
Avian Personality

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Introduction

Birds are widely distributed and highly diversified, and also generally more conspicuous and observable in natural environments than many other vertebrates. Birds also exhibit complex behavior and social processes. Because of these attributes, birds are key model organisms that have allowed behavioral biologists to address a wide range of ecological and evolutionary questions (Konishi et al. 1989; Danchin et al. 2008; Davies et al. 2012). Moreover, owing to the contributions from a diverse group of ornithologists ranging from amateur bird-watchers to professional scientists, the knowledge of bird behavior under natural conditions is more extensive than for any other vertebrate taxa. Many avian species are diurnal, conspicuous, and resilient, and also permit relatively invasive investigations. In consequence, they are well suited for experimental field research using a wide range of methods such as manipulation of breeding conditions (Tinbergen and Boerlijst 1990), bioacoustic analyses (Marler and Slabbekoorn 2004; Catchpole and Slater 2008), capture and marking procedures (Lebreton et al. 1992), and analyses of energy expenditure and of endocrine and immune function (Wingfield 2005). Birds are also excellent study organisms for experimental investigations of behavioral adaptations to changes in environmental conditions, a topic that has become of particular interest in recent years (Visser 2008). Furthermore, captive bird populations proved to be extremely valuable in studies on the genetics of behavior (Berthold and Querner 1981; Jones and Hocking 1999; Price 2002; Drent et al. 2003; Van Oers et al. 2005a), the neurological correlates of behavior (Konishi 1985; Gil et al. 2006), physiological mechanisms underlying behavior and its variation (Wingfield 2005; Soma et al. 2008), and developmental influences on behavior (Naguib and Nemitz 2007), as well as in studies on sexual selection (Andersson 1994). Even in more applied fields such as conservation, animal welfare, and animal husbandry, birds have been shown to be good models for studying behavior, both in the field and in captivity (Sutherland 1998; Dawkins 1999; Rodenburg and Turner 2012).

Considering all of the above, it is not surprising, therefore, that the majority of studies on animal personality have been conducted on birds. The study of personality traits in birds can be framed into an ecological context more easily than in other taxa, allowing analyses of ecological and evolutionary aspects of personality. Birds of resident species can be followed individually, often throughout their lives, their behavior can be measured both under standardized conditions in captivity and in their natural environment, and fitness can be quantified. The opportunity to conduct behavioral tests in the laboratory also allows researchers to effectively document consistent differences in individual behavior within and across contexts (Dingemanse et al. 2002; Van Oers et al. 2005b; Martins et al. 2007; Schuett and Dall 2009).

The aim of this chapter is to provide a broad overview of studies on avian personality, including those that address genetic variation linked to personality (Van Oers et al. 2005a; Fidler et al. 2007; Gil and Faure 2007; Bell and Aubin-Horth 2010; Van Oers and Muller 2010), the behavioral and fitness consequences of personality in natural populations (e.g., Dingemanse et al. 2004; Dingemanse and Wolf 2010; Wolf and Weissing 2010), mathematical models that investigate possible scenarios for the evolution of personality (Wolf et al. 2007; Amy et al. 2010; Dingemanse and Wolf 2010; Houston 2010), and the physiological substrate of personality (e.g., Carere et al. 2005a; Kralj-Fiser et al. 2007; Fucikova et al. 2009; Coppens et al. 2010; Baugh et al. 2012). We also provide a historical background of personality research in birds and discuss recent studies from a historical perspective.

Historical overview of avian personality research

Darwin wrote extensively on animal behavior (Darwin 1872) and, after him, scientists working on animal behavior could be separated into two different fields, namely, comparative psychologists and ethologists. There was one camp of ethologists such as Douglas Spalding (1841–1877), who studied imprinting in chicks (Gray 1967), and another camp of mainly animal psychologists such as Lloyd Morgan (1852–1936), who wrote a book, very influential at the time, introducing the field of comparative psychology (Lloyd Morgan 1923). Wallace Craig, Oskar Heinroth, and Charles Otis Whitman contributed to the emergence of ethology as a major separate biological discipline in the study of behavior. Although both comparative psychology and ethology address basic principles of animal behavior, these disciplines have been separated for a long time. Interestingly, however, the study of individuality in the behavior of birds, and their personality, has found its way in research both by ethologists and by comparative psychologists, and also

has emerged in publications by semiprofessional bird banders. A crucial factor for recognizing individual differences in behavior is spending sufficient time observing the individuals. Yet, a larger part of ornithological research up until the first part of the twentieth century was done in museums so that few data were available on behavioral differences among individuals (Armstrong 1947).

The first published use of the word *personality* to describe characteristics of individual birds was probably by Talbot in 1922. Talbot (1922) described inter- and intraspecific differences in the motivation to fly through a hole that was situated at the entrance of a gathering cage, when birds were caught for banding. In the *Manual of Bird Banders*, Lincoln and Baldwin (1929) even stated that documenting bird personality, defined as the individual peculiarities in appearance, habits, and manners (Baechle 1947), is one of the main achievements of bird banding. A nice example that recognizing individual personality differences requires spending sufficient time with these individuals is provided by Gwendolen (Len) Howard, a musician who kept birds in captivity as hobby. Most of her birds were tame, or at least habituated to human presence, and in a book called *Birds as Individuals*, Howard (1953) describes in great detail the lives of great tits, black birds, robins, and other birds in her garden or inside her house. Most remarkable about this is that she recognized the birds not only by their individual plumage characteristics, but also by their “characteristic mannerisms and poses and their facial expressions.” She states that great tits especially were easily recognized since “their whole bearing and personality was too individual for confusion to arise when I had them at close quarters” (Howard 1953).

