

Pieter van den Berg and Franz J. Weissing

Personality psychology and evolutionary game theory may not seem to be closely connected. Evolutionary game theory is a set of tools for helping us understand the evolution of social behavior; personality psychologists are mostly interested in comprehensively describing consistent individual differences between people (and in predicting the ramifications of these differences for various life outcomes). Traditionally, evolutionary game theory has been used by biologists in their pursuit of understanding the evolutionary origins of animal behavior, but has received much less attention from psychologists trying to understand human behavior. Conversely, the study of personality and individual differences has been a prime interest of psychologists, but has largely been neglected by biologists.

In recent years, however, this has changed and the study of individual differences has become a hot topic in various subdisciplines within biology. In particular, behavioral studies across the animal kingdom have revealed that the individuals in virtually all species differ systematically and consistently in their behavior (Gosling 2001; Sih et al. 2004a, b; Réale et al.

2007). This has produced a literature in which these differences are not only described but also interpreted from an evolutionary perspective. A number of hypotheses about the evolutionary emergence of individual variation have been advanced. Recent years have also seen increased attention to evolutionary explanations of personality differences in psychology, but these literatures have remained segregated (although some cross-references have certainly been made (e.g., Nettle and Penke 2010)). In comparison to psychologists, biologists base their arguments more strongly on formal theory, and in particular on evolutionary game theory, when suggesting explanations for individual differences.

In this chapter, we show that evolutionary game theory is a suitable tool to study the adaptive significance of individual differences. To do this, we first give a brief overview of evolutionary game theory and the study of individual differences in both humans and animals. Next, we discuss a number of evolutionary arguments that provide an adaptive explanation for the existence of individual differences and the structure of personalities. Most of these explanations are based on models from evolutionary game theory. Then, we discuss the evolutionary implications of personality differences for the course and outcome of evolution. By means of examples, we demonstrate that evolutionary predictions (including those of evolutionary game theory) can be far off target when individual differences are neglected.

P. van den Berg (✉) · F. J. Weissing
Theoretical Biology Group, Groningen Institute for
Evolutionary Life Sciences, University of Groningen,
Nijenborgh 7, 9747 AG Groningen, The Netherlands
e-mail: pieter.van.den.berg@rug.nl

F. J. Weissing
e-mail: f.j.weissing@rug.nl

Evolutionary Game Theory

For many decades, economists have used game theory as their main tool for modeling and analyzing strategic interactions. Economic game theory (Rasmusen 2007) is generally normative; it is aimed at identifying optimal decisions, assuming that all involved parties act according to their own interests and in line with *Homo economicus* (i.e., fully rational and with unlimited computational ability). The central concept is that of Nash equilibrium: a combination of strategies where none of the players can obtain a better payoff by changing their behavior (Nash 1951).

Maynard Smith and Price (1973) realized that the insights from game theory could be applied to studying interactions between animals in evolutionary biology. For this, the concept of Nash equilibrium had to be adjusted. To apply it to animals, the definition of equilibrium could no longer be based on assumptions of rationality, but rather on fitness considerations. To achieve this, they introduced the concept of evolutionarily stable strategy (ESS). If all individuals in a population adopt an ESS, natural selection does not favor the invasion of any mutant strategy that is initially rare.

Evolutionary game theory is based on the insight that selection in a social context is “frequency dependent” (Heino et al. 1998): The Darwinian fitness of a strategy does depend not only on an individual’s own behavior but also on the behavior of others in the population. This has important implications. For example, Maynard Smith and Price presented an evolutionary game theoretical model of animal conflict nowadays called the Hawk–Dove game (Maynard Smith 1982; Maynard Smith and Price 1973, see Fig. 34.1 for the payoff structure of this game). Pairs of individuals compete for a resource, and each individual has to decide whether to do this in a relatively peaceful ritualized manner (“Dove”) or to employ dangerous weapons (“Hawk”)¹. When a Dove meets a Hawk, it is overpowered by the Hawk and gives away the resource

