# The social evolution of individual differences: Future directions for a comparative science of personality in social behavior

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A B S T R A C T

Personality is essential for understanding the evolution of cooperation and conflict in behavior. However, personality science remains disconnected from the field of social evolution, limiting our ability to explain how personality and plasticity shape phenotypic adaptation in social behavior. Researchers also lack an integrative framework for comparing personality in the contextualized and multifaceted behaviors central to social interactions among humans and other animals. Here we address these challenges by developing a social evolutionary approach to personality, synthesizing theory, methods, and organizing questions in the study of individuality and sociality in behavior. We critically review current measurement practices and introduce social reaction norm models for comparative research on the evolution of personality in social environments. These models demonstrate that social plasticity affects the heritable variance of personality, and that individual differences in social plasticity can further modify the rate and direction of adaptive social evolution. Future empirical studies of frequency- and density-dependent social selection on personality are crucial for further developing this framework and testing adaptive theory of social niche specialization.

## 1. Introduction

Despite nearly a century of quantitative research on human **personality** (Table 1; McAdams, 1997), the methods and theory of personality science remain largely disconnected from evolutionary research on cooperation and conflict within human societies. Phenotypes such as extraversion, neuroticism, and conscientiousness, for example, are rarely considered in evolutionary models of human social behavior, despite being postulated as universal regulators of individuals' engagement and support, competitiveness and risk-taking, and deceptiveness and predictability in social interactions (Nettle, 2006). Human personality researchers have in turn only recently begun to formally model how social environments shape the expression of individual differences across societies (Smaldino et al., 2019). Similarly, while extensive research has been done on personality in sociability among non-human animals (herein animals; Gartland et al., 2022), sociability per se is not discussed as an important trait in recent, comprehensive treatments of the social evolution of behavior (see e.g. Rubenstein and Abbot, 2017). Instead, greater attention is given to functional variation in diverse, context-specific behaviors regulating mating, childcare,

foraging, predation, competition with neighbors and rivals, and other ecologically pertinent forms of social interaction. As personality researchers have long emphasized, these apparently distinct behaviors are often caused by common heritable mechanisms, and as a result are likely to be mutually shaped and constrained in their coevolution (Sih et al., 2004; Penke et al., 2007; Dochtermann and Dingemanse, 2013). Greater integration among research on personality and social behavior will, therefore, surely benefit our understanding of behavioral evolution more generally, as heritable individual differences are necessary for any phenotype to evolve by natural selection (Darwin, 1859; Lewontin, 1970). However, doing so will also require further developing empirical research in humans and other animals to better understand how plasticity toward and selection from social environments is affecting the adaptation of personality.

In this perspective, we engage with the challenge of integrating personality and plasticity across humans and animals by drawing on recent developments in social evolution, the field of evolutionary biology that investigates the evolution of cooperation and conflict in all domains of life (Frank, 1998; McGlothlin et al., 2010; Bourke, 2011; Rubenstein and Abbot, 2017). See Table 1 for a glossary of key concepts

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**Table 1**

Glossary of key concepts and symbols.

