
ANIMAL PERSONALITIES
Behavior, Physiology, and
Evolution

EDITED BY
CLAUDIO CARERE AND DARIO MAESTRIPIERI

THE UNIVERSITY OF CHICAGO PRESS

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Introduction

Animal Personalities: Who Cares and Why?

CLAUDIO CARERE, DARIO MAESTRIPIERI

Everyone who has experienced close, long-term relationships with animals, such as pet owners or farmers, probably believes that domesticated animals show personality variation, the way people do. In fact, there are studies suggesting that pets' personalities appear to match those of their owners (Gosling 2001). It is possible that pet owners project their own personalities onto their pets, or expect that their pets will complement some aspects of their own personalities (Gosling et al. 2003). In this view, animal personalities would be a product of pet owners' imagination and social-emotional needs. It turns out, however, that personalities are not observed or suspected only in domesticated animals. They have been scientifically demonstrated in nondomesticated animals as well—from invertebrates to monkeys and apes—and in a variety of different environments. In fact, the study of animal personality is one of the fastest growing areas of research in behavioral biology and behavioral ecology.

In animal research, the concept of personality has been used to refer to the existence of behavioral and physiological differences among individuals of the same species, which are stable over time and across different contexts or situations. The behavioral and physiological traits that represent personality are often intercorrelated with one another (i.e., individuals have different clusters of these traits). In animal research, personalities have also been referred to as temperament, behavioral syndromes, coping styles, or simply predispositions (e.g., Wilson et al. 1994; Gosling and John 1999; Gosling 2001; Sih et al. 2004; Groothuis and Carere 2005; Nettle and Penke 2010; Stamps and Groothuis 2010).

A large number of animal studies, particularly in the last decade, have shown that individuals of the same species, often independent from sex or age, differ from each other in their behavior and underlying physiology, even under standardized laboratory conditions. Most of this variation is nonrandom and is consistent across contexts and over time. These individual differences often become conspicuous and easily measurable when

individuals have to cope with challenges in their environment, both social and nonsocial (Broom 2001). In the past, such differences were rarely viewed as an expression of biologically meaningful variation; instead, they were often interpreted either as the consequence of inaccurate measurements or as nonadaptive variation around an adaptive mean (Wilson 1998). In contrast, in humans such variation is interpreted as reflecting consistent individual variation in personality or temperament, the science of human personality being already more than one century old (Galton 1883). Personality characteristics in humans have a significant heritable component and a proximate basis in genetic polymorphisms and associated neurobiology; they have also been shown to predict important life outcomes, such as physical and mental health, as well as social and reproductive functioning (Nettle 2005; Nettle and Penke 2010).

Behavioral ecologists have long recognized the existence, within the same species, of individuals with different reproductive and foraging strategies, which have been referred to as “residents and satellites” or “producers and scroungers” (Barnard and Sibly 1981; Clark and Ehlinger 1987). In the past decade, a growing number of studies have shown that consistent individual differences in one trait covary with other behavioral and physiological traits, and that suites of traits may evolve and be maintained by natural selection (e.g., Dingemanse et al. 2004; Carere and Eens 2005; Wolf et al. 2007; Dingemanse and Wolfé 2010; Wolf and Weissing 2010) or even sexual selection (Schuett et al. 2010). Thus, the study of animal personality has become firmly grounded in evolutionary biology and life-history theory.

A major challenge for animal researchers has been to understand the origin of interindividual variation in personalities and the mechanisms responsible for the maintenance of this variation and its transmission across generations. The study of animal personalities is now at the forefront of contemporary behavioral biology particularly because of its integrative and holistic approach (Sih et al. 2004) and also, admittedly, because of its strong appeal to public opinion and mass media (e.g., Dall et al. 2004; Pennisi 2005). The recent surge of interest in phenotypic plasticity and reaction norms among evolutionary biologists can be viewed as arising from the same need for integrative approaches to the study of phenotypic variation (Schlichting and Pigliucci 1998; Bateson 2003; Stamps 2003; Dingemanse et al. 2010).