without fight. The mean fitness of a population is maximized in the absence of Hawks, since Hawk–Hawk interactions may lead to injury and, hence, a reduction in fitness. Yet, a population of Doves is not evolutionarily stable, since in a population of Doves a single Hawk has a higher fitness than the Dove individuals. As long as Hawks are rare, they will typically meet Doves and therefore easily get access to the resource. Hence, the Hawk strategy will have a selective advantage and will spread when rare. When the Hawk strategy becomes more frequent, however, the risk of injury by getting involved in a Hawk–Hawk interaction increases. If the fitness costs of such injuries are high, the Dove strategy will have a selective advantage in a population of Hawks and, hence, will also spread when rare. Consequently, neither a pure Dove population nor a pure Hawk population is evolutionarily stable. The only evolutionarily stable population is a mixture of Hawks and Doves, or a population in which each individual plays Hawk and Dove with some intermediate probability. This simple example illustrates two points. First, when fitness is frequency dependent, evolution will typically not lead to a state where the mean fitness of the population is maximized; in the majority of all social interactions, such fitness maxima are not evolutionarily stable. Second, frequency-dependent selection will often lead to a polymorphic population where different individuals employ different strategies. Since the 1980s, the Hawk–Dove game has been studied widely—sometimes “disguised” as other games that have the same basic payoff structure, such as the Snowdrift game (which is framed as a context of cooperation rather than conflict; see Fig. 34.1).

Evolutionary game theory has been used to study many types of interactions (Broom and Rychtár 2013; Maynard Smith 1982), but the game that has received by far the most scientific attention is the Prisoner’s Dilemma (Axelrod and Hamilton 1981). This game exemplifies why cooperation may be difficult to achieve, even if mutual cooperation is more beneficial for all parties than mutual restraint from cooperation. In the Prisoner’s Dilemma, two players simultaneously decide on whether to “cooperate” or to “defect.” If a player cooperates, the other player receives a

¹ Notice that Hawk and Dove indicate strategies and not different species of animals; evolutionary game theory is typically concerned with interactions within one species.

benefit b , while the cooperator has to pay a cost c (where $b > c$). A defector does not create benefits and does not have to pay a cost (see Fig. 34.1). Since $b > c$, the payoff in case of mutual cooperation ($b - c$) is larger for both players than the payoff in case of mutual defection (zero). Yet, defection is a dominant strategy: Whatever the other player is doing, defection yields a higher payoff than cooperation (see Fig. 34.1). This outcome reflects the “Tragedy of the Commons” (Hardin 1968): At evolutionary equilibrium, everybody will defect, while mutual cooperation would be a more favorable outcome.

Matters change if the same two players interact with each other repeatedly (the Iterated Prisoner’s Dilemma (IPD) game). Now more sophisticated strategies can emerge that make the behavior

of an individual dependent on the history of the game and, in particular, on the cooperativeness of the other player. Human players often employ a simple strategy called tit-for-tat (TFT; Axelrod and Hamilton 1981). TFT always cooperates unless the other player has defected in the previous round; in that case, a TFT player defects in the next round. Hence, a population of TFT players will always cooperate, but since this cooperation is conditional on the behavior of the other player, a TFT player can less easily be exploited by a free-riding defector. Notice that superior features of a conditional strategy like TFT may not be immediately apparent to an outside observer, since a population of TFT players behaves in exactly the same way as a population of indiscriminate cooperators. This is another general insight from game theory: crucial aspects of a successful strategy may be hidden below the surface.

While TFT plays a prominent role in treatments of the IPD, this strategy is vulnerable, since the slightest mistake made by one of two

