state 1. For the two stage scenario, the environmental conditions for each of the stages are drawn independently from each other. In all our simulations we studied populations of 5000 individuals that are distributed among 50 islands.

After birth individuals disperse to a random island. Individuals are haploid and characterized by a suite of heritable traits corresponding to (1) the tendency to choose the responsive strategy in each of the stages and (2) the tendency to choose option L in each of the stages. Each of these traits is encoded by a separate gene locus; for the two stage scenario, separate loci encode the behaviour in the first and in the second stage. After obtaining the payoff (see below), individuals mate at random within each island, reproduce and then die. Each island contributes equally to the total offspring generation; within islands, the relative contribution of an individual to the offspring generation is proportional to its net payoff. During reproduction, mutations occur with probability $\mu = 1\times10^{-3}$. Whenever a mutation occurs it has a small effect on a random locus: it changes the strategy of an individual by a value that is drawn from a normal distribution with mean 0 and standard deviation 0.1, with the constraint that it remains in the interval from 0 to 1.

For the one stage scenario (Fig. 5.2) individuals face a situation as depicted in Figure 5.1. We assume that the options L and R represent the behavioural alternatives in a patch choice game. For an island with environmental state i, the payoff that an individual obtains in any of the two patches is given by

$a_i = \dfrac{A_i}{f_i}$ and $b_i = \dfrac{B_i}{1-f_i}$, where A_i and B_i are state dependent baseline values and f is the frequency of individuals that choose patch L in this island. All simulations are based on $A_0 = 0.8$, $B_0 = 0.2$, $A_1 = 0.3$, $B_1 = 0.7$, $C = 0.2$ and $s_0 = 0.5$.

For the two-stage scenario (Fig. 5.3) individuals face a situation as depicted in Figure 1 twice. We assume that the options represent the behavioural alternatives in a patch choice game in the first stage and the alternatives in a hawk-dove game in the second stage (see main text). In the hawk-dove game, individuals within an island are paired at random and fight for a resource with a value V_i, which depends on the island's state of the environment for the hawk-dove game. Payoffs are obtained as in the standard hawk-dove game (22): when two hawks meet, one gets V_i while the other gets $-D$; when two doves meet, both get $V_i/2$; when a hawk meets a dove, the hawk gets V_i and the dove gets 0. Figure 5.3 is based on $V_0 = 2$, $V_1 = 8$, $D = 10$ for the hawk dove game, $C = 0.2$, $C_{ur} = 0.2$, $C_r = 0.1$ for the cost of responsiveness and $s_0 = 0.5$, $s'_0 = 0.5$.

ACKNOWLEDGEMENTS

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Appendix

Here we derive the analytical results that we have given in the main text. We first investigated the coexistence of responsive and unresponsive strategies. To this end we analyze the one-stage game depicted in Figure 5.1 in the main text. We show that whenever the payoffs of the two options L and R are negatively frequency dependent, then also the benefits of responsiveness are negatively frequency dependent (Result 1). As argued in the main text, this favours the coexistence of responsive and unresponsive strategies. We then addressed the question why individuals are consistent in their responsiveness. To this end we analyze the two-stage game described in the main text. We assume that positive feedbacks act on responsiveness; that is, responsiveness is less costly (or more beneficial) for individuals that have been responsive before. We show that under this assumption, at any ESS, individuals that are responsive in the first stage have a higher tendency to be responsive in the second stage than individuals that are unresponsive in the first stage (Result 2). As a result individuals differ consistently in their responsiveness.

COEXISTENCE OF UNRESPONSIVE AND RESPONSIVE INDIVIDUALS

Consider the one-stage game depicted in Figure 5.1 in the main text. A strategy in this game is a quadruple $p = (p_r, \overline{l}, l_0, l_1)$, where
p_r is the probability that an individual is responsive,
$\overline{l}$ is the probability that an unresponsive individual chooses option L and
l_i is the probability that a responsive individual chooses option L in state $i = 0{,}1$.

We consider a monomorphic population where each individual is responsive with probability p_r. We assume that for any given level p_r of responsiveness, individuals show the corresponding ESS behaviour $(\overline{l}, l_0^*, l_1^*)$. Selection increases the level of responsiveness p_r whenever the benefits of responsiveness exceed the costs of responsiveness C. The benefits of responsiveness are given by the expected excess payoff E of a responsive over an unresponsive individual. In state i, a responsive individual plays strategy l_i^* and obtains the payoff $l_i^* \cdot a_i + (1 - l_i^*) \cdot b_i$, an unresponsive individual plays $\overline{l}^*$ and obtains the payoff $\overline{l}^* \cdot a_i + (1 - \overline{l}^*) \cdot b_i$. The payoff difference in state i is therefore $(l_i^* - \overline{l}^*) \cdot (a_i - b_i)$ and the benefits of responsiveness are thus given by

$$E(p_r) = \sum_i s_i \cdot (l_i^* - \bar{l}^*) \cdot \Delta_i \tag{1}$$

where

$$\Delta_i = a_i - b_i \tag{2}$$

gives the excess payoff of option L over R in state i. Note that $E(p_r) \geq 0$ since a responsive individual can always achieve a payoff at least as high as unresponsive individual.

Result 1

If the excess payoff Δ_i of choosing L over R in state i is negatively frequency dependent, that is, if Δ_i decreases with the frequency of individuals f_i that choose option L in state i, then the benefits of responsiveness are also negatively frequency dependent. Technically,

$$\frac{d\Delta_i}{df_i} < 0 \quad \Rightarrow \quad \frac{dE}{dp_r} < 0 \tag{3}$$

as long as $E > 0$.

PROOF

Note that

$$\frac{dE}{dp_r} = \sum_i s_i \cdot (l_i^* - \bar{l}^*) \cdot \frac{d\Delta_i}{dp_r} + \sum_i s_i \cdot \Delta_i \cdot \frac{dl_i^*}{dp_r} - \frac{d\bar{l}^*}{dp_r} \cdot \sum_i s_i \cdot \Delta_i \tag{4}$$

which simplifies to

$$\frac{dE}{dp_r} = \sum_i s_i \cdot (l_i^* - \bar{l}^*) \cdot \frac{d\Delta_i}{dp_r} \tag{5}$$

since the last two terms in (4) equal to zero. This can be seen at follows. The expected payoffs of a responsive and an unresponsive individual are given by $\sum_i s_i \cdot l_i \cdot \Delta_i$ and $\bar{l} \cdot \sum_i s_i \cdot \Delta_i$, respectively. From this follows that at any ESS $(\bar{l}, l_0^*, l_1^*)$,

$$l_i^* = \begin{cases} 1 & \text{for } \Delta_i > 0 \\ 0 & \text{for } \Delta_i < 0 \end{cases} \qquad \text{and} \qquad \bar{l}^* = \begin{cases} 1 & \text{for } \sum_i s_i \cdot \Delta_i > 0 \\ 0 & \text{for } \sum_i s_i \cdot \Delta_i < 0 \end{cases} \tag{6}$$

which implies that the last two terms in (4) equal to zero since either $\Delta_i = 0$ or

$$\Delta_i \neq 0 \;\Rightarrow\; \frac{dl_i^*}{dp_r} = \frac{dl_i^*}{d\Delta_i} \cdot \frac{d\Delta_i}{dp_r} = 0 \tag{7}$$

and either $\sum_i s_i \cdot \Delta_i = 0$ or

$$\sum_i s_i \cdot \Delta_i \neq 0 \;\Rightarrow\; \frac{d\overline{l}^*}{dp_r} = \frac{d\overline{l}^*}{d\left(\sum_i s_i \cdot \Delta_i\right)} \cdot \frac{d\left(\sum_i s_i \cdot \Delta_i\right)}{dp_r} = 0 \tag{8}$$

To show Result 1 we thus have to show that whenever the excess payoff Δ_i of choosing L over R is negatively frequency dependent, then also

$$\frac{dE}{dp_r} = \sum_i s_i \cdot (l_i^* - \overline{l}^*) \cdot \frac{d\Delta_i}{dp_r} < 0 \tag{9}$$

or, equivalently

$$\frac{dE}{dp_r} = \sum_i s_i \cdot (l_i^* - \overline{l}^*) \cdot \frac{d\Delta_i}{df_i} \cdot \frac{df_i}{dp_r} < 0 \tag{10}$$

The frequency of individuals f_i that chooses option L in state i is given by

$f_i = p_r \cdot l_i^* + (1 - p_r) \cdot \overline{l}^*$ and thus $\frac{df_i}{dp_r} = l_i^* - \overline{l}^* + p_r \cdot \frac{dl_i^*}{dp_r} + (1 - p_r) \cdot \frac{d\overline{l}^*}{dp_r}$. Note that from equations (1) and (6) follows that whenever $E(p_r) > 0$ then $\Delta_i \neq 0$ in both states and therefore $\frac{dl_i^*}{dp_r} = 0$. Consequently,

$$\frac{dl_i^*}{dp_r} = l_i^* - \overline{l}^* + (1 - p_r) \cdot \frac{d\overline{l}^*}{dp_r} . \tag{11}$$

We now distinguish two cases.

Case 1: Unresponsive individuals play a pure strategy, i.e. $\overline{l}^* = 1$ or $\overline{l}^* = 0$. In this case, $\sum_i s_i \cdot \Delta_i \neq 0$ and thus $\frac{d\overline{l}}{dp_r} = 0$. But this implies with equation (10) and (11) that

$$\frac{dE}{dp_r} = \sum_i s_i \cdot (l_i^* - \overline{l}^*)^2 \cdot \frac{d\Delta_i}{df_i} < 0 \tag{12}$$

since $\frac{d\Delta_i}{df_i} < 0$.

Case 2: Unresponsive individuals play a mixed strategy, i.e. $0 < \bar{l}^* < 1$. In this case, $\sum_i s_i \Delta_i = 0$ and $\sum_i s_i \frac{d\Delta_i}{dp_r} = 0$. This, in combination with the facts that $\frac{d\Delta_i}{dp_r} = \frac{d\Delta_i}{df_i} \cdot \frac{df_i}{dp_r}$ and $\left.\frac{df_i}{dp_r}\right|_{l_i^*=1} > \left.\frac{df_i}{dp_r}\right|_{l_i^*=0}$ implies that $\frac{d\Delta_i}{dp_r} > 0$ in one state and $\frac{d\Delta_j}{dp_r} < 0$ in the other state.

From this follows that

$$\text{sign}\,(l_i^* - \bar{l}^*) = -\text{sign}\,\frac{d\Delta_i}{dp_r} \tag{13}$$

and thus $\frac{dE}{dp_r} = \sum_i s_i \cdot \left(l_i^* - \bar{l}^*\right) \cdot \frac{d\Delta_i}{dp_r} = 0$. This establishes Result 1.

Calculating the benefits of responsiveness for specific applications

As argued in the main text, both the responsive and the unresponsive strategy can spread when rare whenever

$$E(0) > C > E(1) \tag{14}$$

leading to the coexistence of both strategies. For any particular application at hand we might thus want to know $E(0)$ and $E(1)$.

Consider first the benefits of responsiveness $E(1)$ in a population of responsive individuals. We distinguish three cases. First, if responsive individuals play a mixed ESS in both states (i.e., $0 < \bar{l}^* < 1$), as in the patch choice and hawk dove game in the main text, the frequency dependent payoffs between the two choice L and R will be equalized in both states (i.e., $\Delta_i = 0$) and thus

$$E(1) = 0 \tag{15}$$

Second, when responsive individuals mix in one of the states but not in the other, $\Delta_i \neq 0 \Rightarrow l_i^* - \bar{l}^* = 0$ and thus, as above, $E(1) = 0$. Third, when responsive individuals do not mix in any of the two states (i.e., play a pure strategy in both states) we get $E(1) = \min\,(s_0 \cdot |\Delta_0|, s_1 \cdot |\Delta_1|)$.

Consider next the benefits of responsiveness $E(0)$ in a population of unresponsive individuals. In such a population, unresponsive individuals will typically play a mixed strategy. Using the facts that in this case $\sum_i s_i \cdot \Delta_i = 0$ and Δ_i is positive in some state (i.e., $l_i^* = 1$) and negative in the other (i.e., $l_i^* = 0$) we get

$$E(0) = s_0 \cdot s_i \cdot \Delta \tag{16}$$

where $\Delta = \sum_i \left| \Delta_i \right|$ is a measure for the environmental asymmetry in such a population that can be readily calculated. For example, in case of the hawk-dove game considered in the main text $\Delta = \frac{1}{2} \cdot \left| V_0 - V_1 \right|$. In case of the patch choice game considered in the main text, $\Delta_i = A_i \,/\, \tilde{A} - B_i / \tilde{B}$ where $\tilde{X} = \bar{X} \,/(\bar{A} + \bar{B}\,)$ and $\bar{X} = s_0 \cdot X_0 + s_1 \cdot X_1$ for $X = A, B$.

CONSISTENT INDIVIDUAL DIFFERENCES IN RESPONSIVENESS

Consider the two-stage game described in the main text. Both, in the first and in the second stage, individuals face a situation as depicted in Figure 5.1 in the main text. Both stages might either represent the same context at different points in time (e.g., patch choice early and late in the season) or different contexts (e.g., patch choice and aggressive encounters, as in the main text). For simplicity we assume that the environmental states in both stages are uncorrelated. The total payoff of an individual is given by the sum of payoffs this individual obtains in both stages.