The study of animal personalities is important for several reasons: (i) it is conducted with an interdisciplinary approach that integrates proximate mechanisms with ontogenetic, functional, and phylogenetic analyses; (ii) it has important implications for evolutionary theory because different but correlated behaviors do not evolve in isolation, but often as a package and

this can generate tradeoffs and canalizing effects, which set boundaries to unlimited plasticity (e.g., Sih et al. 2004; Wolf et al. 2007); (iii) personality has to be taken into account in both field and laboratory animal behavioral studies because different personality types may react differently to similar environments or different experimental treatments (e.g., Coppens et al. 2010; Luttbegg and Sih 2010); (iv) individuals may show differential vulnerability to stress and artificial housing conditions, with important implications for animal welfare (e.g., Huntingford and Adams 2005); (v) a better knowledge of the mechanisms underlying animal personalities and of the evolutionary causes and consequences of personalities may be extrapolated to humans and help to provide a better understanding of the nature and evolution of human personalities (e.g., Gosling 2001; Nettle and Penke 2010); (vi) the realization by the general public and policymakers that animals have personalities may help create greater empathy for wild animals and enhance conservation efforts.

For instance, studies in birds have shown not only that individual differences in behavior are heritable, but also that they are systematically related to fitness, with different optima occurring under different environmental conditions (Dingemanse and Réale 2005; Réale et al. 2007). For humans, such a demonstration is necessarily more indirect, both for methodological reasons and because of the profound differences between the contemporary environment and the presumed environment in which we evolved (Nettle 2005).

Research on animal personalities poses several theoretical and empirical challenges. Theoretically, it requires an understanding of the evolutionary mechanisms that may account for the origin and maintenance of clusters of interrelated phenotypic traits. Empirically, this research sometimes requires descriptive longitudinal studies, including studies of relationships between different behaviors, and their consistency across situations; studies on genetic and physiological mechanisms underlying the clustering of behavioral traits, such as pleiotropy, gene linkage, or common neuroendocrine substrates; ontogenetic studies on plasticity and environmental malleability; and field studies on survival and reproduction to understand how different personality profiles are maintained and under what circumstances they can be selected for.

In the past decade, growing interest in the study of animal personalities has resulted in the publication of many theoretical and empirical articles, special issues of journals entirely devoted to this topic (e.g., Carere and Eens 2005; Réale et al. 2010), as well as the publication of literature reviews in major scientific journals such as *Nature*, *Science*, *Proceedings of the National*

Academy of Sciences U S A, Current Biology, Biological Reviews, Quarterly Review of Biology, Philosophical Transactions of the Royal Society of London, and Trends in Ecology and Evolution (e.g., Dall et al. 2004; Sih et al. 2004; Pennisi 2005; Bell 2007; Blas et al. 2007; Wolf et al. 2007; Bergmüller and Taborsky 2010; Dingemanse et al. 2010; Réale et al. 2010; Schuett et al. 2010). Finally, the most recent editions of all major animal behavior textbooks dedicate entire chapters to the topic of animal personalities (e.g., Alcock 2009; Dugatkin 2009).

The goal of this edited volume is to synthesize and integrate recent research on animal personalities. We aim to provide a comprehensive overview of research on animal personalities in a wide range of taxa, including humans. We also illustrate the integrative and multidisciplinary nature of animal personality research. Evolutionary biology is clearly the discipline that provides a general framework for the study of animal personalities. Important contributions to personality research, however, are also made by ethology, ecology, genetics, endocrinology, neuroscience, and psychology. In assembling the chapters for this edited volume, we made an effort to address both the *how* and *why* questions about personality, and also to include descriptive and experimental studies from different animal taxa. The chapters in this volume illustrate how personalities vary along multiple dimensions; how they are influenced during ontogeny and in adulthood by genetic, physiological, and environmental factors; what is their functional significance, in terms of how they contribute to reproduction and survival; and what is their relevance for animal conservation in the wild and welfare in captivity.