While the early descriptions of personality-like behavior in birds were largely anecdotal, it was probably Lack (1947) who made the first scientifically based description of individual differences in aggressiveness in robins, when he tested several males and their reaction to a model. Some males were hardly interested in the model, while others vigorously attacked it. Another series of papers related to individual differences in behavior came from Burtt (1967), a psychologist who combined his interest in bird banding with the scientific study of personality. While banding over 17,000 blackbirds for the Federal Wildlife Service, he studied bird behavior for several years from a psychological perspective (Thayer and Austin 1992). In his book *The Psychology of Birds*, he made the connection between personality traits, such as extroversion, dominance, and emotional stability, and the behavior of individual birds (Burtt 1967). Together with Giltz, he investigated, for instance, the importance of personality in the interpretation of bird behavior (Burtt and Giltz 1969b). In connection with a banding program at a decoy trap,

the pair measured the personality traits “complacency” and “aggression” in common grackles (*Quiscalus quiscula*), red-winged blackbirds (*Agelaius phoeniceus*), brown-headed cowbirds (*Molothrus ater*), and starlings (*Sturnus vulgaris*). They defined what they called *the complacency-agitation continuum* as the way an individual bird behaved in a small cage, directly after banding. Complacent birds moved more compared with agitated birds. Aggression was assessed while birds were held in a hand; birds were threatened with a finger and the tendency to bite was measured on a scale from zero to ten (Burt and Giltz 1969a). Both traits showed within- and between-species variation and were found to be highly repeatable. They found cowbirds to be the most complacent and starlings the most agitated species, while grackles and cowbirds were the most aggressive, and starlings and red-winged blackbirds the least aggressive species (Burt and Giltz 1969a; 1969b). They also found that grackles had the greatest tendency to re-enter the trap, and that they were the most resident species compared with the other species (Burt and Giltz 1973).

As suggested by this brief historical overview, recognizing consistent individual differences in bird behavior has a long history, dating back to the roots of ethology. Scientific research focusing on such differences, however, has flourished mainly in the last decade (Table 1), after individual differences in behavior were framed into the well-defined concepts of personality, behavioral syndromes, and coping styles.

Recent advances in avian personality research

BEHAVIORAL CONSISTENCY AND BEHAVIORAL TESTS

Many recent studies on behavioral consistency in birds have been inspired by the work of Verbeek, Drent, and coworkers in the early 1990s on great tits (Verbeek et al. 1994; 1996; 1999). This work was based on earlier studies on the individual consistency in the response toward changes in the environment in mice (e.g., Van Oortmerssen and Bakker 1981; Benus et al. 1987) and studies on foraging and exploratory behavior in great tits (*Parus major*) (e.g., Krebs et al. 1972; Krebs and Perrins 1978). Individual differences in exploratory behavior had been noticed in several studies on foraging behavior in great tits (Partridge 1976; Kacelnik et al. 1981), so the expansion of research with a focus on such behavioral differences could be built on a substantial body of knowledge of this topic. The behavioral tests developed by Verbeek and coworkers to investigate novel object and novel environment exploration (Verbeek et al. 1994) are now used as standard tests in most studies on great tits (e.g., Dingemanse et al. 2002; Van Oers et al. 2008; Hollander

et al. 2008; Titulaer et al. 2012) and also on other bird species (e.g., Fox and Millam 2007; Martins et al. 2007; Kurvers et al. 2009; Schuett and Dall 2009). Since the behavioral response to a novel object or novel environment might be species-specific, some caution is required when comparing studies of different species. A test that might be very meaningful in the life-history of one species might be less suitable for another one, thus resulting in between-species differences in the consistency of a trait (Mettke-Hofmann et al. 2005). Hence, although exploratory behavior is now considered one of the major animal personality traits (Réale et al. 2007; Sih and Bell 2008), species-specific tests to validate this and other behaviors are very important. Related to exploratory behaviors are boldness or risk-taking behaviors (Réale et al. 2007; but see chapter 6). Whereas the exploration of a novel object is likely to reflect a mixture of curiosity and fearfulness, risk-taking behaviors are often related to predation risk and foraging (Van Oers et al. 2004b). Therefore, these behaviors are more closely linked to stress responses (Martins et al. 2007). Social relationships (Stowe et al. 2006; Stowe and Kotschal 2007) and the behavior of unrelated flock mates (Marchetti and Drent 2000; Van Oers et al. 2005b; Kurvers et al. 2009) might also be important factors. The behavior of a group of birds as a whole can, therefore, be affected by the mix of personality types present within the group (Kurvers et al. 2009; Schuett and Dall 2009; Amy et al. 2010).

Apart from exploratory behavior, several other traits have been investigated in birds as personality traits (see table 3.1 for some examples). One trait that has been widely used in bird research is agonistic behavior, which has been shown to be individually consistent and to have a genetic correlate in mice (Benus 1988) and fish (Bakker 1994). Aggression toward a conspecific is a crucial part of the life-history of social animals such as birds. Especially for social dominance (Verbeek et al. 1996; Dingemanse and De Goede 2004) and in territorial behavior (Duckworth 2006b; Garamszegi et al. 2009; Amy et al. 2012), agonistic behavior is an important personality trait determining the outcome of an interaction and subsequent access to resources. In great tits, Verbeek and coworkers (1996) investigated whether individual differences in exploratory behavior were related to agonistic behavior and how this, in turn, related to dominance. In an experimental set-up, two males were placed in a cage, with an opaque partition between them. After removing the partition, the authors noted which of the two males attacked first. They found that this measure of aggressive behavior was consistent over time and that fast explorers started more fights than slow explorers, independent of sex and morphological traits. Individuals that initiated a fight were also more likely to win that fight.