To investigate consistency in responsiveness we allow that individuals can make their responsiveness in the second stage dependent on their responsiveness in the first stage. A strategy in the two-stage game is a tuple $p = (p_r, p_r\big|_r, p_r\big|_{ur}, l)$, where

p_r	is the probability that an individual is responsive in the first stage,
$(p_r\big|_r, p_r\big|_{ur})$	is the probability that an individual that is responsive (unresponsive) in the first stage is responsive in the second stage,
l	is a vector that specifies the behaviour in the *L* vs. *R* choice situations, both in the first and in the second stage.

The expected net payoff of a rare mutant with strategy p in a resident population with strategy $\hat{p}$ is given by

$$w(p, \hat{p}) = p_r \cdot (p_r\big|_r \cdot w_{r,r} + (1 - p_r\big|_r) \cdot w_{r,ur}) + (1 - p_r) \cdot (p_r\big|_{ur} \cdot w_{ur,r} + (1 - p_r\big|_{ur}) \cdot w_{ur,ur}) \tag{17}$$

where $w_{j,i} = w_{j,i}(p, \hat{p})$ is the expected net payoff of an individual with responsiveness $j = r,ur$ in the first stage and $i = r,ur$ in the second stage (r = responsive, ur = unresponsive). These payoffs are given by

$$w_{j,i}(p, \hat{p}) = w_j(p, \hat{p}) + w_i\big|_j(p, \hat{p}) \tag{18}$$

where w_j is the expected first-stage net payoff of an individual with first-stage responsiveness $j = r,ur$ and $w_i\big|_j$ is the expected second-stage net payoff of an individual with first-stage responsiveness $j = r,ur$ and second-stage responsiveness $i = r,ur$.

Positive feedbacks on responsiveness
We say that positive feedbacks act on responsiveness whenever

$$w_r\big|_r(p,\hat{p}) \geq w_r\big|_{ur}(p,\hat{p}) \text{ and } w_{ur}\big|_{ur}(p,\hat{p}) \geq w_{ur}\big|_r(p,\hat{p}) \tag{19}$$

with at least one inequality being strict. In words, either the expected second-stage net payoff of being responsive is higher for individuals that were responsive in the first-stage or the expected second-stage net payoff of being unresponsive is higher for individuals that were unresponsive also in the first stage. Such feedbacks might be the result of increased benefits of responsiveness or decreased costs of responsiveness for individuals that are consistently responsive.

Positive feedbacks via a reduction of costs
In the main text we assumed that the cost of responsiveness in the second-stage is lower for individuals that are responsive in the first stage (C_r) than for individuals that are unresponsive in the first stage (C_{ur}):

$$C_r < C_{ur}\,. \tag{20}$$

Note that this is a special case of positive feedbacks on responsiveness (19) since (20) implies that for an individual with strategy p in a resident population with strategy $\hat{p}$:

$$w_r\big|_r(p,\hat{p}) - w_r\big|_{ur}(p,\hat{p}) = C_{ur} - C_r > 0\,. \tag{21}$$

Result 2
Whenever positive feedbacks act on responsiveness, at any ESS , individuals that are responsive in the first stage have a higher tendency to be responsive in the second stage than individuals that are unresponsive in the first stage, that is

$$p_r^*\big|_r \geq p_r^*\big|_{ur}\,. \tag{22}$$

The inequality being strict when, at the ESS, both responsive and unresponsive individuals occur in the second stage.

PROOF. The expected net payoff of a rare mutant with strategy p in a resident population with strategy $\hat{p}$ is given by (equation (17)):

$$w(p, \hat{p}) = p_r \cdot (w_{r,ur} + p_r\big|_r \cdot (w_r\big|_r - w_r\big|_{ur})) + (1 - p_r) \cdot (w_{ur,ur} + p_r\big|_{ur} \cdot (w_{ur,r} - w_{ur,ur})) \tag{23}$$

or, equivalently (with (18)),

$$w(p, \hat{p}) = p_r \cdot (w_{r,ur} + p_r\big|_r \cdot (w_r\big|_r - w_{ur}\big|_r)) + (1 - p_r) \cdot (w_{ur,ur} + p_r\big|_{ur} \cdot (w_r\big|_{ur} - w_{ur}\big|_{ur})) \tag{24}$$

Now note that from the definition of positive feedbacks (19) follows that $w_r\big|_r - w_{ur}\big|_r > w_r\big|_{ur} - w_{ur}\big|_{ur}$. To see that Result 2 follows from this consider the following three possibilities. (1) $w_r\big|_r - w_{ur}\big|_r < 0$. This implies that $w_r\big|_{ur} - w_{ur}\big|_{ur} < 0$. At such an ESS, $p_r^*\big|_r = p_r^*\big|_{ur} = 0$, being unresponsive is a dominant strategy in the second stage. (2) $w_r\big|_r - w_{ur}\big|_r = 0$. This implies that $w_r\big|_{ur} - w_{ur}\big|_{ur} < 0$. At such an ESS $p_r^*\big|_r \geq 0$ and $p_r^*\big|_{ur} = 0$. (3) $w_r\big|_r - w_{ur}\big|_r > 0$. In this case $w_r\big|_{ur} - w_{ur}\big|_{ur}$ might either be positive, zero or negative. At any ESS with $w_r\big|_{ur} - w_{ur}\big|_{ur} > 0$, $p_r^*\big|_r = p_r^*\big|_{ur} = 1$, being responsive is a dominant strategy in the second stage. At any ESS with $w_r\big|_{ur} - w_{ur}\big|_{ur} = 0$, $p_r^*\big|_r = 1$ and $p_r^*\big|_{ur} \leq 1$. At any ESS with $w_r\big|_{ur} - w_{ur}\big|_{ur} < 0$, $p_r^*\big|_r = 1$ and $p_r^*\big|_{ur} = 0$. This establishes Result 2.

Chapter 6

Variation, responsiveness and the evolution of behavioural consistency

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ABSTRACT

Much recent research focuses on animal personalities (behavioural syndromes, coping styles), that is, individual differences in suites of correlated behaviours that are consistent over time. While behavioural consistency over time is one of the hallmarks of personalities, its adaptive value is not well understood. Current explanations focus on constraints in the architecture of behaviour (e.g., pleiotropic genes) and positive feedback mechanisms such as learning and training. Here we investigate a third explanation, namely that consistency is favoured since it makes individuals predictable, which, in turn, can be beneficial in many social interactions. This explanation hinges on the presence of responsive individuals, that adjust their behaviour in response to the behavioural history of their social partners. Responsiveness however, is only beneficial in the presence of consistent individual differences. We present a simple evolutionary model that investigates this feedback between responsiveness and consistency. We first show that responsive strategies are favoured even in the presence of a very small degree of consistent individual differences (e.g., due to mutation and drift). We then show that the presence of responsive individuals can indeed trigger a coevolutionary process between responsiveness and consistency which gives rise to high levels of adaptive behavioural consistency among unresponsive individuals.

INTRODUCTION

There is increasing evidence from a diverse range of animal species that individuals often differ consistently in their behavioural tendencies (Clark & Ehlinger, 1987; Wilson *et al.*, 1994a; Wilson, 1998; Gosling & John, 1999; Koolhaas et al., 1999; Gosling, 2001; Sih *et al.*, 2004; Groothuis & Carere, 2005; Korte *et al.*, 2005). Consistent individual differences in, for example, cooperative behaviour (Kurzban & Houser, 2005), boldness (Wilson *et al.*, 1994a) or aggressiveness (Koolhaas *et al.*, 1999) have been documented, next to humans, in species as diverse as birds, fish and rodents.

From an adaptive point of view, such consistency in behaviour appears surprising. In contrast to many morphological and physiological characteristics, which can often only be modified under substantial costs to the individual, behavioural traits are thought to be potentially much more flexible in their expression over time (Coleman & Wilson, 1998; Dall *et al.*, 2004). Nothing appears to prevent a stickleback that attacks intruders aggressively at one point in time to adopt a non-aggressive strategy at a later point in time. Similarly, why should a human that behaves altruistically in one situation not be cheating at a later point in time? The observation of consistency suggests that, in some situations, sticking to a previously expressed behavioural phenotype is beneficial to an individual.

Currently, most explanations for behavioural consistency are based on either constraints in the architecture of behaviour or positive feedbacks between current and future actions (Dall *et al.*, 2004; Sih & Bell, 2008). The architecture of behaviour can give rise to consistency whenever behavioural actions at different points in time are affected by a common mechanism within this architecture. It has been shown, for example, that the positive correlation of aggressiveness through ontogeny in the three-spined stickleback (*Gasterosteus aculeatus*) can in part be attributed to pleiotropic genes (Bakker, 1986). Positive feedbacks between current and future actions can give rise to consistency whenever the actions taken at an earlier point in time affect the costs or benefits of future actions, for example due to learning or skill formation (Wolf *et al.*, 2008b).

In this study we focus on a third explanation, which might play an important role for the consistency of social behaviours: consistency gives rise to predictability which, in turn, can be beneficial in social interaction (Dall *et al.*, 2004). There are at least three types of situations in which individuals benefit from being predictable. First, whenever the actions of social partners have to be coordinated, predictability is beneficial because it allows the partner to choose the appropriate actions. Second, whenever individuals compete for social interactions, being predictable can increase the value as a partner (McNamara *et al.*, 2008; McNamara *et al.*, 2009).

Third, being predictable can help to exploit social partners. Individuals might, for example, consistently put little effort into a joint project (e.g., parental care) and thus "force" their partner to put more effort into that project.

The essence of all three situations is that, by being predictable, consistent individuals can affect their partner's behaviour in a self-serving way. This argument clearly hinges on the presence of responsive (reactive, socially aware, eavesdropping) individuals which, when choosing their action, take into account the behavioural history of their social partners. To put it differently, being predictable can only be advantageous if someone responds. Under which conditions should we expect the presence such responsive individuals?

The benefits to a responsive strategy depend on two factors, variation and consistency. Without variation among individuals, there is no need to be responsive. Whenever there is variation among individuals, responsiveness is beneficial only if individuals are consistent (otherwise past behaviour does not help to "predict" future behaviour). As has been shown for the contexts of aggressive (Johnstone, 2001) and cooperative interactions (McNamara *et al.*, 2004; McNamara *et al.*, 2008; McNamara *et al.*, 2009a), responsive strategies should thus be favoured in the presence of consistent individual differences.

Consistency thus selects for responsiveness, which, given our arguments above, should favour consistency. Comparable feedbacks, in which a potentially small degree of individual differences favours responsive strategies, which, in turn, gives rise to a change of selection pressures that gives rise to very different evolutionary outcomes has been described recently (McNamara *et al.*, 2008; McNamara *et al.*, 2009a).

To investigate whether these verbal arguments can indeed explain the evolution of behavioural consistency we here construct a simple evolutionary model. In our model, individuals are engaged in pairwise interactions in which the benefits to an individual depend both on its own action and on the action taken by its partner. We discuss three applications: aggressive interactions in a hawk-dove game, cooperative interactions in a snowdrift game and a patch exploitation game. Individuals in our model can either adopt a responsive or an unresponsive tactic. When choosing an action, responsive individuals take the behavioural history of their social partners into account, unresponsive individuals do not. We first investigate whether the responsive strategy can spread in a population of unresponsive individuals. When then study whether the presence of responsive individuals does indeed trigger a coevolutionary process between consistency and responsiveness which results in a situation with high levels of adaptive behavioural consistency.

MODEL AND RESULTS

Set-up of basic model

We consider an evolving population in which individuals are engaged in a large number of rounds of pairwise interactions with other individuals in the population. In each round, individuals within the population are randomly matched to pairs. Within any interaction, individuals can adopt one out of two actions, payoffs are obtained according to the payoff matrix

$$\begin{array}{lcc} & \text{action 1} & \text{action 2} \\ \text{action 1} & a_{11} & a_{12} \\ \text{action 2} & a_{21} & a_{22} \end{array} \tag{1}$$

where a_{ij} is the payoff to an individual that adopts action i when matched with an individual that adopts action j. The strategy of an individual is given by a single number p , $0 \leq p \leq 1$, which corresponds to the probability with which an individual chooses action 1 in any of the interactions.

Behavioural consistency in our model corresponds to the degree to which individuals show the same behaviour in subsequent interactions, the most consistent strategies are thus $p = 1$ ("always choose action 1") and $p = 0$ ("always choose action 2"). One of the questions we want to ask is whether the presence of responsive individuals gives rise to high levels of consistency, we will thus focus on scenarios in which, in the absence of responsive individuals, mixed strategies $(0 < p < 1)$ are played at evolutionary equilibrium. In other words we focus on scenarios in which none of the pure strategies are evolutionarily stable, that is scenarios where action 1 can invade a population of individuals that always adopt action 2 and vice versa:

$$a_{21} > a_{11} \text{ and } a_{12} > a_{22} \tag{2}$$

A simple calculation shows (Appendix) that at the evolutionary equilibrium, the frequency at which action 1 is adopted in each round is given by

$$f^* = \frac{a_{12} - a_{22}}{(a_{12} - a_{22}) + (a_{21} - a_{11})} \tag{3}$$

Example 1. Aggressive interactions: the hawk-dove game

The classical example with a mixed strategy equilibrium is the hawk-dove game for aggressive interactions (Maynard Smith, 1982). Individuals fight for a resource of value V and can choose between an aggressive "hawk" and a non-aggressive "dove" strategy. The payoff to the row-player is given by:

$$\begin{array}{lcc} & \text{hawk} & \text{dove} \\ \text{hawk} & (V-D)/2 & V \\ \text{dove} & 0 & V/2 \end{array} \tag{4}$$

where $D > V$ is the cost of injury during an aggressive hawk-hawk interaction. The equilibrium frequency (3) of hawks is given by $f^* = V \ / \ D$.