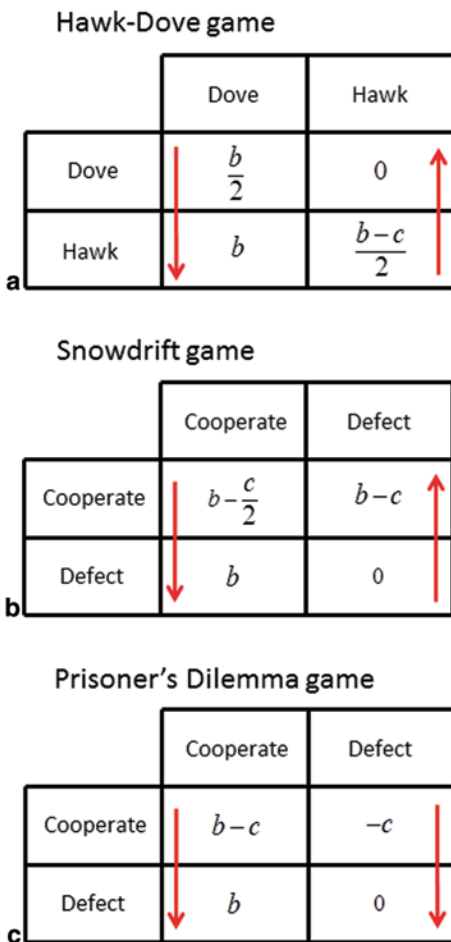


Fig. 34.1 Payoff structures of three prominent two-player games. Payoffs to the row player are shown; arrows indicate the best choice for the row player for both possible actions of the column player. **a** The Hawk-Dove game: two individuals are competing for a resource of value b . Hawks pursue the resource aggressively, while Doves try to resolve the conflict peacefully, and retreat from the conflict when competing with a Hawk. c denotes the cost of getting injured in a Hawk-Hawk fight. In this game, it is usually assumed that $c > b$, in which case it is most favorable to play Dove when the opponent plays Hawk, and vice versa. Hence, neither a population of Hawks nor a population of Doves is evolutionarily stable. The evolutionarily stable strategy (ESS) for this game corresponds to a mixed strategy where individuals play Hawk with a probability $p_H = b/c$. **b** The Snowdrift game: two individuals decide whether to perform a cooperative act that benefits both players (with benefit b , regardless of whether one or both individuals perform it), but comes at a cost of c . If both players cooperate, they share the cost. In this game, it is usually assumed that $b > c$. The ESS corresponds to a mixed strategy where individuals cooperate with probability $p_C = (2b - 2c)/(2b - c)$. **c** The Prisoner’s Dilemma game: two individuals decide whether to perform a cooperative act that provides a benefit b to the other player, and comes at a cost c to the cooperator. As in the Snowdrift game, it is usually assumed that $b > c$. Defect is always the best option, regardless of the behaviour of the other player. Therefore, the ESS is to cooperate with probability $p_C = 0$.

interacting TFT players results in a sequence of alternations between cooperation and defection. Other strategies, notably “generous tit-for-tat,” which only retaliate against defection with a certain probability, and “Pavlov,” which starts with cooperation and switches behavior when the other player defected in the previous round (the name “Pavlov” refers to the fact that the strategy continues behavior that is “rewarded” with good payoffs, but switches behavior after bad payoffs) have been found to be relatively robust outcomes of evolutionary simulations (Nowak and Sigmund 1992, 1993). However, even in this simple kind of interaction, the evolutionary dynamics can be complex. This reflects the fact that the IPD and virtually all games with a rich strategic structure have a multitude of Nash equilibrium strategies. In fact, for *any* outcome between 0 (mutual defection) and $b - c$ (mutual cooperation) a Nash equilibrium can be found that realizes it. This “folk theorem” of game theory (Gintis 2009) is still underappreciated in the behavioral sciences, although it has important implications. First, it is not self-evident that the iteration of a cooperation game leads to mutual cooperation; there are many alternative equilibrium outcomes. Second, the fact that many game models have a huge number of potential Nash equilibria makes the choice of equilibrium (i.e., equilibrium selection; Samuelson 1997) a much harder task than the identification of Nash equilibrium strategies. Even rational players who are able to compute all possible equilibrium strategies have to find ways to coordinate their behavior and to settle on one of these strategies. Personality may be important for resolving the coordination problems that are associated with the complexities of social interactions (discussed below).

There are numerous examples of evolutionary game theoretical analyses that have led to insights that can be overlooked when developing arguments without a basis in formal techniques (McNamara and Weissing 2010). A striking example is biparental care, in which a male and a female have to decide whether they should care for their common offspring, or invest their reproductive effort elsewhere. An evolutionary game theoretical model by McNamara and Houston (2002) found that the outcome of the interaction depends on the order

of decision making of the players. Figure 34.2 shows the payoffs to the male and the female for a generalized version of this model, contingent on the decisions of each parent to either care for the young or desert the nest. If both parents make their choice simultaneously, the female should always care, because this is the best response, both if the male cares and if he deserts. Consequently, given the fact that the female cares, the male will desert. However, if the female decides first, the situation changes, because the male now knows the decision of the female. The male does best to respond to the female’s desertion by caring, and to her caring by desertion. Because of this, the female chooses between a situation in which she cares and the male deserts, and a situation in which the male cares and she deserts. Because the latter situation is the best outcome for her, the female will desert, and the male will respond by caring. Although the male has more information than the female in the latter situation, this works to his disadvantage. This