| Term | Symbols and equations | Description |
|---|---|---|
| Personality | $\mathrm{var}(\eta)$<br><br>Eqs. (B3, 2) | Individual differences in behavior that are repeatable over time. The magnitude of personality $\mathrm{var}(\eta)$ is determined by repeatable genetic and environmental effects on behavior, which are caused by phenotypic interactions between individuals' behavioral mechanisms and social ecological and developmental contexts (Fig. 1). |
| Behavioral reaction norm | $\eta, \mu, \beta$<br><br>Eqs. (B1-2) | A formal description of an individual's behavioral strategy. Behavioral reaction norms predict how repeatable trait expression $\eta$, and thus the magnitude of personality $\mathrm{var}(\eta)$, changes across environments as a function of individual differences in average behavior (intercept $\mu$) as well as plasticity or responsiveness toward the environment (slope $\beta$). |
| Social reaction norm | $\eta', \psi, \beta_\alpha$<br><br>Eqs. (1a-1c) | A behavioral reaction norm describing *social plasticity* ($\Psi$) toward the traits of others in the environment, such as responsiveness to the average behavior of parents, siblings, mates, and/or group members. The degree of repeatable association between the reaction norm parameters of individuals and their social partners is referred to as phenotypic *assortment* ($\beta_\alpha$). |
| Heritable (co)variance and evolvability | $\mathrm{var}(\eta_\mathbf{A})$, $\mathrm{cov}(\eta_\mathbf{A}, \eta')$<br><br>Eqs. (B4, 4a-b, B7a-b) | Among-individual variation $\mathrm{var}(\eta_\mathbf{A})$ and (co)variation with the social environment $\mathrm{cov}(\eta_\mathbf{A}, \eta')$ due to factors generating phenotypic similarity between parent and offspring personality and their interaction with the personality of social partners. Heritable (co)variance in personality determines the potential rate of adaptation in social behavior, also known as evolvability. |
| Social selection | $\beta_\mathrm{S}, \beta_\mathrm{I}, \beta_\mathrm{D}$<br><br>Eqs. (B5, 5, 7-8) | Variation in individual fitness due to the phenotypes of others in their social environment. The strength of social selection $\beta_\mathrm{S}$ may vary across environmental contexts due to interactions caused by frequency- $\beta_\mathrm{I}$ and density-dependent $\beta_\mathrm{D}$ fitness effects. |
| Social evolution | $\mathrm{cov}(\eta_\mathbf{A}, \eta')\beta_\mathrm{S} \neq 0$<br><br>Eqs. (B6, 5) | Adaptation due the effect of individuals' traits on the fitness of others (Fig. 1). Social evolution occurs when a behavior experiences social selection $\beta_\mathrm{S} \neq 0$ and a heritable association occurs between the behavior of individuals and their social partner(s) $\mathrm{cov}(\eta_\mathbf{A}, \eta') \neq 0$. |

and symbols used throughout the text. We begin Section 2 with a basic overview of personality research, the importance of modelling personality using **behavioral reaction norms** (Box 1), and the relevance of personality for understanding the social evolution of behavior in humans and animals. We argue that greater attention is needed to personality in the multifaceted and socially plastic behaviors that mediate daily interactions within many animal societies. Despite great predictive success, a strong emphasis on generalized latent traits such as sociability and extraversion, as well as standardized assays and rating methods, has drawn attention away from directly explaining the social evolution of contextualized behavior. Models of these latent traits are important tools for prediction and causal discovery, but ambiguity in their interpretation can also lead to confounding of distinct levels of functional and mechanistic explanation, limiting their utility for comparative research.

In Section 3, we then discuss the social evolution of behavior (Box 2) and the evolutionary consequences of indirect genetic effects (IGEs) on personality, which are heritable effects due to behavioral plasticity toward the social environment (Moore et al., 1997; Wolf et al., 1998; Bijma, 2011; McGlothlin et al., 2010; Dingemanse and Araya-Ajoy, 2015; Bailey et al., 2018; Araya-Ajoy, Westneat, and Wright, 2020). Despite extensive work and longstanding interest in the social and developmental plasticity of personality (e.g. Caspi and Roberts, 2001; Stamps and Groothuis, 2010; Bergmüller and Taborsky, 2010; Cabrera et al., 2021; Bleidorn et al., 2022), as well as the effects of parenting and rearing environments on personality (e.g. Reddon, 2011; Taylor et al., 2012; Vukasović and Bratko, 2015), much remains to be learned about how IGEs from outside of the natal home or nest (e.g. due to neighbors, mates, local competitors) shape the adaptation of personality. Fortunately, **social reaction norms** (Dingemanse and Araya-Ajoy, 2015; Martin and Jaeggi, 2022) provide an effective solution for estimating these IGEs and modeling the interplay between personality and plasticity in social environments. These models are used to show how **social selection**–i.e. fitness variation generated through social interactions (Wolf et al.,1999; McGlothlin et al., 2010)–can drive rapid adaptation of behavior via feedback between genetic, cultural, and ecological change. These eco-evolutionary feedback processes place the selection and development of personality at the center of social evolutionary models of behavior. Box 3 provides a worked example, integrating well-known insights from evolutionary game theory with a quantitative genetic model of personality in cooperative hunting behavior. We end by emphasizing future directions for empirical research on personality in social behavior, advocating for greater attention to measuring

fluctuating social selection caused by variation in frequency- and density-dependent fitness effects. Such studies will be crucial for more directly testing adaptive theory of personality in humans and other animals, particularly models of social niche specialization.