Example 2. Cooperative interactions: the snowdrift game

One of the standard models of cooperation is the snowdrift game (Dieckmann & Doebeli, 2005) in which individuals can either cooperate or defect. Cooperation yields a benefit B to the cooperator as well as to the partner and incurs a cost $C < B$ if the partner defects and a cost $V/2$ if the partner cooperates. The payoff to the row-player is thus given by:

$$\begin{array}{lcc} & \text{cooperate} & \text{defect} \\ \text{cooperate} & B-C/2 & B-C \\ \text{defect} & B & 0 \end{array} \tag{5}$$

The equilibrium frequency (3) of cooperators is given by $f^* = 1 - C \ / \ (\ 2 \cdot B - C\ )$.

Example 3. Resource exploitation

A third game we consider is a resource exploitation game where individuals can adopt one out of two exploitation strategies, say fast and superficial or slow and thorough exploitation. Whenever the two individuals adopt the same strategy, payoffs are reduced by a factor $\frac{1}{2}$ due to competition. The payoff of the row-player is then given by:

$$\begin{array}{lcc} & \text{fast} & \text{slow} \\ \text{fast} & V_f/2 & V_f \\ \text{slow} & V_s & V_s/2 \end{array} \tag{6}$$

where $V_f > V_s/2$ and $V_s > V_f/2$ correspond the inherent benefit of the fast and slow exploitation strategy, respectively. The equilibrium frequency (3) of fast explorers is given by $f^* = (2 \cdot V_f - V_s) / (V_f - V_s)$.

Evolutionary equilibrium

At evolutionary equilibrium, the frequency of action 1 in each of the interactions is given by (3). This frequency can be achieved in a variety of ways (Maynard Smith, 1982), an equilibrium could be monomorphic, meaning that all individuals play the mixed strategy $p = f^*$, but it could also be polymorphic, for example, a fraction f^* of the individuals always plays the pure strategy 1 ($p = 1$) and a fraction $(1 - f^*)$ of the individuals always plays the pure strategy 2 ($p = 0$). Hence, the resulting population can either consist of behaviourally inconsistent individuals (all individuals play same mixture p) or a mixture of consistent individuals. However, as our individual-based simulations show (Fig. 6.1), in the absence of responsive individuals there is an evolutionary trend towards behaviourally inconsistent individuals playing $p = f^*$.

It can also be seen from Figure 6.1 that at evolutionary equilibrium, mutations and drift give rise to variation among individuals. Responsiveness should be favoured in such a situation since responsive (reactive, socially aware, eavesdropping) individuals, that adapt their behaviour in response to the partner they face, are able to exploit this variation.

Variation favours responsiveness

Consider first, for the sake of the argument, a responsive individual that has perfect knowledge about the strategy   of its opponent (Fig. 6.2). When confronted with an opponent with strategy p, the expected payoffs to action 1 (E_1) and action 2 (E_2) are then given by

$$\begin{aligned} E_1(p) &= p \cdot a_{11} + (1 - p) \cdot a_{12} \\ E_2(p) &= p \cdot a_{21} + (1 - p) \cdot a_{22}\,. \end{aligned} \tag{7}$$

The payoff difference Δ between action 1 and action 2 is thus is given by

$$\Delta = a_{12} - a_{22} - p \cdot \delta \tag{8}$$

with

$$\delta = (a_{12} - a_{22}) + (a_{21} - a_{11}) \geq 0\ . \tag{9}$$

The payoff difference thus strictly decreases in p and changes sign from positive to negative at $p = f^*$ (Fig. 6.2A). Consequently, dependent on the strategy p of its opponent, the best strategy for the responsive individual is to adopt (Fig. 6.2B)

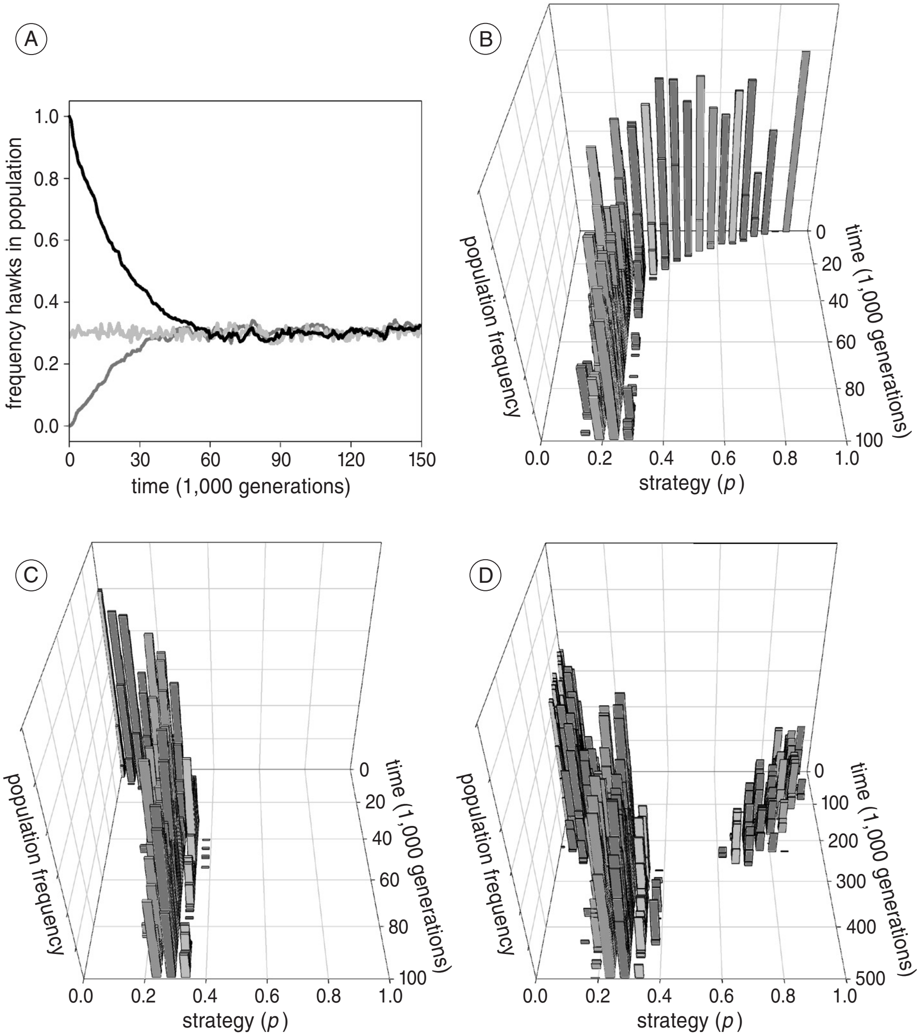

Figure 6.1 Three individual-based simulations for our basic model. Each generation, individuals within a population of size 5000 are engaged in 50 hawk-dove interactions where $V = 0.3$ and $D = 1.0$. Reproductive success of individuals is proportional to the (additive) payoff accumulated in all interactions. During clonal reproduction, individuals pass on their strategy to their offspring, mutations occur with probability 0.005, the effect of mutations on the strategy are drawn from a normal distribution with mean 0 and variance 0.005. (A) In all simulations, the average frequency of hawks rapidly converges to the equilibrium value $V/D = 0.3$. Individuals in the ancestral populations in our simulations are highly consistent, in (B) individuals always choose action 1 (i.e., $p = 1$), in (C) individuals always choose action 2 (i.e., $p = 0$), in (D) we start with a dimorphic population at its equilibrium frequencies V/D. Independent from the ancestral state, all populations evolve towards the monomorphic equilibrium at which individuals show inconsistent behaviour. Mutation and drift maintain variation in the populations.

$$\begin{array}{ll} \text{action 1 if} & p < f^* \\ \text{any action if} & p = f^* \\ \text{action 2 if} & p > f^* \end{array} \tag{10}$$

with corresponding payoffs (Fig. 6.2C)

$$\begin{array}{lll} E_1(p) & \text{if} & p < f^* \\ E_1(p) = E_2(p) & \text{if} & p = f^* \\ E_2(p) & \text{if} & p > f^* \end{array} \tag{11}$$

Compare this, with any unresponsive individual with strategy p_u that plays against the same opponent. Such an individual obtains the expected payoff (Fig. 6.2C)

$$p_u \cdot E_1(p) + (1 - p_u) \cdot E_2(p) \,. \tag{12}$$

The payoff difference between a responsive and an unresponsive individual is thus given by

$$\begin{array}{llll} (1 - p_u) \cdot \big(E_1(p) - E_2(p)\big) & > 0 & \text{for opponents with} & p < f^* \\ & = 0 & \text{for opponents with} & p = f^* \\ p_u \cdot \big(E_2(p) - E_1(p)\big) & > 0 & \text{for opponents with} & p > f^* \,, \end{array} \tag{13}$$

which is always positive (Fig. 6.2C) whenever the population is not at its monomorphic equilibrium ($p = f^*$). Responsive individuals with perfect knowledge can thus always obtain a higher payoff than unresponsive individuals.

In reality individuals do of course not have perfect knowledge about the strategy of their opponent. Responsive individuals can, however, get some information about the strategy of their opponents by observing their past behaviour. For a long sequence of observations, this information would be close to perfect knowledge which, as we have just seen, would be favourable. This is not necessary, however. In the following section we show that even a particularly simple responsive strategy (Johnstone, 2001) that takes into account only the last interaction of its partner is favoured.

Extension of basic model: responsive and unresponsive strategies

We now consider our basic model and allow for both unresponsive and responsive strategies. The strategy of unresponsive individuals is, as above, given by a single number p , $0 \leq p \leq 1$ that determines the probability with which an individual

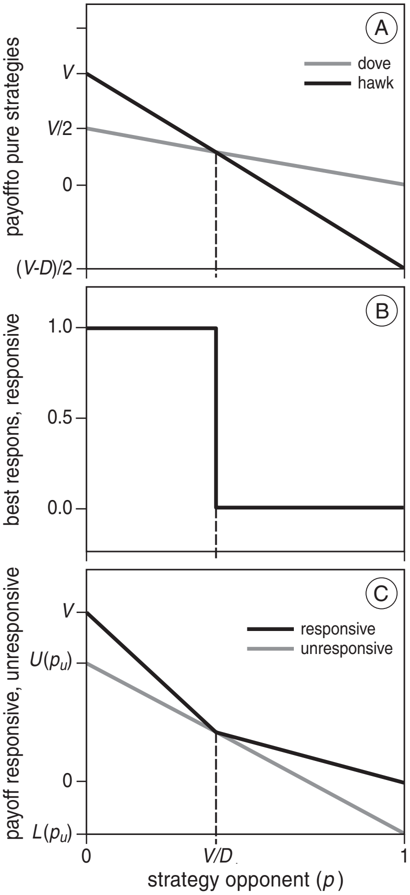

Figure 6.2 Variation favours responsiveness. For the special case of a hawk-dove game, (A) illustrates the linear frequency dependence of the payoffs of the pure strategies. Hawks receive a higher payoff than doves against opponents with $p < V/D$ and vice versa. (B) Consequently, responsive individuals should play hawk when $p < V/D$ and dove otherwise. (C) By adopting this strategy, responsive individuals obtain a higher payoff than any unresponsive individual p_u against all opponents except opponents with $p = V/D$. $U(p_u) = {}^1/_2 \cdot V \cdot (1 - p_u)$ and $L(p_u) = {}^1/_2 \cdot (V - p_u \cdot D)$.

chooses action 1 in each of its interactions. Responsive individuals take into account the last interaction of their partner and choose their behaviour according to a simple eavesdropping strategy (Johnstone, 2001): “choose action 1 if opponent choose action 2 in its last interaction, otherwise choose action 1”. We assume that being responsive is costly and reduces the payoff of responsive individuals per interaction by c_r.

Responsive individuals invade whenever sufficient variation is present
Let us first investigate the invasion prospects of a responsive individual in a population of unresponsive individuals. Let us assume that the population of unresponsive individuals evolved to its evolutionary equilibrium, that is, the fraction of individuals that choose action 1 per game is given by equation (3). As indicated in Figure 6.1, this equilibrium population will typically not be fully monomorphic. Let $\mathrm{V}ar(\hat{p})$ denote the variance in the trait p of the unresponsive individuals at that equilibrium. We show in the Appendix that the expected payoff difference between a responsive and an unresponsive individual in such a population is given by:

$$\delta \cdot \mathrm{V}ar(\hat{p}) - c_r \tag{14}$$

per interaction, where $\delta > 0$ is given by equation (9) above. Responsive individuals can thus invade a population of unresponsive individuals whenever the variation present in this population is large enough, that is

$$\mathrm{V}ar(\hat{p}) > \frac{c_r}{\delta} \tag{15}$$

We have seen above (equation (13) and Fig. 6.2) that responsive individuals with perfect knowledge about their opponent's strategy (or a very large number of observations of the opponent's behaviour) can improve their payoff relative to unresponsive individuals. Responsive individuals in our model, however, take into account only one interaction of their opponent. Interestingly, even this single observation carries sufficient information, to improve its payoff relative to unresponsive individuals. The intuition behind this result is illustrated in Figure 6.3.

Responsive individuals do not go to fixation
Whenever (15) is satisfied, responsive individuals can invade a population of unresponsive individuals. They will, however, not go to fixation. To see this, consider a population of unresponsive individuals. Such individuals always respond with action 1 to opponents that adopted action 2 in their last round and vice versa. As a consequence, after sufficiently many rounds, responsive individuals will always adopt action 1 with probability $\frac{1}{2}$ (see Appendix), the corresponding expected payoff is, thus $\frac{1}{4} \cdot (a_{11} + a_{12} + a_{21} + a_{22})$.