Table 3.1. A noncomprehensive species overview with studies on the assessment of avian personality traits.

<i>Author</i>	<i>Year</i>	<i>Species</i>	<i>Personality traits</i>
		Anseriformes	
Kurvers et al.	2009	Barnacle goose	(<i>Branta bernicla</i>) Boldness
Kralj-Fiser et al.	2007	Greylag goose	(<i>Anser anser</i>) Reaction to handling
		Ciconiiformes	
Blas et al.	2007	European white stork	(<i>Ciconia ciconia</i>) Reaction to handling
		Falconiformes	
Costantini et al.	2005	European kestrel	(<i>Falco tinnunculus</i>) Feeding habits
		Galliformes	
Richard et al.	2008	Japanese quail	(<i>Coturnix japonica</i>) Boldness
Uitdehaag et al.	2008	Jungle fowl	(<i>Gallus gallus</i>) Boldness
Faure	1980	Jungle fowl	(<i>Gallus gallus</i>) Exploration
		Passeriformes	
Guillette et al.	2009	Black-capped chickadee	(<i>Poecile atricapillus</i>) Exploration
Arnold et al.	2007	Blue tit	(<i>Cyanistes caeruleus</i>) Boldness
Burt and Giltz	1973	Brown-headed cowbird	(<i>Molothrus ater</i>) Aggressiveness
		Common grackle	(<i>Quiscalus quiscula</i>) Complacency
		Red-winged blackbird	(<i>Agelaius phoeniceus</i>)
		Starling	(<i>Sturnus vulgaris</i>)
Harvey and Freeberg	2007	Carolina chickadees	(<i>Poecile carolinensis</i>) Aggressiveness Sociability
Quinn and Cresswell	2005	Chaffinch	(<i>Fringilla coelebs</i>) Risk-taking
Garamszegi et al.	2009	Collared flycatcher	(<i>Ficedula albicollis</i>) Boldness Aggressiveness Risk-taking
Stöwe and Kotrschal	2007	Common raven	(<i>Corvus corax</i>) Boldness
Mettke-Hofmann et al.	2005	Garden warbler	(<i>Sylvia borin</i>) Exploration
		Sardinian warbler	(<i>Sylvia melanocephala</i>) Boldness
Verbeek et al.	1994	Great tit	(<i>Parus major</i>) Exploration Boldness
Verbeek et al.	1996	Great tit	(<i>Parus major</i>) Aggressiveness
Van Oers et al.	2004b	Great tit	(<i>Parus major</i>) Risk-taking
Hollander et al.	2008	Great tit	(<i>Parus major</i>) Exploration
Quinn et al.	2009	Great tit	(<i>Parus major</i>) Exploration
Fucikova et al.	2009	Great tit	(<i>Parus major</i>) Reaction to handling
Fox et al.	2009	Mountain chickadee	(<i>Poecile gambeli</i>) Exploration Boldness
Marchetti and Zehindjiev	2009	Sedge warbler	(<i>Acrocephalus schoenobaenus</i>) Exploration
Minderman et al.	2009	Starling	(<i>Sturnus vulgaris</i>) Exploration
Duckworth	2006a	Western bluebird	(<i>Sialia mexicana</i>) Aggressiveness

(continued)

Table 3.1. (continued)

Author	Year	Species	Personality traits
Beauchamp	2000	Zebra finch (<i>Taenopygia guttata</i>)	Exploration
Martins et al.	2007	Zebra finch (<i>Taenopygia guttata</i>)	Exploration Boldness
Schuett and Dall	2009	Zebra finch (<i>Taenopygia guttata</i>)	Exploration
		Psittaciformes	
Fox and Millam	2004	Orange-winged Amazon (<i>Amazona amazonica</i>)	Neophobia
Mettke-Hofmann et al.	2004	10 species	Boldness
		Sphenisciformes	
Ellenberg et al.	2009	Yellow-eyed penguin (<i>Megadyptes antipodes</i>)	Reaction to handling
		Struthioniformes	
De Azevedo and Young	2006	Greater Rhea (<i>Rhea americana</i>)	Boldness

Agonistic behavior in birds is linked to the ability to obtain and maintain a breeding territory (Stamps and Krishnan 1997; Naguib 2005). In studies on agonistic behavior in relation to territorial competitiveness (Duckworth 2006a) and parental behavior (Duckworth 2006b) in Western bluebirds (*Sialia mexicana*) it was shown, for instance, that agonistic behavior is repeatable and costly (Duckworth 2006b). Moreover, Duckworth (2006a) showed experimentally that more aggressive males compete more effectively for territories in areas with a higher density of nest boxes. As a consequence, aggressive and nonaggressive males occurred in breeding habitats that differed in the strength of selection on morphological traits. These results show that aggression can affect selection on a local scale by determining individual settlement patterns, thereby also providing opportunity for correlational selection.