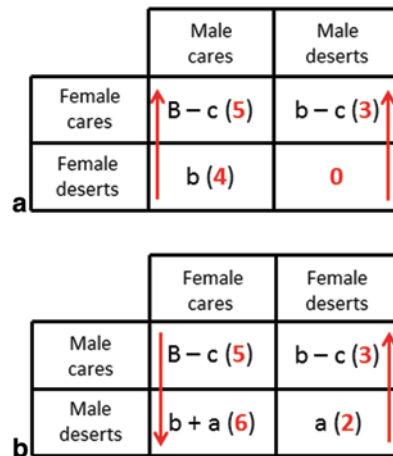


Fig. 34.2 Payoffs to the female **a** and the male **b** in a parental care game (inspired by a game considered by McNamara and Houston 2002). In this model, B represents the benefit of biparental care, b represents the benefit of uniparental care, c represents the cost of providing care, and a represents the fitness accrued through additional mating (we assume that such extra-pair mating opportunities are only available to males). In the model, $B > b > c$ and $B < 2b$ (uniparental care provides more benefit per invested effort than biparental care). In the example (digits shown in red), we assume that $B=6$, $b=4$, $c=1$, and $a=2$

shows that having more information can have negative consequences.

Although evolutionary game theory has generated valuable insights over the years, there are also limitations of the approach. Game theoretical analyses focus on fitness considerations, without regard for the mechanisms that underlie traits. This has been referred to as the “phenotypic gambit”: sacrificing realism of mechanisms for tractability of the evolutionary process. It fits in the tradition in biology to separate questions of proximate causation (How is a trait caused by immediate factors? What are the underlying mechanisms?) from ultimate causation (Why did a trait emerge in evolution? Why does it provide a fitness advantage?; Mayr 1961; Tinbergen 1963). However, the relative neglect of mechanisms in evolutionary studies is receiving increasing criticism (Bateson and Laland 2013; Fawcett et al. 2012; Laland et al. 2011; McNamara 2013). Mechanisms are of particular importance when considering the evolution of social traits, because they influence the probabilities with which strategies arise through mutation (van den Berg and Weissing, submitted). This is important, because in social contexts the success of a mutant strategy often strongly depends on the probability that it encounters itself in a resident population.

Another aspect of evolutionary game theory that has come under recent criticism is its focus on finding stable strategies for isolated contexts. Animals are faced with a complex and dynamic world, and it is unlikely that natural selection has equipped them with a perfect behavioral answer to every possible situation that they encounter (Fawcett et al. 2012, 2014). Indeed, animals often value immediate gains over long-term gains in a suboptimal way (Henly et al. 2008), make different decisions when there are “decoy” options available (Bateson and Healy 2005), and value food options differently depending on whether they were hungry when they previously encountered them (Marsh et al. 2004). Human behavior is also known to be subject to numerous psychological biases, causing them to deviate from rational behavior (Kahneman 2011; Tversky and Kahneman 1974). It seems likely that natural selection has equipped organisms with simple

heuristics that perform relatively well when faced with a range of contexts (Gigerenzer et al. 1999).

Individual differences are often overlooked in evolutionary game theoretical analyses. Evolutionary game theoretical models consider the fate of mutants in monomorphic resident populations. However, behavioral variation can have a profound effect on the outcome of evolution, for instance in the case of cooperative behavior (McNamara and Leimar 2010). If variation in a social trait is present in a population, it can be advantageous to be choosy about with whom to interact. If this social sensitivity indeed evolves, it may in turn affect the evolution of the social trait (Wolf et al. 2011). For this reason and others mentioned below, it is important to consider individual variation when constructing evolutionary game theoretical models (McNamara 2013; McNamara and Weissing 2010).

Human and Animal Personality

The study of individual differences has been one of the main areas of study in psychology for decades. The field of personality psychology has a long and diverse history, its prominence reflected by the large number of scientific journals, books, and conferences dedicated to it today. The study of personality addresses individual differences in characteristics that are relatively stable over time, but how those characteristics should be defined and measured has remained a matter of controversy (Engler 2009). Personality research is characterized by a large variation in objectives. Much research is focused on comprehensively describing the individual variation in a population, but much research is also dedicated to correlating outcomes (in education, work, or personal life) with personality factors. Over time, a number of influential systems for describing personality variation have been devised, of which the five-factor model (Digman 1990; McCrae and John 1992; Tupes and Christal 1961) is the most used and confirmed. Personality is most often measured using self-report data, although ratings by others and behavioral observations are also used.