In view of assumption (2), either a_{12} or a_{21} is the maximal payoff and this maximal payoff can be obtained by unresponsive individuals. Consider, for example, the case where a_{12} is the maximal payoff. Unresponsive individuals that play the pure strategy 1 obtain that payoff, since responsive individuals always respond

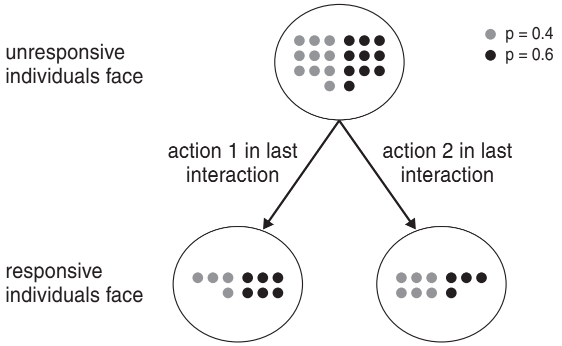

Figure 6.3 Benefits to simple eavesdropping strategy. Example illustrating how responsive individuals that take into account only one past interaction of their partner can improve their payoff. Consider a population of unresponsive individuals at its equilibrium, suppose the equilibrium frequency of action 1 is $f = 0.5$ and suppose further that two strategies are present at that equilibrium in equal proportions, $p = 0.4$ (grey dots) and $p = 0.6$ (black dots). The best response to the former is action 1, to the latter is action 2 . Unresponsive individuals do not differentiate between these two types of individuals and will adopt the best response behaviour in only half of their interactions. By taking into account one past interaction of their opponent, responsive individuals can increase the proportion of cases in which they play a best response, in our simple example they play a best response in a fraction 0.6 of the cases.

with action 2 to these individuals. In fact, as we show in the Appendix, all unresponsive individuals with $p > \frac{1}{2}$ can invade a population of responsive individuals.

Coexistence of responsive and unresponsive individuals

From our analysis above follows that at any evolutionary equilibrium, both responsive and unresponsive individuals must be present in the population. This coexistence is maintained by negative frequency dependence: When confronted with an unresponsive individual, responsive individuals do better than unresponsive individuals since they can fine-tune their behaviour to the unresponsive opponent. When confronted with a responsive individual, however, unresponsive individuals do better than responsive individuals since, by choosing the right pure strategy, they can always obtain the maximal payoff in these interactions.

Presence of responsive individuals selects for consistency

Whenever an unresponsive individual interacts with a responsive individual consistency is beneficial. Suppose the unresponsive individual has chosen action 1 in its last interaction, the responsive individuals will thus respond with action 2. Since $a_{12} > a_{22}$, the unresponsive individual should adopt action 1 again. Con-

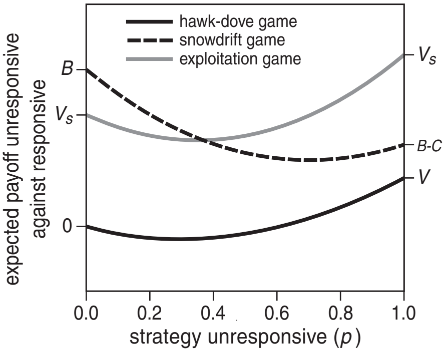

Figure 6.4 Responsive individuals select for consistency, illustrated for our three examples. The expected payoff that an unresponsive individual obtains in an interaction with a responsive individual is frequency independent and strictly convex in the strategy p of the unresponsive individual. Consequently, consistent strategies are favoured over inconsistent strategies, local payoff maxima occur at both $p = 0$ or $p = 1$, the global maximum occurs at either $p = 0$ or $p = 1$.

versely, since $a_{21} > a_{11}$, unresponsive individuals that chose action 2 in their last interaction should adopt action 2 again. The presence of responsive individuals thus selects for consistency.

To make this point more precise, let us denote the expected payoff of an unresponsive individual p against a responsive individual by $W_{u,r}(p)$. This payoff is frequency independent and strictly convex in the strategy p of the unresponsive individual (see Appendix and Figure 6.4), with a minimum at

$p = \frac{1}{2} \cdot \left(1 + \frac{a_{21} - a_{12}}{\delta}\right)$. In other words, unresponsive individuals obtain the maximal

payoff against responsive individuals at either of the highly consistent strategies $p = 1$ or $p = 0$, both of which are a local payoff maximum.

Evolutionary equilibrium

We have seen above that at any evolutionary equilibrium, unresponsive individuals will coexist with responsive individuals. We have also seen that in interactions with responsive individuals, unresponsive individuals with inconsistent behaviour are outperformed by more consistent individuals. This provides the intuition for our result (Appendix) that, at any evolutionary equilibrium, unresponsive individuals will always employ strategies that give rise to highly consistent behaviour, that is $p = 0$ or $p = 1$.

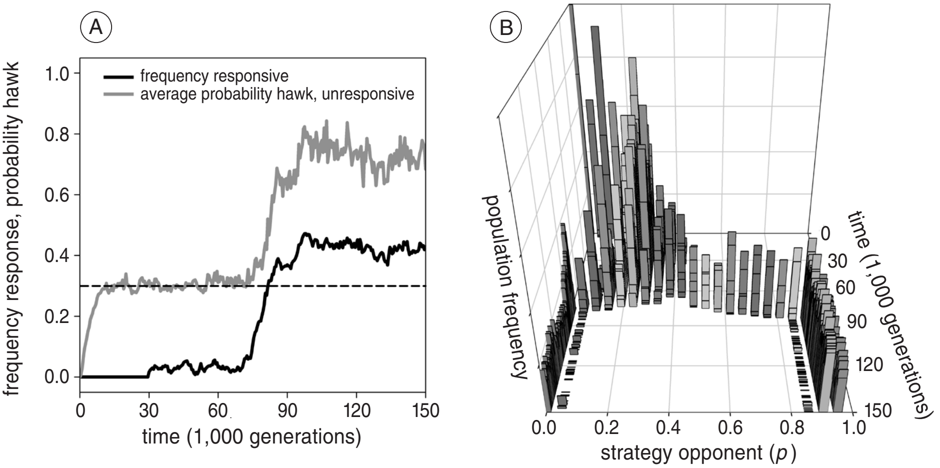

Figure 6.5 Evolution of behavioural consistency. Individual-based simulations with parameter values as in Figure 6.1. After 30.000 generations we allow rare mutations (probability 0.005) that give rise to responsive individuals. (A) Responsive individuals increase in frequency over time (black line) and select for an increased frequency of hawks among unresponsive individuals (grey line). (B) The presence of responsive individuals gives rise to benefits of consistency which, in turn, select for high levels of consistency among unresponsive individuals, that is, unresponsive strategies with maximal behavioural consistency ($p = 0$ or $p = 1$) are favoured over less consistent one.

As a consequence, there are only three candidate evolutionary equilibria, two dimorphic equilibria in which responsive individuals coexist with one unresponsive type ($p = 0$ or $p = 1$) and one trimorphic equilibrium at which responsive individuals coexist with two unresponsive types ($p = 0$ and $p = 1$). As we show in the Appendix, both dimorphic candidates are evolutionarily unstable: the dimorphic equilibrium in which unresponsive individuals always adopt action 1 ($p = 1$) can be invaded by unresponsive individuals that always adopt action 2 ($p = 0$) and vice-versa. Thus, at evolutionary equilibrium the population must be composed of three behavioural types: responsive individuals and two unresponsive types that show highly consistent behaviour, that is $p^* = 0$ and $p^* = 1$.

These results are confirmed by our individual-based simulations, Fig. 6.5 shows a typical example for the case where the interactions correspond to hawk-dove games. To illustrate the effect of responsive individuals, we did not allow responsive individuals during the first 30.000 generations. During the first few thousand generations, the population frequency of hawks rapidly converges to the predicted equilibrium value for unresponsive individuals (Fig. 6.5A), which is indicated by the black hatched line. As we have already seen in Figure 6.1, variation among individuals is a typical feature of such an equilibrium (Fig. 6.5B). From 30.000 generations onwards, we allow the rare occurrence of responsive individuals. As predicted, these individuals increase in frequency over time (Fig 6.5A, black line). The presence of responsive individuals, in turn, selects for behavioural consistency among unresponsive individuals (Fig. 6.5B): inconsistent behavioural strategies are outperformed by more consistent strategies and, at evolutionary equilibrium, responsive individuals coexist with two types of highly consistent unresponsive individuals that either always adopt the hawk or dove behaviour.

In summary, in social interactions, a potentially small amount of consistent variation among individuals (e.g., due to mutations and drift) can select for the presence of responsive individuals (McNamara *et al.*, 2008; McNamara *et al.*, 2009a). The presence of responsive individuals, in turn, selects for consistency in behaviour among unresponsive individuals whenever predictability is beneficial. As a result, evolution gives rise to populations in which inconsistent responsive behavioural types coexist with highly consistent unresponsive behavioural types.

DISCUSSION

Matrix games

In this study we focused, for simplicity, on interactions that can be described as matrix games with two pure strategies (1) as, for example, the hawk-dove game and the snowdrift game. However, we do not expect that our explanation of behavioural consistency is restricted to these situations. There are two key steps in our argument.

First, responsiveness is favoured in populations of unresponsive individuals. This will be the case whenever variation (e.g., due to mutations and drift) among unresponsive individuals meets two criteria. It must be consistent, since otherwise, nothing can be gained by taking the past behaviour of social partners into account. Second, the optimal response to different individuals must differs, since otherwise, nothing can be gained by being responsive. Whenever both conditions are fulfilled, as for example in our models, responsiveness is favoured.

Second, the presence of responsive individuals selects for behavioural consistency among unresponsive individuals. This will be the case whenever predictability in the interactions with social partners is beneficial. This is not always the case, in fact, under some circumstances one would expect that unpredictable strategies should be favoured. However, as discussed above, predictability is beneficial in many social interactions (coordination, partner choice, exploitation) and these are the situation where the presence of responsive individuals selects for consistency.

Consistency in the absence of responsive strategies

In order for responsiveness to be favoured, the variation present among unresponsive individuals has to be consistent in the sense that the past behaviour of an individual is (to a potentially very small extent) predictive for its future behaviour. In our model, this "baseline consistency" is caused by the assumption that individuals use the same strategy p in all interactions: any potentially small difference in p thus gives rise to a small degree of predictable differences among individuals which, in turn, can be exploited by responsive individuals. In principle, one could envisage an analysis based on a model without this baseline consistency, the strategy of individuals in such a model would then be given by N numbers, where the n-th number gives the behavioural tendency of an individual during its n-th interaction. We do not expect qualitatively different results from such a more complicated model. As in our model, unresponsive individuals would differ due to mutations and drift. At any point in time, due to chance, these differences might either be consistent or inconsistent , that is, due to chance, there is a positive or a negative correlation among the behavioural tendencies used in subsequent rounds. In periods where consistency is present, responsiveness should be favoured which, in turn, should trigger the same evolutionary process leading to high levels of adaptive consistency as in our model.

Responsive strategy

In our model we focussed on a particularly simple responsive strategy (Johnstone, 2001) that takes into account only one interaction of its opponent and responds in a very simple manner. This, however, should be seen as an conservative approach since, as we have seen above, the better a responsive strategy can "estimate" the strategy of its opponent, the more beneficial this strategy should be. Consequently, if responsive strategies that take into account only one piece of information are favoured, responsive strategies that take into account more information should also be favoured.

We assumed, for simplicity, that responsive individuals have perfect information about their opponent's behaviour in one interaction. Analogous results, however, can be derived for situations in which this information is imperfect or responsive individuals sometimes make errors in responding to this information.

Importance of variation

It has been recently demonstrated that the presence of a potentially small amount of variation in social contexts can trigger coevolutionary processes that give rise to unexpected evolutionary outcomes. Small consistent differences in trustworthiness (McNamara *et al.*, 2009a), for example, favour socially aware individuals that trust on the basis of prior trustworthy behaviour. The presence of socially aware individuals, in turn, can give rise to disruptive selection on the trustworthiness of individuals. Similarly, a potentially small degree of consistent individual differences in cooperativeness favours choosiness among individuals which, in turn, can give rise to a coevolutionary process of choosiness and cooperativeness maintaining unexpectedly high levels of cooperation in the population (McNamara *et al.*, 2004).

Our results provide yet another example for the drastic effect that a small degree of variation can have on the expected evolutionary outcome, in our case, on the behavioural consistency of individuals. In the absence of sufficient variation, individuals in our model evolve a mixed strategy which gives rise to inconsistent behaviour in repeated social interactions. Whenever sufficient variation among individuals is present, however, a coevolutionary process between responsiveness and consistency is triggered which, in turn, gives rise to populations in which responsive individuals coexist with unresponsive individuals that show high levels of adaptive consistency in their behaviour. Interestingly, our explanation for behavioural consistency thus requires the presence of inconsistent individuals, since it is just the presence of these individuals that make consistency beneficial.

Appendix

BASIC SET-UP OF THE MODEL

Consider the model as described in the main text. Individuals within an evolving population are engaged in a large number of rounds of pairwise interactions. In each round, individuals in the population are randomly matched to pairs. Within any interaction, individuals can adopt one out of two actions, payoffs are obtained according to the payoff matrix

$$\begin{array}{lcc} & \text{action 1} & \text{action 2} \\ \text{action 1} & a_{11} & a_{12} \\ \text{action 2} & a_{21} & a_{22} \end{array} \tag{1}$$

with

$$a_{21} > a_{11} \text{ and } a_{12} > a_{22} \ . \tag{2}$$

Individuals can either adopt a responsive or an unresponsive strategy. The strategy of unresponsive individuals is given by a single number p, $0 \leq p \leq 1$ that determines the probability with which an individual chooses action 1 in each of its interactions. Responsive individuals take into account the last interaction of their partner and choose their behaviour according to a simple eavesdropping strategy: "choose action 1 if opponent chose action 2 in its last interaction, otherwise choose action 2". Responsiveness is costly and reduces the payoff of responsive individuals per interaction by c_r.