Tests of agonistic behavior are, by definition, conducted in a social context, and the consistency in behavior could also be dependent on the context (Van Oers et al. 2005b). To test whether males of black-capped chickadees (*Poecile atricapillus*) behaved consistently with different mates, they were paired to a female and several aspects of their behavior were observed (Harvey and Freeberg 2007). After being paired with a new mate, the males showed behavior that was consistent with the behavior previously shown with their former mate, indicating that agonistic behavior is consistent also when the social context has been changed (Harvey and Freeberg 2007).

A crucial issue in assessing personality traits is the identification of contexts that are most suitable for revealing consistent differences in behavior among individuals. Exploration tests in artificial environments, such as

a novel room or cage, and novel object tests, provide standard situations. The artificial nature of such a context has the advantage that behavior can be tested in the absence of a specific resource value, which may confound any measurement of intrinsic behavioral traits. Resources vary in their value to different individuals so that in tests conducted in natural situations it is difficult to separate individual differences in behavior from differences in resource values. Individuals may behave differently not as a result of personality but as a result of differences in resource values. Conducting tests in the natural habitat could potentially reveal a more meaningful variation in behavior compared with the standard tests done in captivity, and therefore yield results with high ecological and evolutionary relevance. Yet, when testing birds for personality traits during resource defense in the field, one needs to be careful in developing tests so that the recorded behavior is not primarily related to the resource value rather than to their personality traits. Demonstrating consistencies in behavior in contexts that are independent of resources crucial for reproduction, thus remains a powerful tool in research aimed at unraveling the evolutionary significance of personality traits.

Causes of personality variation: genes and physiology

GENETICS

The majority of our knowledge of the genetic background of traits such as exploratory behavior, aggressiveness, and fearfulness comes from studies on domestic birds. Selection experiments on chicken, turkey, ducks, and Japanese quail have shown that the observed variation in open field, pair-wise, and novel object tests has a substantial genetic basis (e.g., Brown and Nestor 1973; Francois et al. 1999; Jones and Hocking 1999; Arnaud et al. 2008). Although the presence of a genetic component is an important factor to consider in studies on evolutionary change of personality traits, genetic studies of animal personality traits in natural populations are scarce (Bell and Aubin-Horth 2010). Most quantitative genetic and molecular analyses of bird personality traits have been conducted with the great tit (quantitative: Van Oers et al. 2005a; Quinn et al. 2009; molecular: Fidler et al. 2007; Van Bers et al. 2010; Korsten et al. 2010). In this species it is apparent that personality traits typically have moderate levels of additive genetic variation (Dingemanse et al. 2002; Drent et al. 2003; Van Oers et al. 2004b; Quinn et al. 2009) and of genetic dominance (Van Oers et al. 2004c), and that traits are genetically correlated (Van Oers et al. 2004a). An important gene has been identified for great tit personality: the dopamine receptor D4 gene

(Fidler et al. 2007) explains between 5% and 8% of the phenotypic variation in some but not all European great tit populations (Korsten et al. 2010). This and other genes are thereby likely not only to affect behavioral responses early in life (i.e., temperament traits), but also to affect learning and plasticity later in life.

One difficult question is to assess the extent to which the underlying genetic and physiological mechanisms are a constraint on the evolution of behavioral traits vs. the extent to which they are the product of variation and selection (Bell 2005; Dingemanse et al. 2007). An important issue here is how the word *constraint* is used. In a biological context, the word can refer to a factor that impedes but does not necessarily prevent evolution in particular directions, or it can indicate that specific evolutionary trajectories are unavailable to selection (Roff and Fairbairn 2007). Therefore, determining the role of genetic constraints in the evolutionary change of personality will require not only more detailed ecological studies, but also better knowledge than we currently possess of the relevant genes and their importance in natural populations (Blows and Hoffmann 2005; Van Oers et al. 2005a). A more comprehensive overview of the current knowledge of the genetic basis of personality variation in captive and wild animals is provided in chapter 6.

HORMONAL CORRELATES

Many vertebrate species are characterized by the flexibility with which they cope with stressors, and birds provide good examples of this. When birds are under conditions of low environmental predictability, they experience stress (Wiepkema 1992). Behavioral and physiological efforts to master the situation (coping strategies) can be important determinants of health and disease both in humans and in animals (Koolhaas et al. 1999). Moreover, individuals often show different physiological responses in these situations, also referred to as coping styles. Individuals appear to cope with stressors in a predominantly sympathetic or parasympathetic way. Individual variation in agonistic behavior can be considered as an example of more general variation in coping with environmental challenges, where highly aggressive individuals adopt a proactive coping style and submissive individuals adopt a more passive or reactive style (Koolhaas et al. 2007). Therefore, most physiological research relevant to avian personality involves stress physiology and coping (see chapter 12). In mammals, it has been suggested that individual differences in stress responses reflect variation in personality or coping styles (Korte et al. 2005). Passive copers are expected to have higher hypothalamic-pituitary-adrenal (HPA) responses to stressors, a lower sympathetic adrenomedullary reactivity, a higher humoral immunity, but also a

higher vulnerability to stress-induced illnesses compared with active copers (Ellis et al. 2006).