In biology, research concerning individual differences is a more recent phenomenon. Individual differences between animals of the same species have long been ignored or treated as irrelevant behavioral noise. The idea that evolution does not lead to variation, but rather depletes variation and leads to a single optimal type, is likely to have contributed to this attitude. However, in the last few decades, evidence has accumulated that patterned variation in animal behavior (dubbed “coping style,” “behavioral syndrome,” or “animal personality”) occurs across a wide range of taxa (Gosling 2001; Groothuis and Carere 2005; Koolhaas et al. 1999; Réale et al. 2007; Sih et al. 2004a; Wolf and Weissing 2012). Animal personality has been defined as behavioral variation that is consistent through time as well as across different contexts. It is defined in terms of measurable behavioral tendencies; the fact that self-report data are impossible with animals has helped avoid some of the controversy about the concepts of personality in psychology. Perhaps more importantly, animal personality research distinguishes itself from personality psychology by acceptance of the overarching framework of evolutionary theory. Questions are often inspired from an evolutionary perspective, and the relevance of different characteristics is determined accordingly.

In recent years, there has been some cross-pollination between the fields of personality psychology and animal personality research, particularly in the development of theory to explain the evolution of individual variation (Buss 2009; Figueredo et al. 2005; Gosling 2001; Michalski and Shackelford 2010; Nettle 2006; Penke et al. 2007). Recently, Nettle and Penke (2010) have argued that personality psychologists can benefit much from behavioral ecology, especially in adopting an evolutionary perspective. They also argue that adopting the concept of the reaction norm from biology (a rule that defines the response of an organism to environmental conditions) can help solve the long-standing debate in psychology about whether personality or situational parameters are more important in shaping human behavior. Conversely, biologists can learn from the 100 years of experience that psycholo-

gists have with devising comprehensive descriptions of behavioral variation. Some have argued that personality differences are especially prevalent in highly social species (Figueredo et al. 1995, 2005; Penke et al. 2007). Since the evolution of social behavior is governed by frequency-dependent selection, evolutionary game theory is a preeminent tool to formally study the evolutionary emergence of personality differences. Moreover, the use of formal techniques such as evolutionary game theory is important for further developing verbal arguments, so that they mature into theories that generate testable predictions.

Evolutionary Causes of Personality Differences

Consistent individual differences are challenging to explain from an evolutionary point of view. First, there is the question of variation: Why are there individual differences between members of the same species, where one would expect evolution to deplete variation, leading to a single optimal type? Second, there is the question of consistency: Why do individuals behave in the same way across different contexts and over their lifetime, instead of being flexible and optimally adapting their behavior to each specific circumstance? Adaptive explanations for individual differences have started to emerge in both evolutionary psychology and evolutionary biology over the last two decades. In recent years, both fields have started recognizing the same evolutionary mechanisms that can lead to consistent variation. In biology more than in psychology, evolutionary explanations have often been backed by formal theory—often evolutionary game theoretical models.

Buss (1984) remarked that evolutionary biology and personality psychology are connected in an interesting way: personality psychology studies variation, which is the substrate that evolution acts on. Tooby and Cosmides (1990) argued that personality differences are unlikely to have resulted from natural selection, and consider personality variation to be random noise. However, since then, adaptive explanations for personality

differences have started emerging in the literature. Notable examples from psychology include the theories of sociosexuality (Gangestad and Simpson 1990) and sociopathy (Mealey 1995). The biological literature of the 1990s also saw an increased interest in adaptive explanations for variation in reproductive strategies (see Gross 1997, for a review), often accompanied by evolutionary game theoretical models, and other studies invoking adaptive arguments for individual differences (e.g., Morris 1998). More recently, Nettle (2006) took the first steps towards more explicitly connecting the fields of evolutionary biology and personality psychology by offering a number of potentially adaptive explanations for the variation in human personality using the five-factor model.

Recent reviews from evolutionary psychology (Buss 2009) and evolutionary biology (Wolf and Weissing 2010) reveal that a similar range of adaptive explanations for individual variation is currently being considered in both fields. Three types of adaptive explanations prominently figure in both reviews: (1) state-dependent behavior that is contingent on nonevolved differences, (2) environmental heterogeneity in fitness optima through space and/or time, and (3) negative frequency-dependent selection. These are not all the explanations that are considered in either paper. Buss also includes costly signaling, but this can be considered as a subset of state-dependent behavior, and some nonadaptive explanations such as mutation load. Wolf and Weissing, in turn, also discuss the emergence of individual variation as a result of nonequilibrium dynamics. Below, we elaborate on these three explanations, and give examples of evolutionary game theoretical models that support each of them.