PAYOFFS

At any point in time, our population can be characterized by the tupel $(f, \theta(p))$, where f gives the frequency of responsive individuals in the population and $\theta(p)$ gives the frequency distribution of unresponsive strategies in the population at that point in time. For any distribution $\theta(p)$ of strategies, we denote its expected value by $E(p)$ and its variance by $Var(p)$.

The expected payoff of an unresponsive individual with strategy p in a resident environment $\left(\hat{f},\hat{\theta}(\hat{p})\right)$ is given by

$$W_u\left(p,\hat{f},\hat{\theta}\right)=\hat{f}\cdot w_{u,\hat{r}}+\left(1-\hat{f}\right)\cdot w_{u,\hat{u}} \tag{3}$$

per interaction, where $w_{u,\hat{\imath}}$ is the expected payoff to an unresponsive individual dependent on whether it interacts with a responsive or an unresponsive resident individual. These payoffs are given by:

$$\begin{aligned}
w_{u,\hat{u}} &= p\cdot\int_0^1\left(\hat{p}\cdot a_{11}+(1-\hat{p})\cdot a_{12}\right)\hat{\theta}(\hat{p})d\hat{p}+(1-p)\cdot\int_0^1\left(\hat{p}\cdot a_{21}+(1-\hat{p})\cdot a_{22}\right)\hat{\theta}(\hat{p})d\hat{p}\\
&= p\cdot\left(E(\hat{p})\cdot a_{11}+(1-E(\hat{p}))\cdot a_{12}\right)+(1-p)\cdot\left(E(\hat{p})\cdot a_{21}+\left(1-E(\hat{p})\right)\cdot a_{22}\right)\\
w_{u,\hat{r}} &= p\cdot\left(p\cdot a_{12}+(1-p)\cdot a_{22}\right)+(1-p)\cdot\left(p\cdot a_{11}+(1-p)\cdot a_{21}\right)\ .
\end{aligned} \tag{4}$$

The expected payoff of an responsive individual in the resident environment $\left(\hat{f},\hat{\theta}(\hat{p})\right)$ is given by:

$$W_r\left(\hat{f},\hat{\theta}\right)=\hat{f}\cdot w_{r,\hat{r}}+\left(1-\hat{f}\right)\cdot w_{r,\hat{u}}-c_r \tag{5}$$

per interaction, where $w_{u,\hat{\imath}}$ is the expected payoff to a responsive individual dependent on whether it interacts with a responsive or an unresponsive individual. These payoffs are given by:

$$\begin{aligned}
w_{r,\hat{u}} &= \int_0^1\left(\hat{p}\cdot\left(\hat{p}\cdot a_{21}+(1-\hat{p})\cdot a_{22}\right)+(1-\hat{p})\cdot\left(\hat{p}\cdot a_{11}+(1-\hat{p})\cdot a_{12}\right)\right)\cdot\hat{\theta}(\hat{p})d\hat{p}\\
&= a_{21}\cdot\left(Var(\hat{p})+E(\hat{p})^2\right)+(a_{22}+a_{11})\cdot\left(E(\hat{p})\cdot\left(1-E(\hat{p})\right)-Var(\hat{p})\right)+\\
&\quad\ a_{12}\cdot\left(1-E(\hat{p})\cdot\left(2-E(\hat{p})\right)+Var(\hat{p})\right)\\
w_{u,\hat{r}} &= \Phi_r\cdot\left(\Phi_r\cdot a_{22}+(1-\Phi_r)\cdot a_{21}\right)+(1-\Phi_r)\cdot\left(\Phi_r\cdot a_{12}+(1-\Phi_r)\cdot a_{11}\right)
\end{aligned} \tag{6}$$

where Φ_r is the proportion of responsive individuals that chose action 1 in their last round, which changes according to the difference equation:

$$\Phi_r^t=\hat{f}\cdot(1-\Phi_r^{t\text{-}1})+(1-\hat{f})\cdot\left(1-E(\hat{p})\right) \tag{7}$$

that converges to

$$\Phi_r=\frac{\hat{f}+(1-\hat{f})\cdot\left(1-E(\hat{p})\right)}{1+\hat{f}}\ . \tag{8}$$

EVOLUTIONARY EQUILIBRIUM

The responsive strategy invades

Consider a population of unresponsive individuals, that is $\hat{f} = 0$. We assume that this population is at its evolutionary equilibrium, that is to a frequency distribution $\theta\,(p)$ at which both actions achieve equal payoff.
The expected payoff to action 1 is given by

$$E(\hat{p}) \cdot a_{11} + \left(1 - E(\hat{p})\right) \cdot a_{12} \;, \tag{9}$$

the expected payoff to action 2 by

$$E(\hat{p}) \cdot a_{21} + \left(1 - E(\hat{p})\right) \cdot a_{22} \;. \tag{10}$$

At evolutionary equilibrium, the frequency distribution of p thus satisfies

$$E(\hat{p}) = (a_{12} - a_{22}) \cdot \delta^{-1} \tag{11}$$

where $\delta = (a_{12} - a_{22}) + (a_{21} - a_{11})$.

Consider now the invasion prospects of a rare responsive mutant in such a population. With equations (3) and (5), the payoff difference $\Delta_{r,\hat{u}}$ between this mutant and the unresponsive resident is given by

$$\Delta_{r,\hat{u}} + w_{r,\hat{u}} - w_{\hat{u},\hat{u}} - c_r \tag{12}$$

per interaction, which, with equations (4) and (6), simplifies to

$$\delta \cdot Var(\hat{p}) - c_r \;. \tag{13}$$

Responsive individuals can thus invade a population of unresponsive individuals whenever the variation present in this population is large enough, that is

$$Var(\hat{p}) > \frac{c_r}{\delta} \;. \tag{14}$$

The responsive strategy does not go to fixation

Consider the invasion prospects of a rare unresponsive mutant with strategy p in a population of responsive individuals, that is $\hat{f} = 1$. With equations (3) and (5), the payoff difference between this mutant and the responsive resident is then given by:

$$\Delta_{ur,\hat{r}}(p) = w_{ur,\hat{r}} - w_{\hat{r},\hat{r}} + c_r \tag{15}$$

per interaction, which, with equations (4), (6) and (8) reduces to

$$\Delta_{ur,\hat{r}}(p) = \delta \cdot \left(p^2 - p + \tfrac{1}{4}\right) + \left(\tfrac{1}{2} - p\right) \cdot (a_{21} - a_{12}) + c_r \ . \tag{16}$$

From this follows directly that an unresponsive mutant with $p = \frac{1}{2}$ obtains a higher payoff than the resident since

$$\Delta_{ur,\hat{r}}(0.5) = c_r > 0 \ , \tag{17}$$

which shows that a population of responsive individuals is not evolutionarily stable. In fact, whenever $a_{12} > a_{21}$, all unresponsive mutants with $p > \frac{1}{2}$ obtain a higher payoff than the resident since $\Delta_{ur,\hat{r}}(p)$ is a strictly convex function in p, that is

$$\frac{d^2 \Delta_{ur,\hat{r}}}{dp^2} = 2 \cdot \delta > 0 \tag{18}$$

and

$$\left.\frac{d\Delta_{ur,\hat{r}}}{dp}\right|_{p=\frac{1}{2}} = a_{12} - a_{21} \ . \tag{19}$$

Similarly, whenever $a_{12} < a_{21}$, all unresponsive mutants with $p < \frac{1}{2}$ obtain a higher payoff than the resident.

Coexistence

From the last two sections follows directly that, at any evolutionary equilibrium, both responsive and unresponsive strategies coexist, that is

$$0 < f^* < 1 \ . \tag{20}$$

Unresponsive individuals adpot pure strategies

At an evolutionary equilibrium, unresponsive individuals will always adopt one of the pure strategies, that is $p = 0$ or $p = 1$. To see this, consider that an internal evolutionary equilibrium, $0 < p < 1$, is characterized by a vanishing selection gradient, $\frac{dW_u}{dp} = 0$ (no directional selection), and a negative second derivative $\frac{d^2W_u}{dp^2} < 0$ (p is a local ESS) at that equilibrium. From this follow directly that an internal p can never be a local ESS in our model since

$$\frac{d^2W_u}{dp^2} = 2 \cdot \hat{f} \cdot \delta > 0\,. \tag{21}$$

Dimoprhisms are evolutionarily unstable

From our analysis above follows that there are three candidate evolutionary equilibria, two dimorphic equilibria at which responsive individuals coexist with one unresponsive type ($p = 0$ or $p = 1$) and a trimorphic equilibrium at which responsive individuals coexist with two unresponsive types ($p = 0$ and $p = 1$).

Let f_1 and f_2 denote the frequency of individuals that always choose action 1 ($p = 1$) and 2 ($p = 0$), respectively, and $f_r = 1 - f_1 - f_2$ the frequency of responsive individuals in the population. Dependent on f_r, f_1, f_2 the payoffs to these three behavioural types per interaction are given by

$$\begin{aligned} W_1 &= f_1 \cdot a_{11} + f_2 \cdot a_{12} + f_r \cdot a_{12} \\ W_2 &= f_1 \cdot a_{21} + f_2 \cdot a_{22} + f_r \cdot a_{21} \\ W_r &= f_1 \cdot a_{21} + f_2 \cdot a_{12} + f_r \cdot w_{r,r} \end{aligned} \tag{22}$$

where

$$w_{r,r} = \Phi_r^2 \cdot a_{22} + \Phi_r \cdot (1 - \Phi_r) \cdot (a_{12} + a_{21}) + (1 - \Phi_r)^2 \cdot a_{11} \tag{23}$$

gives the expected payoff of an responsive individuals when encountering another responsive individual, and Φ_r the proportion of responsive individuals that chose action 1 in their last round, which is, with equation (8), given by

$$\Phi_r = \frac{f_r + f_2}{1 + f_r} \tag{24}$$

We now show that, whenever

$$a_{12} > a_{21} \tag{25}$$

neither of the two dimorphic equilibria is evolutionarily stable. The proof for $a_{12} < a_{21}$ runs analogously.

Consider first a dimorphic candidate equilibrium with $f_1 = 0$. At that candidate, individuals that adopt the pure strategy for action 2 obtain the payoff

$$W_2 = f_2 \cdot a_{22} + f_r \cdot a_{21} \tag{26}$$

Compare this with the payoff to an unresponsive mutant that always adopts action 1 which is given by

$$W_1 = f_2 \cdot a_{12} + f_r \cdot a_{12} = a_{12} \tag{27}$$

which, since a_{12} is the maximal payoff that can be obtained, is always higher than that of the unresponsive resident individual. The dimorphic candidate equilibrium with $f_1 = 0$ is thus never evolutionarily stable.

Consider next the dimorphic candidate equilibrium with $f_2 = 0$. At that candidate, individuals that adopt the pure strategy 1 obtain the payoff

$$W_1 = f_1 \cdot a_{11} + f_r \cdot a_{12} \ . \tag{28}$$

Compare this with the payoff to an unresponsive mutant that always adopts action 2 which is given by

$$W_2 = f_1 \cdot a_{21} + f_r \cdot a_{21} = a_{21} \ . \tag{29}$$

The payoff difference between the unresponsive mutant and the unresponsive resident is thus given by

$$W_2 - W_1 = a_{21} - a_{11} + f_r \cdot (a_{11} - a_{12}) \ . \tag{30}$$

The unresponsive mutant can invade if and only if this payoff difference is positive, that is, whenever

$$f_r < \frac{a_{21} - a_{11}}{a_{12} - a_{11}} \tag{31}$$

at that candidate. The unresponsive mutant can thus invade if and only if the frequency of responsive types at the candidate is not too high. We now show that condition (31) is always true at our candidate.

To simplify matters, we make use of the fact that we can always rescale our payoff matrix (1) by multiplying all elements with the same number and/or adding the same number to all elements without changing the equilibrium properties (Hofbauer & Sigmund, 1998) of our game. In particular we first subtract a_{11} from all elements and then divide all elements by $(a_{12} - a_{11})$. Our new payoff matrix is thus given by

$$\begin{array}{lcc} & \text{action 1} & \text{action 2} \\ \text{action 1} & 0 & 1 \\ \text{action 2} & \tilde{a}_{21} & \tilde{a}_{22} \end{array} \tag{32}$$

where

$$\tilde{a}_{21} = \frac{a_{21} - a_{11}}{a_{12} - a_{11}} \tag{33}$$

and

$$\tilde{a}_{22} = \frac{a_{22} - a_{11}}{a_{12} - a_{11}} \tag{34}$$

with, in view of our assumptions (2) and (25),

$$0 < \tilde{a}_{21} < 1 \tag{35}$$

and

$$\tilde{a}_{22} < 1 \tag{36}$$

At the candidate, the payoff differences between the responsive resident and the unresponsive resident type is given by

$$\Delta_{r,u} = (W_r - W_1)\Big|_{f_2=0} \tag{37}$$

which is strictly decreasing in the frequency of responsive individuals in the populations since

$$\frac{\delta \Delta_{r,u}}{\delta f_r} = A \cdot (f_r^3 + 3 \cdot f_r^2) + B \cdot f_r - 1 - \tilde{a}_{21} < 0 \tag{38}$$

where

$$\begin{aligned} A &= \tilde{a}_{22} - \tilde{a}_{21} - 1 &< 0 \\ B &= -\tilde{a}_{21} - 1 &< 0 \end{aligned} \tag{39}$$

Notice that the responsive mutant can invade if and only if

$$f_r < \tilde{a}_{21} \tag{40}$$

At that threshold the payoff difference between the responsive resident and the unresponsive resident type is given by

$$\Delta_{r,u}\Big|_{f_r = \tilde{a}_{21}} = \tilde{a}_{21}^{3} \cdot (\tilde{a}_{22} - 1) - \tilde{a}_{21}^{4} \tag{41}$$

which, in view of (35) and (36) is always negative. Since the payoff difference is strictly decreasing in the frequency f_r of responsive individuals in the populations and all resident types have to achieve equal payoff at an equilibrium, the equilibrium frequency of responsive types at the candidate equilibrium must always satisfy (40). From this follows that the unresponsive mutant that always adopts action 2 obtains a higher payoff than the unresponsive resident (see equation (30)). The candidate is thus never an evolutionary equilibrium.