In birds, fast exploration, high risk-taking, and high responsiveness to a novel object appear to be associated with high corticosterone levels during the test (Martins et al. 2007; Richard et al. 2008). Birds also show individual consistency in the secretion of stress hormones. Kralj-Fisher and coworkers (2007) have shown in greylag geese that corticosterone levels measured in fecal samples collected after repeated handling episodes were consistent within individuals. This repeatability was especially pronounced when individuals were feeding in low competition areas; in high competition areas individuals were less consistent. Whether these individual differences in stress responses reflect genetic personality differences remains unclear. Yet, some support for this possibility has been found in other avian species where selection experiments have shown that the stress response has an additive genetic background (Brown and Nestor 1973; Edens and Siegel 1975; Satterlee and Johnson 1988). Moreover, great tit genetic lines selected for different personalities (Drent et al. 2003) differed in the level of stress hormone secretion after being in a social contest with a conspecific (Carere et al. 2003). Birds of the less aggressive and more cautious line (slow explorers) showed a trend for a higher response compared with birds of the more aggressive and bolder line (fast explorers), which could be taken to suggest a physiological basis of different coping strategies in birds (Carere et al. 2003). Alternatively, personality types might differ in the perception of the stressor, causing indirect differences in stress response to a standard stressor (Sapolsky 1994). Most likely both mechanisms play a role. However, the extent to which one or the other is more important in shaping variation in personality needs to be studied in more detail. Studies in great tits have shown that exploratory behavior is related to stress responses in both juvenile (Fucikova et al. 2009) and adult birds (Carere and Van Oers 2004). Adult birds that explore a novel environment more quickly (fast explorers) show a lower stress response after being handled, but nestlings that become fast explorers in adulthood show an increased response after being socially isolated as nestlings. This indicates that differences in personality traits measured just after independence might act as a predictor of individual variation in the stress response in adulthood, and as a result of variation in responsiveness as juveniles. A more direct way of measuring the link between variation in personality and stress is through stress hormones. In birds, corticosterone is the major glucocorticosteroid hormone secreted in response to stress, and many studies have shown that individual birds differ in their hormonal response to stress. This response varies not only with intrinsic factors such as sex and age, but

also in relation to behavioral types, and it is modified by factors such as body condition (Schwabl 1995; Silverin 1998; Cockrem and Silverin 2002; Cockrem 2007). These modifications may allow the adjustment of physiological and behavioral responses to adverse environmental circumstances and help explain individual differences in responses.

Glucocorticosteroid responses are seen as an evolutionary mechanism that maintains physiological homeostasis within an adaptive range. Only recently, however, have studies raised the question of how to explain the consistent individual differences in these responses that are unrelated to age or size (Cockrem 2007). It will be interesting to develop this and determine whether individual variation in short-term elevation of circulating glucocorticosteroids also explains fitness differences, and whether fitness consequences vary for different behavioral types. A first step in that direction was made by the work of Blas et al. (2007) on European white storks (*Ciconia ciconia*). This study showed that the magnitude of the adrenocortical response to a standardized perturbation during development is negatively correlated to survival and recruitment (Blas et al. 2007). The next step would be to investigate whether these fitness consequences differ for different behavioral types. Blas et al. (2007) discuss this possibility, by arguing that the success of proactive vs. reactive types varies as a function of population density and predictability of food resources. If this is associated with differences in glucocorticosteroid responses, it could provide an explanation for varying success of the behavioral types. Direct measurements and experimental changes, however, are needed to test this hypothesis. More on this subject can be found in chapter 12, on neuroendocrine and autonomic correlates of personalities.

Developmental aspects of personality

PLASTICITY

Although it has been shown that the genetic and physiological structure of personality is relatively rigid (Koolhaas et al. 1999; Van Oers et al. 2005a), personality nevertheless has substantial phenotypic plasticity and can be affected by environmental factors, specifically when they act during early development (Carere et al. 2005b; Arnold et al. 2007; Krause et al. 2009; Stamps and Groothuis 2010a; 2010b; Naguib et al. 2011). Such environmental factors include changes in the context in which a trait is expressed, for example, and the social factors that will change the adaptive value of a certain behavioral response (e.g., Schuett and Dall 2009). More subtle factors include maternal effects acting during embryonic development, such as the

amount of hormones transferred to the egg by the female (Schwabl 1993; Gil 2008; chapter 11), circulating hormones that influence habituation and sensitization to stressful events, and learning how to cope with certain stressors (Kant et al. 1985; Stam et al. 2000). Avian personalities are therefore open to change, though within certain boundaries, and traits such as shyness or boldness are therefore highly consistent within an individual. Individuals that are classified as being one or the other personality type, however, may still fluctuate in their behavior (Carere et al. 2005a), and repeatability of behavioral traits is typically moderate (Bell et al. 2009). Phenotypic correlations between personality traits may be strong in some environments but weak in others. For example, in great tits, both males and females of genetic lines selected for fast exploratory behavior return more quickly to the feeding table after a startle (risk-taking behavior). Lines selected for risk-taking behavior also differ in their exploratory tendency, such that a positive genetic correlation of 0.84 exists between the two traits (Van Oers et al. 2004a). In a follow-up study investigating the context generality of this correlation, fast- or slow-exploring great tits were tested for their risk-taking behavior in a nonsocial context followed by a social context (Van Oers et al. 2005b). Van Oers and coworkers found that the relation between exploratory behavior and risk-taking behavior depended on the social context. Females in general returned later in the social test, while the reaction of males to the presence of a companion was dependent on their behavioral type. Slow males came back sooner with faster companions and fast males did not react to the companion (Van Oers et al. 2005b). Similar results were found in a study on zebra finches (Schuett and Dall 2009): males and females differed in how consistently they behaved across social and nonsocial contexts. Schuett and Dall (2009) also tested whether males and females differed in their influence as companions, and found that individuals of both sexes influenced each other's exploratory behavior in a similar way within the social context: the more exploratory the companion, the more exploratory the focal individual. In great tits, birds of different personality type differ in their foraging strategy (Marchetti and Drent 2000). Moreover, the presence and strategy of a conspecific can affect the foraging strategies of individuals differently, depending on their personality. As a result, birds of different exploration types differ in their tendency to copy a tutor's foraging decision (Marchetti and Drent 2000; see below).