State-Dependent Behavior

The idea that individual variation may arise from underlying differences in state is not new. In fact, it is central to the handicap theory of sexual selection (Zahavi 1975). In handicap models, it is assumed that there is some kind of variation in quality between males; either heritable (“good

genes”) or nonheritable (e.g., the amount of resources a male has available to invest in offspring). In these models, evolution leads to the development of a costly indicator trait that signals quality in males, and a costly preference for the degree of exaggeration of that indicator trait in females. Thus, the measurable individual variation in the indicator trait is contingent on the underlying variation in male quality.

A more recent example is the idea that individual differences in social dominance may result from minute differences in fighting ability, or even from chance asymmetries regarding who happens to win most fights early in life. Van Doorn et al. (2003) considered the iterated version of the Hawk–Dove game (see Fig. 34.1): The same two individuals repeatedly had to fight over resources and in each round could choose between playing Hawk or Dove. In the majority of their simulations, a strategy emerged that resembles the so-called winner–loser (WL) effect that has been described in many animal populations (Chase et al. 1994). According to this WL strategy, individuals play Hawk with a certain probability in their first rounds, until they are involved in a Hawk–Hawk interaction. From this round onwards, the winner of this interaction plays Hawk in all remaining rounds, while the loser sticks to playing Dove. If both players of an iterated Hawk–Dove interaction adopt the strategy WL, the outcome is a stable dominance convention: the individual that happens to win the first fight keeps obtaining the resource in subsequent interactions, while the other individual keeps losing the contest. This happens despite of the fact that there are no initial differences in strength or fighting ability. The evolved strategy WL is a strategic convention that leads to consistent individual differences in social dominance on the basis of a single event, the random assignment of a winner, or loser position in one escalated fight.

Environmental Heterogeneity

If there is variation in fitness optima through space and/or time, this may lead to variation in behavior. However, exactly how phenotypic vari-

ation is expected to emerge depends on the details of the situation (Wolf and Weissing 2010). If individuals have reliable knowledge of their environment and the costs of adapting behavior to environmental conditions are low, phenotypic plasticity is likely to evolve. In this case, the resulting individual variation is a consequence of a form of state-dependent behavior, where “states” correspond to environmental conditions. If information on the environment is noisy or the costs of plasticity are high, polymorphism will typically arise, where different types of individuals coexist that are adapted to some but not all environmental conditions. This polymorphism may reflect either genetic diversity (different genotypes specifying phenotypes adapted to different conditions) or a bet-hedging strategy (where a single genotype produces phenotypically variable offspring).

Olofsson et al. (2009) present an evolutionary model to explain the evolution of bet-hedging strategies. In their model, a population of individuals is living in a temporally variable environment. The variation between years is implemented as a variable minimal weight for the viability of offspring; any offspring below that threshold does not survive. In addition, only a limited number of offspring can survive in each year. In the model, each individual can produce the same total weight of offspring, but has three genes to determine how many offspring to produce. One gene determines the average weight of one offspring, one determines the variability in weight among offspring in a given year, and one determines the variability in weight between years. The outcome of evolution in the model is that individuals produce variable offspring both within and across the generations. The result is a population in which there are individual differences in size, that are not conditional responses to the current environment, but that are also not based on a genetic polymorphism.

Frequency-Dependent Selection

Frequency-dependent selection is arguably the only ultimate explanation of the sustained persistence of heritable variation. Competing strat-

egies will easily coexist (resulting in individual variation) if each strategy has a fitness advantage when occurring in a low frequency. Such a rareness advantage arises, for example, in case of frequency-dependent selection where the fitness of each strategy decreases with the frequency of this strategy in the population (“negative” frequency-dependent selection). Both Gangestad and Simpson’s (1990) theory of sociosexuality and Mealey’s (1995) theory of sociopathy are based on arguments of negative frequency dependence. Evolutionary game theory is a particularly useful tool for studying the implications of negative frequency-dependent selection.

An example of a game theoretical model that explains the evolution of individual differences by negative frequency-dependent selection is the model of Johnstone and Manica (2011) for the emergence of leaders and followers (but see Weissing 2011). With their model, they consider a population in which individuals are grouped at random and have to play an n-person version of the game “battle of the sexes.” The original context of this game is a situation where a couple has to decide how to spend their evening. The man would like to go to the prizefight, the woman would prefer to go to the ballet, but above all they want to spend their evening together. In the model, there is a group of individuals that each have their own preference, but also obtain benefits when they coordinate on the same option with many fellow group members. Each individual has a genetically determined value of leadership: if it is high, the individual tends to choose their own preferred option; if it is low, the individual copies the most recent choice of a randomly selected group member. In this case, leadership is subject to negative frequency-dependent selection; the fewer leaders there are, the more it pays to be a leader. The outcome of their model is individual variation because of a genetic polymorphism in leadership; some individuals are leaders, some are followers. Indeed, for some parameter combinations, as many as five different types can arise.