Chapter 7

General discussion

No two individuals are alike. Take two individuals of the same sex, age and social background and you will typically find consistent differences in their motivation, cognition and behaviour. In humans, such differences are referred to as personalities (Pervin & John, 1999). Personality or individuality, however, appears not to be restricted to humans. In recent years, consistent differences in suites of correlated behavioural traits have been described in a diverse range of animal species (Clark & Ehlinger, 1987; Boissy, 1995; Gosling & John, 1999; Koolhaas *et al.*, 1999; Gosling, 2001; Sih *et al.*, 2004b; Groothuis & Carere, 2005). Such differences have been termed animal personalities (also: coping styles, Koolhaas *et al.*, 1999; behavioural syndromes, Sih *et al.*, 2004a; temperament, Reale *et al.*, 2007). The emerging notion that individual differences may be expressions of different behavioural types – rather than the result of stochastic noise – provoked a large number of empirical research during the last years (Sih *et al.*, 2004b), most of which aimed at understanding the structure (e.g., what traits are correlated with each other? How stable are these correlations over time?) and the proximate causes of animal personalities (e.g., what are the physiological correlates of personalities? How does experience affect personalities?).

This thesis presented work that aimed to investigate how natural selection can give rise to animal personalities, that is, behavioural differences among individuals that are correlated across situations and contexts (sensu Sih *et al.*, 2004a) and stable for some period of time. This question has been addressed to some extent in the literature (e.g., Clark & Ehlinger, 1987; Buss, 1991; Wilson, 1998; Bouchard & Loehlin, 2001; Dall *et al.*, 2004; McElreath & Strimling, 2006; Nettle, 2006; Stamps, 2007; Wolf *et al.*, 2007a; McNamara *et al.*, 2008; Pruitt *et al.*, 2008; Wolf *et al.*, 2008b; McNamara *et al.*, 2009a), at present, however, most researchers would probably agree that the evolutionary origin and adaptive significance of personalities is a poorly understood phenomenon.

The main part of the thesis began with a conceptual chapter (Chapter 2) that reviewed the main factors and mechanisms that may contribute to an adaptive explanation of animal personalities. In particular we discussed in detail how natural selection can give rise to three key behavioural aspects of personalities, variation among individuals, consistency of behaviour over time and behavioural correlations across situations and contexts.

The remainder of the thesis presented a series of conceptual evolutionary models. With these models I aimed to address behavioural aspects of personalities that appear to have some universality (i.e., occur in a range of animal species). As discussed in the General Introduction (Chapter 1), at present, there seem to be at least two candidates that suite this condition: the boldness-aggression syndrome and individual differences in responsiveness. These two candidates were the focus of the remainder of this thesis.

The work presented in Chapters 3 and 4 focused on the boldness-aggression syndrome and related observations. In these chapters we developed a theory that provides a link between life-history variation among individuals and personalities. Below, under the heading "Life-history variation", I will summarize and discuss the main aspects of this theory and point to possible future developments. The work presented in Chapters 5 and 6 focused on individual differences in responsiveness to environmental stimuli. In these chapters we investigated how natural selection can give rise to such differences, why such differences should be consistently expressed over time and across contexts and how the presence of responsive individuals can affect the course of evolution. Under the heading "Responsiveness" below, I will summarize and discuss the main results of these chapters and put them into a broader context.

I conclude this final chapter with some brief remarks on future avenues of behavioural ecology.

LIFE-HISTORY VARIATION

Many researchers would probably agree that the boldness-aggression syndrome is one of most reported findings in the animal personality literature. In a nutshell, individuals that tend to be relatively aggressive towards intruders also tend to be relatively bold in response to predators and relatively active in unfamiliar environments (Koolhaas *et al.*, 1999; Sih *et al.*, 2004b; Groothuis & Carere, 2005). Moreover, individual differences on this behavioural axis are often consistent for at least some period of time. These observations led us to hypothesize (Chapter 3) that the mortality risk associated with behavioural actions might be the organizing factor underlying these behavioural associations: individuals that risk more in intraspecific fights also risk more when confronted with a predator and when exploring an unfamiliar environment. From life-history theory it is known (Houston & McNamara, 1989; Clark, 1994) that individuals should adjust their willingness to take risks to their residual reproductive value (i.e., future fitness expectations) which, in turn, is determined by its life-history strategy.

Asset-protection

Consider an individual that faces the choice whether or not to take a risky action. In particular, let v be the residual reproductive value (henceforth simply reproductive value) of that individual, c the mortality risk associated with the action, and b the increase in reproductive value associated with the action, conditional on surviving. Taking the action thus results in an expected reproductive value v' that is given by

$$v' = (1 - c) \cdot (v + b) \quad . \tag{1}$$

The individual should take the action whenever this action increases its expected reproductive value, that is whenever $v' > v$, or equivalently, whenever

$$v < \frac{(1 - c)}{c} \cdot b \quad . \tag{2}$$

The characteristics of the risky choice (b, c) thus determine a threshold with the property that individuals with a reproductive value below that threshold should take the risky action whereas individuals with a reproductive value above that threshold should not take the risky action. This principle has been termed asset protection: individuals with a relatively low reproductive value have less to lose and should therefore be more willing to take risks than individuals with a relatively high reproductive value (Houston & McNamara, 1989; Clark, 1994).

Asset-protection and animal personalities

In Chapter 3 we developed an evolutionary model that provides a link between asset protection and animal personalities. The basic idea can be illustrated with equation (2). Suppose that, at a particular point in time, individuals within a population differ in their reproductive value, say individuals have either a relatively low v_L or a relatively high v_H reproductive value, $v_L < v_H$. Such differences give rise to differences in the willingness to take risky actions. In particular, whenever confronted with a risky choice (b, c) such that

$$v_L < \frac{(1 - c)}{c} \cdot b < v_H \tag{3}$$

individuals with low fitness expectations should take the risky action while individuals higher expectations should not take the action. Since this argument applies to all kinds of risky contexts, differences in reproductive value should give rise to consistent differences in suites of correlated risky behavioural traits. In Chapter 3 we showed that this basic principle can indeed account for the evolution of animal personalities whenever individuals differ in their fitness expectations.

The focus of Chapter 3 was on how differences in fitness expectations select for differences in suites of correlated risky behaviours. Risky actions, however, affect the fecundity and mortality profile of individuals and thus feed back on the fitness expectations of individuals. In the Intermezzo following Chapter 3 and in Chapter 4 we turned to the question how such feedbacks affect the emergence and stability of personalities.

Consistency

At present, many explanations of behavioural consistency over time are based on positive feedback mechanisms between the behaviour and the state of an individual (Sih *et al.*, 2004b; Sih & Bell, 2008): behavioural differences give rise to state differences among individuals that act to reinforce initial behavioural differences. Such reinforcement might, for example, act through learning or training (Rosenzweig & Bennett, 1996), or through behaviour induced changes in an individual's condition (Rands *et al.*, 2003; Stamps, 2007).

Returning to our explanation above, it may seem, that asset-protection involves a negative feedback that erodes the basis of behavioural differences over time (McElreath *et al.*, 2007; Sih & Bell, 2008). Consider, for example, a scenario where risky actions act to increase the future fecundity of surviving risk-prone individuals. Since individuals with low fitness expectations are more willing to take risky actions than individuals with higher expectations, the former will accumulate benefits in terms of future fecundity relative to the latter, which, in turn increase their future fitness expectations. Differences in fitness expectations thus give rise to behavioural differences that act to decrease the initial differences in fitness expectations.

It has been argued (McElreath *et al.*, 2007; Sih & Bell, 2008) that this negative feedback (1) is inherent to asset-protection and (2) eventually erodes the basis of behavioural differences among individuals. I agree that it is plausible that negative feedbacks as the ones above are present in some situations, however, they are neither inherent to asset-protection nor is it obvious that they are strong enough to erode underlying differences in fitness expectations. I mention three reasons for that.

RISKY ACTIONS WITH SMALL EFFECTS

Let's assume for the moment that the benefits associated with risky actions give rise to a permanent increase in the reproductive value of risk-prone individuals (see the following two points for a discussion of this assumption). In such situations negative feedbacks occur: differences in fitness expectations give rise to behavioural differences that decrease the initial differences in fitness expectations. Whether or not this process erodes differences in fitness expectations, however, depends on the magnitude of the benefits associated with risky actions relative to magnitude of the differences in fitness expectations among individuals. Intuitively, whenever the benefits are small relative to the differences in fitness expectations, risky actions have only a negligible effect on these differences. In such cases, differences in fitness expectations cannot be eroded by the feedbacks of asset-protection. On the other hand, whenever the benefits are large relative to the differences in reproductive value, risky actions will quickly erode initial differences in reproductive value among individuals.

BENEFITS TO KIN

In some cases, the benefits associated with risky actions do not directly increase the reproductive value of the acting individual but that of kin members (e.g., risky parental care, risky foraging in cooperative breeding groups). In such a situation, taking the risky action results in an expected reproductive value v' that is given by

$$v' = (1 - c) \cdot (v + r \cdot b) \ . \tag{4}$$

where r is the coefficient of relatedness between the acting individual and its kin. As above, the individual should take this action whenever $v' > v$, or, equivalently,

$$v < \frac{(1 - c)}{c} \cdot r \cdot b \ . \tag{5}$$

Individuals that take risky actions in such a situation, however, do not experience a direct increase in their reproductive value. In other words, there is no direct feedback from the risky action on the surviving risk-prone individual and behavioural differences due to asset protection do not effect underlying differences in fitness expectations.

TEMPORARY BENEFITS

Up to now I remained with an abstract characterization of the risky choice in the sense that I did not specify how the benefits b affect the reproductive value of individuals. It turns out, however, that these details are important for judging whether or not asset-protection tends to erode initial differences in fitness expectations. To see this, consider the fact that at some point in time t an individual's reproductive value v_t can be decomposed in the reproductive output F_t of that individual and its future reproductive value v_{t+1} which is deflated by the survival probability s_t from t to $t + 1$:

$$v_t = F_t + s_t \cdot v_{t+1} \tag{6}$$

The benefits of risky choices b might act to increase either the current reproductive output ($F_t + b$), the future reproductive value to ($v_{t+1} + b$) or both. Importantly, increases in current reproductive output have only a temporary effect on the fitness expectations and will not affect the willingness of that individual to take risks in the future ($> t$). Consequently, the more the benefits of risky actions tend to act on current reproduction, the weaker the negative feedback of asset-protection.

Positive feedbacks

In Chapter 4 we provide a formal analysis of feedbacks and their effect on the emergence and stability of personalities. The main result of that chapter is that asset-protection can give rise to both negative and positive feedbacks. Which of the scenarios is to be expected depends on the timing of the costs and benefits associated with risky actions.

To see the scope for positive feedbacks, consider, for example, a situation with a trade-off between the immediacy of benefits associated with risky actions and their risk. To put it simple, risky actions act to increase current fecundity (F_t in equation (6)) while less risky actions act to increase future fecundity (v_{t+1} in equation (6)). In such a situation, risk-averse individuals increase their future fecundity and thus their future fitness expectation, relative to individuals that are more risk-prone. In other words, individual differences in fitness expectations give rise to behavioural differences that act to increase initial differences in fitness expectations. Importantly, such positive feedbacks act to stabilize behavioural differences among individuals over time, even more, such feedbacks can give rise to consistent individual differences even when differences in fitness expectations are initially absent (Chapter 4).

Quality differences

Asset-protection provides a clear-cut and testable prediction: all other things being equal, if individual A has higher fitness expectations than individual B, A should be consistently more risk-averse in all kinds of risk-related situations than B. When testing this prediction in natural situations, however, a complication might arise.

In our analyses in the Chapters 3 and 4 we assumed, for simplicity, that all individuals face the same benefit and mortality risk associated with a particular risky action. In many natural situations, however, individual differences in fitness expectations will be associated with differences in states of individuals which may at the same time affect the benefits and mortality risks associated with risky actions.