MATERNAL HORMONES

Since birds lay eggs, embryos are separated from the mother before they start to develop. Females are, however, able to influence embryonic devel-

opment by transferring nutrients and hormones to the yolk and albumen of their eggs (Gil 2008). Although it is not completely clear how females can actively vary the amounts of nutrients and hormones, these substances can exert short- and long-term effects on the offspring (Schwabl 1993; Eising et al. 2001; Groothuis et al. 2005; Eising et al. 2006; chapter 11). It is possible that maternal hormones in the egg may influence personality variation by modulating genetic differences or physiologically programming the offspring in certain ways. These maternal effects, however, may have a genetic basis, as individual differences in the deposition of maternal hormones in eggs have been shown to be, in part, genetically determined. Genetic variation in yolk hormones has been found in lines of domesticated species (Daisley et al. 2005; Gil and Faure 2007). In lines selected for fast and slow exploratory behavior in great tits, Groothuis et al. (2008) found that females of the slow line deposited lower amounts of testosterone in the yolk of their eggs compared with females from the fast line. This was especially true for the eggs laid early in the laying sequence (see chapter 11). This could indicate that females of different personality types have different strategies in rearing offspring. In this view, fast females would aim at rearing all offspring, whereas slow females invest less in those offspring that have lower chance of surviving (Tobler and Sandell 2007). Not only can maternal hormones influence behavioral differences, they can also affect the persistence of certain behaviors. In an experiment, the behavior of birds that came from testosterone-injected (T-treated) and control eggs were compared for their behavior toward a novel food source (Tobler and Sandell 2007). Birds from T-treated eggs did not differ in their latencies to approach and eat novel food during their first encounter. However, testosterone treatment affected subsequent encounters with the novel food source. Owing to habituation, latencies decreased in both groups over a period of 5 days, but considerably more so in T-offspring (Tobler and Sandell 2007). Whether this is different for offspring hatched from eggs at the beginning or end of the laying sequence is still unknown.

EARLY DEVELOPMENT

Environmental factors acting during ontogeny have been shown to significantly affect a whole range of morphological (Tinbergen and Boerlijst 1990), physiological (Kitaysky et al. 2001; Naguib et al. 2004; Verhulst et al. 2006), behavioral (DeKogel and Prijs 1996; Nowicki et al. 1998; Naguib and Nemitz 2007; Krause et al. 2009), and life history traits (DeKogel 1997; Naguib et al. 2006) and therefore may also play a role in personality development. It is

well established that conditions experienced during early development are important in shaping the behavior of an animal against the background of the reaction norm (Mason 1979; Metcalfe and Monaghan 2001). Such factors can involve a wide range of stressors, such as low-quality food (Krause et al. 2009), brood size (Neuenschwander et al. 2003), and parasites (Tschirren and Richner 2006). Yet, relatively little is known about how conditions experienced during early development affect personality (Stamps and Groothuis 2010a; 2010b). One trait, used as a proxy for personality, boldness in response to novel objects, has been studied by Fox and Millam (2004), who investigated the effects of rearing condition on the reaction to novel objects in orange-winged Amazon parrots (*Amazona amazonica*). Hand-reared, parent-reared, and parent-reared/human-handled birds, which were handled five times a week for 20 minutes, were tested for their latency to feed in the presence of five different novel objects between 4.5 and 6 months after hatching. At an age of 12 months the response to a novel object in their home cage was measured. They found that handling birds did not influence the reaction to novelty, but whether an individual was reared by their own parents or hand-reared did. They concluded that the development of neophobia in orange-winged Amazon parrots may be related to novelty the chicks experience during early life (Fox and Millam 2004). Moreover, we recently showed in great tits that personality is affected by the sex ratio in the nest. Birds that grew up in female-biased nests became faster explorers than birds that grew up in male-biased nests. These findings that early social interactions shape personality in animals but future research is required to unravel the precise behavioral mechanism leading to this effect.

Another important influence on behavior during early development is the quantity, quality, or composition of food (e.g., see Birkhead et al. 1999). Variation in food characteristics can be caused by parental choice, sibling competition, or habitat quality but also by differences in the parents' ability to search and find suitable food. Experiments on birds investigating the influence of food during ontogeny can be conducted relatively easily in altricial species compared with precocial species. Carere et al. (2005b), for example, manipulated the early rearing condition in two great tit lines selected for fast and slow exploratory behavior by a food rationing protocol. Birds from both fast and slow exploration lines, but also control chicks, decreased their growth rate and increased their begging behavior compared with unmanipulated chicks within the same nests. This resulted in slow chicks becoming much faster than their parents, but without any changes in aggressiveness. In contrast, fast chicks had exploration scores similar to their

parents but an increased level of aggressiveness. As a consequence, there was no apparent line difference in exploration behavior at independence. The effect, however, turned out to be partly temporary: although the offspring of the slow line were still relatively fast six months later, birds of the fast line became even faster, restoring the line differences again. A side effect of the treatment on the experimental birds was that control chicks also begged more. To rule out these effects of sibling competition, the authors conducted a second experiment with experimental and control siblings in separate nests. Here, only the food-rationed chicks became faster in exploration, indicating that the shift in the controls in the within-nests design was indeed due to enhanced sibling competition. Krause et al. (2009) also showed that the feeding conditions experienced during early development affect exploration behavior in zebra finches. They showed that female zebra finches raised as nestlings under low-quality food conditions were more explorative in a novel environment than females that had been raised under high-quality food conditions. The same individuals were also more sensitive to short periods of food deprivation by losing more weight than those raised under high-quality food, underlining the link between behavioral differences in personality with physiological differences in responses to a stressor.