## 2. Personality and social behavior

### 2.1. Evolutionary research on animal and human personality

Personality is key to understanding the adaptation of behavior, as a population without individual variation cannot evolve by natural selection. Yet, it is only in the last two to three decades that biologists have given significant attention to the evolution of repeatable individual differences in behavior, independent of more commonly studied differences due to sex, age, morphology, and social rank (Wilson et al., 1994; Gosling, 2001; Bolnick et al., 2003; Réale et al., 2007; Dingemanse and Wolf, 2010). While evolutionary game theorists have long studied mixed strategies, where multiple discrete behavioral types or probabilistic decision rules are maintained within a population (e.g. hawks and doves, producers and scroungers, cooperators and defectors, cads and dads; Axelrod and Hamilton, 1981; Smith, 1982; Alger et al., 2020; McNamara and Leimar, 2020), empirical research on personality brought fresh attention to the once underappreciated degree of adaptive individual variation in all forms of animal behavior (see Buss and Hawley, 2010; Carere and Maestripieri, 2013; Vonk et al., 2017 for comprehensive overviews). Field studies have found that commonly studied personality traits affect fitness components such as survival, fertility, and bodily condition across taxa, indicating that personality continues to potentiate ongoing evolution by natural selection in the wild. For instance, many species exhibit temporally consistent among-individual variation in exploratory behavior, with some individuals being repeatedly more or less prone than others to be active and sample information in a novel environment (Reader, 2015). Long-term research on great tits (*Parus major*) has shown that personality in exploration is being adaptively maintained within multiple populations throughout Western Europe, due to ongoing temporally fluctuating selection across breeding seasons, with selection favoring more exploratory birds in some years and less exploratory birds in others (Mouchet et al., 2021). Similarly, consistent individual differences in risk-taking behavior, often termed boldness, generate fluctuating selection in Siberian chipmunks (*Tamias sibiricus*), with bolder individuals achieving higher reproductive success when resources are scarce but

shyer individuals faring better in seasons of plenty (Le Cœur et al., 2015).

Empirical evidence further suggests that personality structure–capturing associations among individual differences across multiple behaviors, also termed behavioral syndromes (Sih et al., 2004; Bell, 2007)–can bias the rate and direction of evolutionary change, speeding up, slowing down, preventing, or even reversing adaptation relative to independently evolving traits (Dochtermann and Dingemanse, 2013; Teplitsky et al., 2014). Royauté et al. (2020), for instance, demonstrated that divergence among reproductively isolated populations of field cricket (*Gryllus integer*) has occurred along conserved axes of genetic integration between boldness, exploration, and activity level, suggesting that personality structure has constrained and channeled ongoing phenotypic evolution within this species. The fitness consequences of behavioral syndromes have in turn been observed through studies of correlational selection on personality structure, where the consequences of a personality trait for survival and reproduction vary based on the expression of other personality traits. In common lizards (*Zootoca vivipara*), for instance, boldness and activity are shaped by negative correlational selection, with bold and inactive as well as shy and active individuals exhibiting higher growth rates than bold and active or shy and inactive individuals (Le Galliard et al., 2015).

In addition, animal personality research is also increasingly linking the proximate mechanisms underlying individual differences to broader patterns of ecological and evolutionary change (e.g. Wolf and Weissing, 2012; Canestrelli et al., 2016; Schirmer et al., 2019), building essential conceptual bridges between behavioral ecology, ecophysiology, and evolutionary genetics (Dochtermann et al., 2015; Stamps et al., 2018). Experimental evolution in bank voles (*Myodes glareolus*), for example, has shown that selection for increased predatory ability and enhanced aerobic capacity can both independently cause the evolution of greater activity level and boldness in a risky environment, suggesting adaptation of common physiological pathways that affect phenotypes and performance across multiple functionally distinct domains (Maiti et al., 2019). Dispersal behavior, which plays a key role in shaping population dynamics, is also regulated by widely conserved pathways of metabolic and hormonal physiology (Goossens et al., 2020) and shares common genetic bases with exploratory behavior in great tits (Korsten et al., 2013) and aggressiveness in western bluebirds (*Sialia mexicana*, Duckworth and Badyaev, 2007).