Contrasting our prediction above, such underlying state differences can give rise to situations where individuals with higher fitness expectations are more willing to take risky actions than individuals with a lower fitness expectations. Consider, for example, a situation in which individuals with a relative high reproductive value v_H have a relatively low mortality risk c_H associated with a particular action whereas individuals with a relative low reproductive value v_L have a relatively high mortality risk c_L associated with the same action, $c_L > c_H$. To be concrete, individuals might differ in their body condition and individuals in better condition might be better in avoiding risks. This asymmetry in mortality risks can give rise to situations in which individuals with low fitness expectations avoid the risky action,

$$\frac{(1-c_L)}{c_L} \cdot b < v_L \ . \tag{7}$$

whereas the same action is beneficial for individuals with higher fitness expectations.

$$v_H < \frac{(1-c_H)}{c_H} \cdot b \ . \tag{8}$$

RESPONSIVENESS

I now turn to a discussion of the second part of this thesis which focussed on individual differences in responsiveness to environmental stimuli. Empirical studies in a range of animal species suggest that such differences may be an important factor structuring animal personalities (Aron & Aron, 1997; Koolhaas *et al.*, 1999; Groothuis & Carere, 2005). In a nutshell, individuals within populations often differ along a responsiveness (reactivity, flexibility, awareness) axis: at the unresponsive end of this spectrum we find individuals with a intrinsic behavioural control that quickly develop routines and show relatively rigid behaviour; at the responsive end we find individuals with a more extrinsic control of behaviour that remain reactive to environmental stimuli and show flexible behaviour. The work in presented in the Chapters 5 and 6 of this thesis focused on these observations.

Adaptive variation in responsiveness

Responsive individuals adjust their behaviour to the prevailing environmental conditions. Responsiveness is beneficial because it allows individuals to achieve a better phenotype-environment match (Benus *et al.*, 1987; Verbeek *et al.*, 1994; Mottley & Giraldeau, 2000), these benefits, however, will typically come at a cost (DeWitt *et al.*, 1998) since, for example, responsive individuals have to spend time and energy sampling the environment for cues. It is thus easy to see that the optimal degree of responsiveness depends on features of the environment such as the degree of environmental variation, the presence cues and sampling costs. It is not obvious, however, why individuals that face the exact same environment should differ in their responsiveness.

In Chapter 5 we showed that both spatial and temporal variation in the environment can give rise to adaptive individual differences in responsiveness. The essence of our arguments can be illustrated with the following simple toy-model.

Consider a population of N individuals where each individuals has the choice between two patches, say patch 1 and patch 2, that differ in their number of resources, R_1 and R_2. Within each patch, resources are shared equally among individuals, that is if individuals choose patch i the per capita payoff in that patch is given by R_i / N_i. Consequently, payoffs will be equalized across patches whenever the relative number of individuals in each patch matches the relative number of resources, that is

$$\frac{R_1}{N_1^*} = \frac{R_2}{N_2^*} \tag{9}$$

which corresponds to the so called ideal free distribution of individuals (Fretwell & Lucas, 1970).

Suppose now, realistically, that the resource distribution across the two patches varies in time. In such situations, individuals will repeatedly find themselves in situations that do not correspond to the equilibrium distribution (9). Consequently, one patch, say patch 2, yields a higher payoff than the other. This situation provides a payoff premium for responsive individuals that sample the alternative patch and switch patches in case its is beneficial. In particular, an individual in patch 2 that is responsive could obtain a payoff premium Δ that is given by

$$\Delta = \frac{R_2}{N_2} - \frac{R_1}{N_1} > 0 \tag{10}$$

The crucial point to realize now is that the payoff premium that can be gained by being responsive will decrease with the number of responsive individuals in the population. By switching patches, responsive individuals decrease the payoff in the more profitable patch from R_2 / N_2 to $R_2 / (N_2 + 1)$ and increase the payoff in the less profitable patch from R_1 / N_1 to $R_1 / (N_1 - 1)$. In fact, the payoff premium will be zero as soon as sufficiently many individuals switched from the less profitable to the more profitable patch such that the ideal free distribution (9) is attained. At that point nothing can be gained from being responsive. Consequently, in this simple example, being responsive is beneficial for some individuals in the population, but not for all.

In Chapter 5 we build on this basic intuition and show, quite generally, that negative frequency-dependence at the level of the behavioural choices (above: choice between two patches) gives rise to benefits of responsiveness that are negatively frequency dependent. The intuition for this result can be seen in our example above. Responsive individuals exploit environmental opportunities (e.g., switch to the more profitable patch). The benefits that are associated with these opportunities, however, will often decrease with the frequency of individuals in the population that exploit these opportunities and thus with the frequency of responsive individuals in the population.

Benefits of responsiveness that are negative frequency-dependent, in turn, favour the coexistence of responsive and unresponsive individuals. In short, responsive individuals are favoured because they can exploit opportunities in their environment. Unresponsive individuals can exploit the fact that responsive individuals tend to homogenize the environment and thus the payoffs associated with behavioural alternatives.

Consistency

As discussed above, at present, many researchers believe that feedback mechanisms between the behaviour and the state of an individual will be an important factor in explaining consistency (Sih & Bell, 2008). While these ideas seem plausible, up to now, little formal analysis has investigated the scope of such mechanisms (but see Rands *et al.*, 2003). In Chapter 5 we studied, in the context of responsiveness, if and how feedback mechanisms can give rise to behavioural consistency over time.

We focussed on a multi-stage scenario in which individuals could choose repeatedly between an unresponsive and a responsive behavioural tactic. In each stage, frequency dependent selection maintained both tactics in the population. In the absence of feedbacks (not shown in Chapter 5) individuals exhibit, at the evolutionary equilibrium, inconsistent behaviour over time: all individuals play a mixed strategy that randomizes between both behavioural alternatives.

To investigate the effect of positive feedbacks we assumed that individuals that chose the responsive tactic in an earlier stage experience lower costs or higher benefits of being responsiveness at a later stage. This assumption seems to capture the essence of what is meant by positive feedbacks (for a discussion of what processes give rise to such feedbacks, see Chapter 5). Our analysis shows that such feedbacks are indeed a powerful mechanisms explaining adaptive behavioural consistency. In fact, the presence of the smallest such feedback gives rise to high levels of behavioural consistency over time, at the evolutionary equilibrium, individuals that adopt the unresponsive tactic in an earlier stage will always have a higher tendency to adopt the unresponsive tactic at a later than previously unresponsive individuals.

Notice that while our analysis was performed in the context of responsiveness it should apply to any choice situation where (i) individuals have repeatedly the choice between two behavioural actions (e.g., hawk vs. dove, cooperate vs. defect, produce vs. scrounge), (ii) both actions are maintained by frequency-dependent selection in the population and (iii) positive feedback in the above sense are present.

Responsiveness selects for consistency and vice versa

In Chapter 6 we focussed on a feedback between responsive and unresponsive individuals that might be common in social interactions. Interestingly, this feedback provides an explanation for and a link between two basic phenomena associated with animal personalities, individual differences in responsiveness and behavioural consistency over time.

The basic idea is as follows. In social interactions, behavioural consistency may often be beneficial because it gives rise to predictability. Being predictable, however, can only be beneficial in the presence of responsive (socially aware) individuals that, when choosing their action, take into account the behavioural history of their social partners. The benefits of a responsive strategy, in turn, depend on two factors (Johnstone, 2001; McNamara *et al.*, 2008; McNamara *et al.*, 2009a): variation among individuals (in the absence of variation there is no need to be responsive) and consistency (past behaviour is only informative when individuals are at least to some degree consistent). In short, behavioural consistency favours responsiveness, which, in turn, favours consistency.

In Chapter 6 we developed an evolutionary model that investigates this feedback between responsiveness and consistency. Our analysis shows that responsive strategies are indeed favoured even in the presence of a potentially very small degree of consistency among individual differences. The presence of responsive individuals, in turn, selects for behavioural consistency among unresponsive individuals and, at the evolutionary equilibrium, responsive individuals coexist with unresponsive individuals that show high levels of consistency in their behaviour. Interestingly, this explanation for behavioural consistency thus requires the presence of inconsistent individuals, since it is just the presence of these individuals that make consistency beneficial.

Responsiveness and the importance of variation

Standard techniques of evolutionary analysis like evolutionary game theory (McNamara & Weissing, 2009b) and adaptive dynamics (Geritz *et al.*, 1998) are based on the simplifying assumption that evolution takes place in populations with little variation. Evolutionarily stable strategies (ESS), for example, are determined by considering the invasion prospects of rare mutants in a monomorphic population. It is not self-evident however that the predictions derived with such techniques apply to natural populations, which typically harbour much more variation.

There is at least one important context where the neglect of individual variation regularly leads to wrong conclusions. In social evolution, the focus of interest is often on responsive strategies that prescribe a certain behaviour in response to the inspection of other individuals. In situations like this, the degree and patterning of variation in the inspected traits is often of crucial importance for the outcome of evolution . Sexual selection theory provides us with a well-known example: costly female preferences can only evolve if there is sufficient variation in male traits (Andersson, 1994). This is not difficult to understand. Paying the costs of being choosy can only be advantageous if these costs are balanced by benefits. Such benefits only accrue if choosy females actually 'have a choice', that is, if there is sufficient variation among males.

The same basic principle applies to many other social situations, where the variance in a behavioural trait is important in determining the outcome of evolution (McNamara *et al.*, 2008; McNamara *et al.*, 2009a). Chapter 6 of this thesis provides another example. In the absence of sufficient variation, individuals evolve a mixed strategy which gives rise to inconsistent behaviour in repeated social interactions. Whenever sufficient variation among individuals is present, however, a coevolutionary process between responsiveness and consistency is triggered which, in turn, gives rise to a population in which responsive individuals coexist with unresponsive individuals that show high levels of adaptive consistency in their behaviour.

The interaction between variation and social sensitivity also plays a crucial role in situations where individuals face the decision on whether to break up a partnership. Many models show that the ability to opt out of an interaction can radically change evolutionary predictions. For example, in McNamara *et al.* (2008) individuals can break up a partnership in order to seek a more cooperative partner. Whether such a break up pays, however, depends crucially on the variation in cooperativeness within the population. In situations with low variation, potential future partners are similar to the current one and it is not beneficial to pay the costs of a break up (e.g., search costs), individuals should stick to their once chosen partner. However, if there is sufficient variation there are likely to be better partners and it may be worth paying the cost of a break up. The presence of individuals that are willing to break up, in turn, changes the selection pressures on cooperativeness, uncooperative individuals are more likely to lose their partners and thus to pay the cost of seeking a new partner, which, in turn, selects for increased cooperation; so again increased variation leads to the evolution of cooperation.

Similarly, variation in cooperativeness is also crucial for stabilizing cooperative strategies in the Repeated Prisoner's Dilemma (McNamara *et al.*, 2004), for the build-up of trust and trustworthiness (McNamara *et al.*, 2009a), and for the stability of monitoring and policing (McNamara & Weissing, 2009b). All these models exemplify the general principle that the presence of variation selects for responsive strategies which in turn can trigger coevolutionary processes that give rise to very difference evolutionary outcomes when compared to situations without such initial variation.

CONCLUDING REMARKS

This thesis presented a series of conceptual evolutionary models that were aimed at two basic questions. First, which factors promote adaptive behavioural differences that are consistent over time? Second, which factors promote adaptive behavioural differences that are correlated across situations and contexts? These questions were posed and investigated in the context of animal personalities, however, as I indicated already in the introduction, I see my work as part of a larger research project that aims to develop an integrated and holistic view on animal behaviour (Tinbergen, 1963; Gould & Lewontin, 1979; West-Eberhard, 2003; McNamara & Houston, in press).

Behavioural ecology traditionally focuses on the optimal behaviour for isolated decision problems. What mating strategy should an individual adopt? How much parental care should an individual provide? What is the best response to a predator? Typically, such questions are studied in isolation (this is nicely illustrated by animal behaviour textbooks, devoting separate chapter to mating, antipredator defence, etc.). The behavioural phenotype of an individual, in turn, is pictured as a collection of behavioural traits that are fine-tuned to such isolated decision problems.

Such an approach is particularly adequate if natural selection fine-tunes behaviour to any particular decision problem at hand. In reality, however, this seems not possible. Individuals are confronted with an enormous number of decisions throughout their life and it seems unrealistic to expect that natural selection fine-tunes the behaviour to each of these decisions – even if such a piecewise optimization would be feasible it would probably not be advantageous.

An alternative and in my view more fruitful approach is to view behaviour as resulting from behavioural rules which are selected to generalize across related but differing decision problems. According to such an approach, behaviour is not expected to be fine-tuned to any particular decision problem, rather, it is the result of underlying decision rules which are selected to perform well on average, that is when confronted with a larger class of decision problems. In this sense I fully agree with John McNamara and Alasdair Houston (in press): "Behavioural ecologists have built complex models of optimal behaviour in simple environments. We argue that they need to evolve simple mechanisms that perform well in complex environments."

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Dutch summary

Geen twee individuen zijn gelijk. Neem twee individuen van hetzelfde geslacht, dezelfde leeftijd en dezelfde sociale achtergrond en je zult stabiele verschillen in hun motivatie, kennis en gedrag vinden. In mensen worden dergelijke stabiele verschillen persoonlijkheden genoemd. Maar persoonlijkheden of individualiteit komen niet alleen binnen mensen voor. In de laatste jaren zijn dierlijke persoonlijkheden beschreven in een groot aantal soorten (>100), variërend van spinnen tot hommels, van octopussen tot stekelbaarzen, en van muizen tot apen. Een koolmees (*Parus major*), bijvoorbeeld, die als jong dier een tendens heeft nieuwe omgevingen snel en oppervlakkig te onderzoeken zal zijn omgeving ook later in zijn leven snel en oppervlakkig onderzoeken. Nog interessanter is dat snelle en oppervlakkige koolmezen ook agressiever lijken te zijn dan hun langzame en grondige onderzoekende soortgenoten en bovendien vertonen ze gewaagder gedrag in nieuwe situaties en nemen ze meer risicos. Op dezelfde manier verschillen individuele knaagdieren zoals muizen (*Mus musculus*) en ratten (*Rattus norvegicus*) vaak consistent tussen elkaar in de manier hoe zij omgaan met uitdagingen in hun omgeving; dergelijke verschillen zijn gemeten met betrekking tot sociale tolerantie, agressiviteit, cooperativiteit en zelfs nestbouwend gedrag.