Aside from the amount of food, its quality may also be very important for the development of behavioral consistency. Essential amino-acids are known to be limiting factors during development (Murphy and Pearcy 1993) and are also relatively scarce in the bulk food of many passerines (Izhaki 1998; Ramsay and Houston 2003). Several tit species therefore supply their nestlings with a high proportion of spiders early during development (Ramsay and Houston 2003). Spiders contain a relatively high amount of taurine. To investigate whether taurine has a developmental effect on personality variation in blue tits (*Cyanistes caeruleus*), Arnold and coworkers (2007) conducted a feeding experiment in which they supplemented taurine to blue tit nestlings during the period of maximum growth. Juveniles that had received additional taurine as nestlings were significantly bolder when investigating novel objects, and also were more successful at a spatial learning task than controls. They concluded that prey selection is a mechanism by which parents can alter the behavioral phenotype of their offspring. Further experiments in natural settings should be conducted to see whether parents indeed use this mechanism to prepare their offspring for the future. Taken together, these findings suggest that personality traits may well be shaped by the conditions experienced during early development, a topic that is worth exploring more in the future.

A question arises as to the extent to which individuals differing in personality also differ in learning abilities or learning strategies. Individuals that differ in environmental exploration are likely to also differ in the way they acquire, process, recall, and use environmental information (Guillette et al. 2010; Cole and Quinn 2012; Amy et al. 2012; Titulaer et al. 2012). Animals have to learn to find food, possibly from successful conspecifics, and to remember food locations. Marchetti and Drent (2000) found that, in great tits, slow and fast explorers differ in their routines to revisit known feeding sites and in using information they obtain by observing conspecifics when foraging. Birds were first trained to find food at a specified feeder, which during the experiment was then left without food. When tested alone, fast explorers kept on visiting the now unrewarded feeder they had previously learned to visit. Slow explorers, in contrast, were quicker in finding new food locations and did not revisit the previously rewarded feeder as often. In other words, fast birds were less flexible in finding food locations and expressed more behavioral routines than did slow explorers. Interestingly, when subjects had the opportunity to observe a tutor bird to explore a specific food source (colored feeder), then slow and fast explorers behaved in opposite ways. Fast explorers were faster in copying the tutor's behavior (and in feeding from the feeder indicated by the tutor) whereas slow explorers did not learn to explore the rewarded feeder from the tutor. In other words, slow explorers were better in finding new food sources on their own, whereas fast explorers did better in exploring new food sources when given the opportunity to learn from others. Such differences in foraging strategies may explain in part why slow and fast explorers perform differently under natural conditions depending on food availability. Alternatively, this could be mediated by differential susceptibility to stress, where differential stress levels may alter the way information is processed. In a recent experiment, Titulaer et al. (2012) further showed that personality affected learning only in difficult tasks, but in a sex-specific way. Such effects presumably are related to selection acting differently on the sexes with respect to behavioral strategies in terms of space use, foraging, and social behavior. Such relations between cognition and personality have also been addressed in a number of other recent studies (Guillette et al. 2010; Cole and Quinn 2012; Amy et al. 2012).

Animal husbandry and welfare

Obviously, research on personality is not restricted to natural contexts. Personality has been a key issue in studies on animal welfare and husbandry (We-

melsfelder et al. 2000; Bolhuis et al. 2005; Würbel 2009; see chapter 14) and is of emerging relevance in the development of nature conservation programs that deal, for instance, with habitat defragmentation and reintroduction of animals to new areas (see chapter 13). Although researchers with more applied interests have often studied behavioral consistency, their concepts and terminology are often different from those used by behavioral ecologists. Studies investigating personality in quail and chicken, for example, often use the terms fear and fearfulness (Boissy 1995), where fearfulness is measured as the emergence into a larger compartment, the reaction to novel food or objects, or the response to a predator (Miller et al. 2005; 2006).

One of the central problems in applied bird ethology is feather pecking, a common behavior in laying hens, with substantial economic and welfare implications. Feather pecking has a genetic component but is also affected by various social and housing factors (Van Krimpen et al. 2005; Van de Weerd and Elson 2006; Rodenburg et al. 2008). Research has shown that individuals are consistent in this behavior, reflecting a potential personality trait. Understanding the causes of feather pecking is thus of high applied significance as it will contribute to develop rearing strategies and selection processes that will reduce this problem. With the new regulations of housing laying hens in larger groups, feather pecking needs to be monitored carefully, and identifying behavioral and genetic correlates of this behavior will help to find optimal solutions that balance welfare and economic interests.