Overall, constraints play an important role in the evolution of consistent individual differences. If the optimal strategy cannot be attained, because of imperfect information, cognitive limitations,

costs of plasticity, or for whatever other reason, frequency-dependent selection will often lead to the emergence of consistent individual variation. For a simple way of illustrating this, again consider the Hawk–Dove game. If individuals can have mixed strategies (their strategy can be to play Hawk with a certain probability), evolution leads to the emergence of a single type (Wolf et al. 2011). However, the strategy space is constrained so that only pure strategies are allowed (individuals can only always play Hawk or always play Dove), evolution leads to a population that consists of some individuals that always play Hawk, and some that always play Dove. Because of a constraint on the flexibility of behavior, both variation and consistency in behavior emerge.

Most animals are faced with numerous different contexts throughout their lives, and they usually lack detailed information about the specific context that they are in. It is not difficult to see that informational and cognitive constraints render it close to impossible for animals to have a perfect behavioral response for each possible context that they may face. Instead, they often resort to imperfect behavioral responses: general-purpose mechanisms or “rules of thumb.” These imperfect mechanisms leave room to be exploited by other imperfect mechanisms, and individual variation can emerge as a result (Botero et al. 2010). A recent empirical example of variation in general-purpose mechanisms in human behavior is individual variation in social learning strategies (Molleman et al. 2014; Van den Berg et al. 2015). These authors show experimentally that humans are different in the extent to which they are interested in social information. Moreover, there is variation in the type of information individuals are interested in; some try to identify the type of behavior that is associated with the highest payoffs, whereas others are only interested in finding out what the majority is doing. Interestingly, these differences were consistent across a number of different contexts that the subjects were confronted with. This indicates that there may be limitations to flexibly adapting social learning strategies to each different context, potentially explaining the observed variation.

Evolutionary Consequences of Personality Differences

Even though there has recently been interest in evolutionary explanations for personality differences, questions concerning the evolutionary consequences of individual variation have received less attention. However, as summarized in two recent reviews (Sih et al. 2012; Wolf and Weissing 2012), there are many potential ecological and evolutionary consequences of the presence of behavioral variation in a population. Consequences of individual differences can impact three qualitatively different domains. First, it can affect ecological parameters, such as population density, the spatial distribution of different behavioral types over different habitats, and disease transmission dynamics. Second, it can affect qualitative aspects of the evolutionary process, such as evolvability, constraints on evolution, and the likelihood of evolution to lead to speciation. Third, the presence of consistent individual variation can alter selective forces acting within populations. This latter consequence of consistent individual variation is especially suited for analysis with formal techniques from evolutionary game theory. Below, we elaborate on the consequences of both consistency and individual variation for the outcome of evolution, giving examples of evolutionary game theoretical models in both cases.

Implications of Individual Variation

To illustrate the evolutionary consequences of individual differences, we can again refer back to handicap models of sexual selection (Zahavi 1975). In those models, males signal their mate value (whether heritable or not) with a costly indicator trait. In response, a costly female preference for the extent of expression of this trait can emerge. Under the right circumstances, the benefits of such a preference (leading to mating with higher-quality males) will outweigh the cost of being choosy. However, a costly female preference can only be maintained if there is something to choose—there must be variation

between males for the preference to have a selective advantage. Without individual variation in male quality, female preference for the indicator trait will be lost from the population. As a result, male investment in the indicator trait also loses its selective advantage, and will also be lost. In summary, without individual differences in male quality, there can be no evolution of exaggerated indicator traits and female preferences for those traits. Noe and Hammerstein (1994, 1995) recognized the importance of the evolution of choosiness in “biological markets,” where one class of individual has something to offer for another class of individuals. They consider the case of mating, but also of cooperation and mutualism between different species. However, although variation is a prerequisite for any market to function, they do not explicitly consider the importance of variation in their models.