Dit proefschrift onderzocht hoe natuurlijke selectie tot dierlijke persoonlijkheden kan leiden. Of preciezer, hoe natuurlijke selectie kan resulteren in gedragsverschillen tussen individuen, waarbij deze gedragsverschillen tussen verschillende situaties en contexten gecorreleerd en voor een bepaalde tijd stabiel zijn. Deze vraag is in zekere mate in de literatuur behandeld, maar momenteel zouden de meeste onderzoekers het ermee eens zijn dat de evolutionaire oorsprong en de aanpassingswaarde van persoonlijkheden een slecht begrepen fenomeen zijn.

Het hoofddeel van deze proefschrift begon met een conceptueel hoofdstuk (**Hoofdstuk 2**) dat de meest belangrijke factoren en mechanismen herzag die tot een aanpassingsverklaring van dierlijke persoonlijkheden kunnen bijdragen. Wij concentreerden ons op twee hoofdvragen. Ten eerste, welke factoren bevorderen de evolutie van variate in gedrag? Ten tweede, welke factoren bevorderen de evolutie van correlaties tussen verschillende typen gedrag en tussen verschillende tijdstippen (gedragscorrelaties)?

Betreffende de oorzaken van variatie hebben wij de rol van frequentie afhankelijke selectie en omgevingsvariatie in ruimte en tijd besproken. Variatie kan het resultaat van selectie zijn wanneer elk gedragstype een fitnessvoordeel heeft wanneer het zeldzaam is; als de individuen die met een onvoorspelbare omgeving geconfronteerd zijn een zogeheten "bet-hedging" strategie spelen; of als verschillende gedragstypes elkaar op een synergistische manier opvullen (bijvoorbeeld als er sprake is van arbeidsverdeling tussen de verschillende gedragstypen).

Betreffende de oorzaken van gedragscorrelaties concentreerden wij ons op de rol van beperkingen in de onderliggende genetische en fysiologische architectuur van gedrag, aanpassingen aan lokale habitats, en verschillen in toestand tussen individuen. Wij bespraken dat gedragscorrelaties onvermijdelijk zijn als gedrag alleen door een beperkt aantal controlevariabelen (bijvoorbeeld hormonen) wordt geregeld. Correlaties zijn ook te verwachten wanneer individuen in toestand verschillen en het optimale fenotype afhangt van een bepaalde toestand van het individue. Stabiel gedrag over tijd zal vaak het gevolg zijn van positieve terugkoppeling (bijvoorbeeld vanwege leergedrag) waar de toestand en het gedrag elkaar versterken.

De rest van deze proefschrift stelde een reeks conceptuele evolutionaire modellen voor. Met deze modellen streefde ik ernaar om gedragsaspecten van persoonlijkheden te onderzoeken die een wat algemener voorkomen lijken te hebben (dwz., gedragen die in in meerdere dierlijke soorten voorkomen). Momenteel lijken er minstens twee gedragsaspecten goede kandidaten te zijn die aan deze voorwaarde voldoen: het zogenaamde "boldness-aggression syndrome" en individuele verschillen in "responsiveness" (voortaan responsiviteit). Deze twee kandidaten stonden centraal in deze dissertatie.

De naam boldness-aggression syndrome verwijst naar een positieve correlatie tussen individuele verschillen in onverschrokkenheid (bijvoorbeeld in de reactie op een roofdier of in het onderzoeken van een nieuwe omgeving) en de mate van agressie tegen soortgenoten. Dergelijke verschillen zijn het eerst beschreven binnen stekelbaarzen (*Gasterosteus aculeatus*): (i) gedurende de paringscyclus verschillen mannelijke stekelbaarzen in hun aggressiviteit tegen territoriale indringers; (ii) de mate van aggressiviteit bleef stabiel wanneer stekelbaarzen werden geconfronteerd met verschillende types van indringers en ook gedurende latere tijdstippen tijdens de paringscyclus; en (iii) individuen die agressiever waren tegen territoriale indringers tijdens het paarseizoen reageerden ook onverschrokkener op roofdieren buiten het paarseizoen.

Sinds deze vroege stekelbaarsstudie is het boldness-aggression syndrome voor verschillende andere taxa beschreven, inclusief vogels en knaagdieren. Momenteel is het boldness-aggression syndrome één van de meest gemelde bevindingen in de dierlijke persoonlijkheidsliteratuur.

In de Hoofdstukken 3 en 4 ontwikkelden wij een theorie die een verbinding tussen variatie in de levensloop en het boldness-aggression syndrome laat zien. Deze theorie is gebaseerd op de waarneming dat zowel onverschrokkenheid als ook aggressiviteit in termen van risicogedrag kunnen worden gecategoriseerd: die individuen die meer risico nemen in conflicten met soortgenoten, nemen ook meer risico wanneer ze met roofdieren zijn geconfronteerd. Van de theorie die zich bezig houdt met de studie van verschillende levensstrategieën in dieren (zogeheten 'life-history theory') weten wij dat individuen hun risicogedrag aan hun overblijvende reproductieve waarde (dwz., verwachte fitness) zouden moeten aanpassen. Individuen met een hogere reproductieve waarde zouden risicos moeten vermijden, aangezien zij moeten overleven om deze verwachtingen te realiseren. Door dezelfde reden zouden individuen met vrij lage verwachtingen meer risico's moeten nemen, aangezien zij weinig te verliezen hebben. Hieruit volgt dat wanneer individuen in hun verwachtingen verschillen wij stabiele verschillen en gecorreleerde gedragspatronen verwachten: sommige individuen zijn risicodragend terwijl anderen risicos vermijden.

In **Hoofdstuk 3** toonden wij door middel van een eenvoudig model aan dat deze intuïtieve argumenten inderdaad een evolutionaire verklaring geeft voor het ontstaan van verschillende dierlijke persoonlijkheden . Wij gingen in drie stappen te werk: ten eerste toonden wij aan dat de balans tussen huidige en toekomstige reproductie gemakkelijk tot polymorfe populaties kan leiden waar sommige individuen meer nadruk op toekomstige reproductie dan anderen leggen. Ten tweede toonden wij aan dat deze variatie in levensgeschiedenis selecteert voor systematische verschillen in het risicogedrag: individuen die meer nadruk op toekomstige reproductie leggen evolueren voorzichtiger gedrag dan individuen die meer nadruk op de huidige reproductie leggen. Ten derde toonden wij aan dat deze verschillen in het risicogedrag zich tot diverse risicovolle situaties uitbreiden en stabiel in de tijd zijn, en daardoor tot dierlijke persoonlijkheden leiden.

De analyse in **Hoofdstuk 3** concentreerde zich op de vraag hoe verschillen in fitnessverwachtingen voor stabiele verschillen van gecorreleerd gedrag selecteren. Maar risicogedrag beïnvloedt ook de vruchtbaarheid en het mortaliteitsprofiel van individuen en voert op deze manier weer terug op de fitnessverwachtingen van de individuen. Dergelijke terugkoppelingen worden belangrijk wanneer de aanvankelijke verschillen in fitness verwachtingen klein zijn. In **Hoofdstuk 4** leverden wij een algemene analyse van dergelijke terugkoppelingen. Onze resultaten toonden aan dat afhankelijk van de timing van de kosten en de voordelen van het risicogedrag twee kwalitatief verschillende scenario's mogelijk zijn. Ten eerste kunnen gewaagde keuzen met mortaliteit en gevolgen voor de vruchtbaarheid verbonden zijn, waardoor verschillen in het risicogedrag verminderd worden (negatieve terugkoppeling). Individuen die risicos vermijden vertonen meer risicovol gedrag en vice versa. Ten tweede kunnen gewaagde keuzen met mortaliteit en gevolgen voor de vruchtbaarheid verbonden zijn die vroegere verschillen in het risicogedrag verhogen (positieve terugkoppeling).

Het werk dat in de **Hoofdstukken 5 en 6** wordt voorgesteld concentreerde zich op een tweede gedragskenmerk van dierlijke persoonlijkheden dat een zekere algemeenheid heeft: hier gaat het om individuele verschillen in responsiviteit van omgevingsstimuli. Terwijl sommige individuen zeer ontvankelijk voor deze stimuli te zijn schijnen en gemakkelijk hun gedrag aan de heersende situaties aanpassen, tonen anderen een rigider gedrag. Stabiele verschillen in ontvankelijkheid zijn gedocumenteerd in verschillende taxa met inbegrip van vogels, knaagdieren, varkens en mensen.

Bijvoorbeeld zowel bij muizen en ratten verschillen de individuen wezenlijk in hun ontvankelijkheid aan omgevingsveranderingen in een labyrinttaak. Sommige individuen vormen snel een routine, worden niet door minder belangrijke omgevingsveranderingen beïnvloed en presteren vrij slecht wanneer ze geconfronteerd zijn met een veranderende labyrintconfiguratie. Anderen vormen geen routine, worden door minder belangrijke veranderingen sterk beïnvloed en presteren vrij goed wanneer ze geconfronteerd zijn met veranderende labyrintconfiguraties. Op dezelfde manier passen sommige koolmezen hun gedrag gemakkelijk aan een verandering in de het voedingssituatie aan terwijl anderen zich aan vroeger gewoonten houden.

Vanuit een aanpassingsperspectief levert de waarneming dat individuen in hun ontvankelijkheid verschillen twee kernvragen op. Ten eerste, waarom kunnen ontvankelijke en niet-ontvankelijke individuen binnen een populatie coexisteren? Zouden wij niet één enkel „optimaal“ fenotype moeten verwachten? Ten tweede, waarom zijn de verschillen in ontvankelijkheid stabiel tussen verschillende contexten en over tijd? Zouden wij niet moeten verwachten dat individuen hun ontvankelijkheid aan de behoeften van de situatie aanpassen?

In **Hoofdstuk 5** ontwikkelden wij een evolutionair model om deze vragen te beantwoorden. Ten eerste pakten wij het probleem van coexistentie aan. Ons inzicht is dat het voordeel van ontvankelijkheid voor vele realistische scenario's negatief frequentie afhankelijk is, dat wil zeggen dat ontvankelijkheid voordelig is als het zeldzaam is, maar nadelig is wanneer het algemeen is. Als gevolg daarvan breidt ontvankelijkheid zich snel uit wanneer het zeldzaam is, en het tegenovergestelde vindt plaats als veel individuen juist al ontvankelijk zijn. Dit verklaart coexistentie. Ten tweede pakten wij het probleem van stabiliteit van de ontvankelijkheidverschillen aan. Wij laten zien dat stabiele verschillen in ontvankelijkheid te voorschijn komen wanneer de kosten van ontvankelijkheid lager zijn voor die individuen die al eerder ontvankelijk zijn geweest. Wij voeren aan dat vele processen (bijvoorbeeld leergedrag) tot dergelijke positieve terugkoppelingen kan leiden.

In het **Hoofdstuk 6** concentreerden wij ons op terugkoppelingen tussen ontvankelijke en niet-ontvankelijke individuen die in sociale interactie vaak aanwezig zouden kunnen zijn. Het basisidee was als volgt. Gedragsconsistentie kan in sociale interacties vaak voordelig zijn omdat gedragsconsistentie tot voorspelbaarheid leidt. Voorspelbaarheid kan echter slechts in aanwezigheid van ontvankelijke individuen voordelig zijn die, wanneer ze hun acties kiezen, met de gedragsgeschiedenis van hun sociale partner rekening houden. Uit dit volgt dat de voordelen van een ontvankelijke strategie van twee factoren afhangen: variatie tussen individuen (bij gebrek aan variatie is er geen behoefte aan ontvankelijkeid) en stabiliteit (het eerdere gedrag is slechts informatief wanneer individuen op zijn minst tot een zeker niveau consistent zijn). In het kort, stabiliteit in het gedrag begunstigt ontvankelijkheid, dat op zijn beurt weer de stabiliteit in ontvankelijkheid begunstigt.

In **Hoofdstuk 6** ontwikkelden wij een evolutionair model om deze terugkoppeling tussen ontvankelijkheid en consistentie te onderzoeken. Onze analyse toont aan dat ontvankelijke strategieën inderdaad zelfs in aanwezigheid van een potentieel zeer kleine graad van consistentie worden begunstigt. De aanwezigheid van ontvankelijke individueen selecteert op zijn beurt voor gedragsconsistentie onder niet ontvankelijke individuen: op het evolutionaire evenwicht coexisteren ontvankelijke individuen met niet ontvankelijke individuen die hoge niveaus van consistentie in hun gedrag laten zien. Interessant is ook dat deze verklaring voor gedragsconsistentie de aanwezigheid van inconsistente individuen vereist, aangezien dat het de aanwezigheid van precies deze individuen is die consistentie voordelig maakt.

Samengevat stelde deze thesis een reeks conceptuele evolutionaire modellen voor die gericht waren op twee kernvragen. Ten eerste, welke factoren bevorderen aangepaste gedragsverschillen die stabiel in de tijd zijn? Ten tweede, welke factoren bevorderen aangepaste gedragsverschillen die tussen situaties en contexten gecorreleerd zijn? Deze vragen werden gesteld en onderzocht in de context van dierlijke persoonlijkheden, maar, zoals ik ook al in de inleiding (**Hoofdstuk 1**) en de algemene bespreking (**Hoofdstuk 7**) besprak zie ik mijn werk als deel van een grotere onderzoeksproject dat poogt om een geïntegreerde en holistisch beeld van dierlijk gedrag te ontwikkelen.

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