Structure and content of the volume

The book is organized into four sections. The first section (Personalities across Animal Taxa) includes 5 chapters that illustrate the occurrence and the behavioral expression of personalities in different taxa, from invertebrates to humans. In the first chapter of this section, Mather and Logue review a number of descriptive, physiological, genetic-linkage, ontogenetic, and ecological studies to determine the degree to which invertebrates, often viewed as animals of limited behavioral repertoires, exhibit personalities. Bell, Foster, and Wund examine personalities in stickleback fishes. By comparing groups of sticklebacks that either show or do not show consistent individual differences in behavior across contexts, stickleback researchers have an opportunity to understand and experimentally investigate the selective factors that can favor the evolution of personality in fishes. Van Oers

and Naguib provide an overview of research on personality in birds, including studies that have addressed behavioral variation, its underlying genetic bases, and its fitness consequences in natural avian populations. Weiss and Adams examine personality studies in nonhuman primates and integrate the findings obtained with different approaches, such as ecology-based and life-history-based approaches, human personality assessment procedures, and multivariate and behavior genetic approaches. The chapter by Gosling and Mehta concludes this section by discussing the value of animal personality research for understanding human personality. In doing so, these authors provide a broad review of animal personality studies across different taxa and discuss the parallels between their findings and those of human personality studies.

The second section (Genetics, Ecology, and Evolution of Animal Personalities) includes both theoretical and empirical chapters on animal personalities, which address the relation between genetic variation, phenotypic plasticity, ecological factors, and the selective mechanisms favoring the evolution and maintenance of personalities in natural animal populations. In the first chapter of this section, Van Oers and Sinn address the quantitative and molecular genetics of animal personality, discussing the role of direct genetic effects, maternal effects, and gene-environment interactions in the evolution and expression of animal personality differences and their transmission across generations. In the following chapter, Dingemanse and Réale address the question of whether animal personality differences represent different social and reproductive strategies, and the role of different selective processes in their evolution. In addition, they examine the reaction norm and character state view of animal personality and discuss how selection acting on personality could be studied from each perspective. In his chapter, Sih focuses on evolutionary studies of animal personality in a socio-ecological context. Specifically, he examines how variation in animal personalities relates to predation, mating, and cooperation as well as how variation in social conditions (e.g., availability of different social partners) affects plasticity in behavioral aspects of personality. The last chapter in this section is by Wolf, Van Doorn, Leimar, and Weissing, who provide a broad overview of the selective pressures favoring the evolution of animal personalities and a discussion of how these pressures affect the structure (e.g., the type of phenotypic traits that cluster together) and the developmental stability of individual differences in personalities.

The third section (Development of Personalities and Their Underlying Mechanisms) addresses the ontogenetic trajectories of different personality types, how they arise as a result of early parental influences, and how

they are controlled and regulated by different neuroendocrine mechanisms. The chapters in this section integrate empirical research on behavioral and physiological aspects of animal personality conducted both in the field and in the laboratory. Curley and Branchi review studies of laboratory rodents illustrating the mechanisms through which stable individual differences in neurobiology and behavior emerge during development. In particular, they address the role of gene-environment interactions and epigenetic mechanisms in personality development of laboratory rodents. Maestriperi and Groothuis explore maternal environmental effects on offspring personality development and their underlying mechanisms in both oviparous vertebrates (fish, reptiles, and birds) and placental mammals (rodents and primates). Specifically, they discuss how maternal behavior, maternal stress, and prenatal exposure to varying amounts of maternal steroid hormones, both androgens and glucocorticoids, can result in stable individual differences in offspring physiology and behavior later in life. Finally, Caramaschi, Carere, Sgoifo, and Koolhaas review research on the relation between physiological and behavioral traits commonly considered in animal personality assessments, with particular regard to behavioral reactivity to stress and the activity of the hypothalamic-pituitary-adrenal axis, the hypothalamic-pituitary-gonadal axis, and the autonomic nervous system. They also discuss evidence linking the neurotransmitters serotonin and dopamine, as well as cortical brain structures such as the hippocampus, to variation in animal personality.