Personality differences also might be of great importance in reintroduction of individuals reared in captivity into wild populations or in transferring wild individuals to new locations. Before reintroduction, individuals of many species, for example, have to learn to avoid predators. Training individuals in these capacities is therefore a crucial factor for increasing the probability of postrelease survival (Box 1991). The ability to learn to avoid certain dangers might, however, be dependent on the personality type of an individual. That this can be the case is nicely shown in a study on greater rheas (*Rhea americana*) (De Azevedo and Young 2006). Captive individuals were tested for their response to several novel objects, before and after being trained to avoid predators. Birds were less bold after training compared with before training, and the responses to the novel object before the training sessions were a good predictor of how the bird would react during training. Bolder birds behaved more calmly than shy birds. Similar results were obtained studying the natural antipredator behavior of chaffinches (*Fringilla coelebs*): calm individuals were better able to assess the risk of a hawk flying over compared with very active individuals. They showed greater behavioral plasticity in high-risk versus low-risk situations, while hyperactive

individuals in general showed more fleeing behavior (Quinn and Cresswell 2005), possibly because of differences in the risk perception between the activity types (Butlers et al. 2006). As dispersal, territorial, and foraging strategies can be linked to personality (Dingemanse et al. 2003; Amy et al. 2010; see below; chapter 7), including information about personality in decisions made about when to release individuals may affect the success of a reintroduction project (Bremner-Harrison et al. 2004; Merton 2006).

Field studies and fitness correlates

The growing interest in research on animal personality in part has been driven by the ecological and evolutionary significance of personality—that is, that personality matters in the dynamics of wild populations. Even though the origin and nature of individual variation in itself is interesting, the ecological and evolutionary framework adds another reason for interest, as it shows that personality affects selection while at the same time being under selection itself. Ecologically relevant personality correlates include nest defense behavior (Hollander et al. 2008), song (Garamszegi et al. 2008; Amy et al. 2010; Naguib et al. 2010), social dominance (Dingemanse and De Goede 2004), feeding behavior (Costantini et al. 2005), as well as dispersal and mating behavior (Dingemanse et al. 2003; Van Oers et al. 2008).

Dingemanse et al. (2003) showed, for instance, that natal dispersal distance (i.e., the distance between place of origin and the place of breeding) was linked to personality in great tits. In their study population of great tits with known personalities (assessed under standard laboratory conditions using a novel environment test), they found that the personality of the father mattered. Offspring from males that were fast explorers in the novel environment test dispersed farther from their original nest box than did slow explorers. Furthermore, immigrants into the population had higher exploration scores than resident birds. Such effects presumably resulted from genetic differences and environmental effects acting during development. Indeed, as personality has a considerable heritable component (Van Oers et al. 2005a), personality-related differences in dispersal strategies may affect the genetic variance of a population, depending on the extent to which residents and immigrants succeed in breeding.

Dingemanse et al. (2004) found in great tits that personalities had differential fitness effects, that these effects were different for males and females, and that they were reversed in different years depending on food availability. Studying local survival across three years, they found that slow males did better in the two years with limited food availability in winter than they

did in the year with high winter food availability. Females over the same period were affected in the opposite way. These results suggest that fast males, being more aggressive and dominant over females (Krebs and Perrins 1978; Drent 1987; Verbeek et al. 1996), do better in poor years than females, as the limiting resource is the food over which they compete. In good years, the higher winter survival results in higher competition among males for territories so that slower and less aggressive males do relatively less well than females. Indeed, Amy et al (2010) showed that territorial behavior is affected by personality, with faster males being more aggressive at the site of intrusions while slower males follow a different strategy by singing more from the distance and exploring more the boundaries of their territory. Dingemanse et al. (2004) also found that in the poor year, pairs of individuals with similar personality produced more local recruits than pairs in which the male and female had different personalities; these effects, however, may have been caused by differential survival or differential dispersal (Dingemanse et al. 2003). Along this line, Both et al. (2005) reported that pairs with similar personality have a higher reproductive success, measured as offspring condition. These findings may explain the production of more recruits by pairs with similar extreme personality, as shown by a different study for the same population (Dingemanse et al. 2004), as fledgling condition has been shown to predict survival (Tinbergen and Boerlijst 1990). While the nature of one's own and the partner's personality appears to have fitness consequences measured as offspring condition, recruits, and survival, personality also can affect more immediate reproductive decisions. Monogamous animals are known to produce extra-pair offspring in addition to the offspring produced with their social partner (Petrie and Kempenaers 1998; Griffith et al. 2002). Decisions about extra-pair matings most commonly have been linked to the expression of sexually selected traits of the social mate and the extra-pair mate (Kempenaers et al. 1992; Hasselquist et al. 1996). Apparently, decisions about extra-pair matings also depend on within-pair personality differences in great tits, as pairs with more extreme similar personality (slow-slow and fast-fast pairs) are more likely to raise extra-pair offspring (Van Oers et al. 2008). In other words, females are more likely to engage in extra-pair copulations when their social mate is similar in personality compared with her own personality. Such disassortative decision making in reproduction may ensure high offspring variability and also contributes to maintaining high variation in personality within a population, in a similar way as has been argued for links between mate preferences for partners with different immune characteristics (Wedekind et al. 1995; Milinski 2006).

Conclusions

Birds are excellent model organisms for studying the causes and consequences of personality in descriptive and experimental ways in the field and in the laboratory. Integrating information obtained from studies under controlled experimental lab conditions with experimental studies in the field and analyses of fitness-relevant traits under natural conditions has generated multifaceted insights into principles of personality. So far, much of the field research addressing evolutionary and ecological questions has been conducted on great tits, which remain the species in which the study of causation and consequences of personality under natural conditions has been best integrated. With research on personality now gradually expanding to other avian species, the opportunity to obtain comparative data sets allowing us to link basic species differences in life history to our current understanding on personality is becoming available.

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