Recently, McNamara et al. (2008) developed an evolutionary game model that explicitly considers the importance of individual variation for the evolution of choosiness in the context of cooperation. In the model, they consider a population in which pairs of individuals engage in a variant of the IPD. Each individual carries two genetically determined traits: degree of cooperativeness and degree of choosiness. At the beginning of each interaction, both individuals simultaneously invest an amount of effort, which is determined by their degree of cooperativeness. Both individuals incur a cost for the amount of effort that they invest, but gain a benefit from the amount of effort invested by the other player. The degree of choosiness next determines the minimal cooperative effort that is accepted from the other player. If the choosiness of both players is satisfied, the two players interact again—unless one of them does not survive to the next round, which happens with a small fixed probability. If the choosiness of at least one of the players is not satisfied, both players find a new interaction partner, at a small cost. The outcome of the model is that the evolution of choosiness and cooperation strongly depend on the mutation rate, which determines the amount of individual variation in the population. If the mutation rate is high enough, there are sufficient individual differences in co-

operativeness, which provides a selective advantage for being choosy. Consequently, as a result of the evolution of increased choosiness, it pays to cooperate more, and high levels of cooperativeness evolve. In contrast, if the mutation rate is too low, choosiness does not pay, and levels of cooperation remain low as a consequence. In summary, this model shows that the amount of individual variation that is present in a population can profoundly affect the evolution of cooperation and choosiness.

Implications of Behavioral Consistency

As noted, many types of interactions have a huge number of Nash equilibria. Even if there are several Nash equilibria that are favorable for all individuals involved, the participants of an interaction first have to zoom in on one particular equilibrium. In the absence of efficient and reliable communication, this may be a difficult task, corresponding to a “coordination game.” (A classic example of a coordination game with different equilibria is whether to drive on the left side or the right side of the road; see McNamara and Weissing 2010.) Behavioral consistency can be helpful in solving problems of coordination. By being consistent, individuals can inform others about how they are likely to behave in the future. Others can use this information to choose their own behavior in such a way that successful coordination is the result.

By means of an evolutionary game model, Wolf et al. (2010) show how consistency and responsiveness to consistency may arise in evolution, and how a small amount of consistency may lead to the emergence of even more consistent strategies. They model a population in which individuals are engaged in pairwise Hawk–Dove game interactions. Each individual has a genetically determined trait that dictates with what probability they play Hawk. As described before, the evolutionary outcome in the simplest version of this model is a population in which each individual plays Hawk with some intermediate probability (the exact value depends on the specifics of the payoff parameters; see Fig. 34.1). In an

expanded version of the model, each individual also carries a gene that allows for social responsiveness. Responsive individuals watch their future interaction partners in one interaction with a third individual and subsequently make their behavior contingent on the choice of strategy in this interaction: if the future interaction partner played Hawk, the responsive individual plays Dove, and vice versa. Surprisingly low levels of individual variation in the probability to play Hawk already provide social responsiveness with a selective advantage. The ensuing presence of responsive individuals in the population selects for consistency, since the best reply to the strategy employed by responsive individuals is to stick to one's previous behavior. In turn, responsive individuals profit from the consistency of their interaction partners. Accordingly, there is a positive feedback loop: the more consistent individuals there are, the more it pays to be socially responsive, which can in turn lead to even greater consistency. In the end, a population may result that differs substantially from the original population (e.g., in the frequency of Hawk–Hawk interactions).

Conclusions and Future Directions

We have given a number of examples where evolutionary game theory has been used as a formal tool to support arguments for the adaptive significance of consistent individual differences. Both when studying the evolutionary causes and the consequences of consistent individual variation, evolutionary game models can be used to sharpen intuition, make arguments more precise, and help formulate predictions and new questions. Personality psychologists can benefit from the use of evolutionary game models in advancing our understanding of individual differences in human populations. Especially in humans, where the study of individual variation has a long and rich tradition, there is a huge amount of empirical substrate for formulating evolutionary hypotheses that could benefit from formal approaches.

We have argued that a better understanding of evolutionary constraints is crucial for getting a

better grasp on the evolution of individual variation. Mechanistic constraints are often (perhaps even always) at the basis of the evolution of heritable individual differences. However, developing such a theory of constraints is a rather unfamiliar practice to evolutionary biologists. Traditionally, evolutionary biologists have separated proximate (how does it work?) and ultimate (why does it exist?) questions, and evolutionary models have reflected this separation in their neglect of mechanistic constraints. However, there is now a growing appreciation that asking evolutionary questions without regard for proximate mechanisms can be misleading. We contend that the study of the evolution of individual differences would be an ideal test case for the development of a more mature theory of the relation between ultimate explanations and proximate mechanisms.

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