The fourth section (Implications of Personality Research for Conservation Biology, Animal Welfare, and Human Health) examines applied aspects of animal personality research. In their chapter, Smith and Blumstein emphasize that behavioral diversity, including personality variation, is an important component of biological diversity and therefore plays a significant role in the long-term persistence of animal populations. They then address how the study and management of animal personalities may play a key role in conservation biology, by arguing that anthropogenic activities can reduce behavioral diversity, and that personality traits can be useful in identifying potentially invasive species. In their chapter, Huntingford, Mesquita, and Kadri emphasize that although most research on fish personality is conducted on species such as sticklebacks and zebrafish, personality profiles have been identified also in many species of cultured fish, particularly salmonids. Since different personalities persist within populations because they allow individuals to grow and survive well in different environmental conditions, the study of behavioral and physiological personality traits in farmed fish can contribute to the scientific understanding of animal person-

ality as well as to the maximization of production and welfare. In the last chapter, Cavigelli, Michael, and Ragan address the importance of research with rodent models of human personality for understanding the relationship between genes and environment, and behavior and physiology, in both health and disease processes. The authors review studies conducted with different strains of laboratory rodents to determine whether some of these strains have behavioral and physiological traits that would permit certain personality types to be resilient or susceptible to specific disease processes. They also compare differential behavioral profiles associated with health trajectories in laboratory rodents to potentially analogous personality traits and associated health and disease trajectories in humans.

It should be obvious from the breadth of topics included in this volume that knowledge of the findings of animal personality research is potentially interesting to many different people, such as scientists (e.g., evolutionary biologists, comparative psychologists, and physiologists), people involved in the conservation of wild animal populations, people involved in the production and welfare of farm animals, and people who own pets or who are simply fascinated by biodiversity, wildlife, and animal behavior.

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I

PERSONALITIES ACROSS ANIMAL TAXA

The Bold and the Spineless

Invertebrate Personalities

JENNIFER A. MATHER AND DAVID M. LOGUE

Introduction

Reviewing the study of personalities of invertebrates offers a series of challenges. First, there is a huge number of invertebrate species, sometimes estimated to represent 98% of the animal species on the planet (Pechenik 2000). Second, invertebrates exhibit a tremendous array of life history strategies, developmental trajectories, modes of reproduction, and physiological bases of behavior, many of which are poorly known. A further challenge arises from the diversity of perspectives and research backgrounds that characterizes invertebrate personality researchers.

One of the goals of this review is to determine the degree to which invertebrates, often viewed as animals of limited behavioral repertoires, exhibit personality as defined in the introduction and throughout this volume. We begin with a survey of reports that relate to personality in invertebrates. We categorize these as (1) descriptive reports, (2) physiological/genetic linkages (see Van Oers et al. 2005), (3) ontogenetic studies (*sensu* West-Eberhard 2003), and (4) ecological/selection studies (Groothuis and Carere 2005; Smith and Blumstein 2008). There will be some bias toward studies of poorly known taxa, even if their evidence is fragmentary. We then evaluate several particularly thorough and influential research programs in depth. In the final section, we provide recommendations for future research directions and attempt to summarize the current state of the field.

This review does not evaluate the division of labor (polyethism) in colonies of social insects, or the discrete morphologies (polyphenism) found in many invertebrates. Although we recognize that both of these phenomena may relate to personality (e.g., Bergmüller and Taborsky 2010; Bergmüller et al. 2010), we have chosen to focus on subtler forms of personality (i.e., those that form continuous rather than discrete distributions). We refer

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