Similar to the field of animal personality, serious attention to the evolution of human personality has only begun to consolidate in recent decades (e.g. Buss, 1991; Nettle, 2006; Alvergne et al., 2010; Gurven et al., 2014; Penke and Jokela, 2016; Lukaszewski et al., 2020). This despite longstanding interest among personality psychologists in understanding the "*individual differences that are of most significance in the daily transactions of persons with each other*" (Goldberg, 1981, p. 141), as well as their role in shaping folk lexicons of personality terms and descriptors (Ashton and Lee, 2005; John, Angleitner, and Ostendorf, 1988). For nearly a century, multivariate dimension reduction techniques such as factor analysis have been used in combination with this lexical approach to personality measurement (Cattell, 1943; Goldberg, 1993), helping to tame the unwieldy complexity of the thousands of partially redundant personality terms observed in many human languages (Allport and Odbert, 1936; Angleitner et al., 1990). Studies of personality ratings from individuals and their close social partners have repeatedly shown that only a few major factor dimensions–usually five or six–are necessary to describe much of the variation observed in personality across human societies (Goldberg, 1993; Digiman, 1996; Ashton and Lee, 2007; John et al., 2008).

So-called Big Five or Five Factor models of personality capture covariance across a host of cognitive, affective, behavioral, and motivational traits using five latent trait dimensions: extraversion, agreeableness, conscientiousness, neuroticism or emotional stability, and openness to experience (Goldberg, 1990; Costa and McCrae, 1995; Wilt and Revelle, 2015). A closely related six factor HEXACO model further differentiates an honesty-humility factor (de Vries et al., 2016). These latent factors have been associated with individual variation in key genetic and neurobiological pathways regulating human behavior (Sanchez-Roige et al., 2018; De Young et al., 2021). Factor scores have also been associated with variation in important life outcomes related to individuals' job success, social status, mental health, and quality of interpersonal relationships, as well as in more direct fitness proxies such as mortality risk, fertility rate, and bodily health and condition (Hakulinen et al., 2015; Ozer and Benet-Martinez, 2006; Roberts et al., 2007; Penke and Jokela, 2016; Soto, 2019). For example, among Tsimane women of lowland Bolivia, higher neuroticism and extraversion were found to predict later age at first reproduction and higher fertility, respectively, in deep forest communities; yet in communities nearer to market towns, these patterns were reversed, suggesting fluctuating patterns of selection in response to ecological and cultural variation (Gurven et al., 2014). Similarly, among rural women in Senegal, neuroticism was on average associated with children of lower body size and mass but also a greater number of living children. However, among women of higher social class, neuroticism did not predict variation in offspring condition (Alvergne et al., 2010).

The strong empirical foundation of latent trait models in personality psychology has centered most evolutionary research toward explaining how and why these five or six major dimensions of social behavior may have evolved and continue to be maintained in human societies. Latent factors have been argued to reflect individual differences in processes of intrinsic maturation (McCrae and Costa, 2003), self-regulation and neurocognitive development (van Egeren, 2009; deYoung, 2015), and/or persistent individual by environment interactions that are experienced across all human societies (Buss, 1991; McAdams and Pals, 2006; Nettle, 2006; de Vries et al., 2016), as well as among many other species (Weiss, 2021). However, as we argue further below, recent studies have also begun to challenge the universality of human personality structure, as well as the ability of current latent trait models to explain the development and evolution of plasticity in human social behavior.

### 2.2. Measuring and comparing personality in social behavior

#### 2.2.1. Distinguishing sociability, social networks, and social strategies

While great advances have been made in our understanding of animal personality in active, exploratory, and risk-taking behavior, much remains unknown about adaptive personality in animal social behavior, despite a growing body of empirical research demonstrating personality in social traits and its effects on fitness in wild populations (see Gartland et al., 2022 for a detailed review). More aggressive male tree swallows (*Tachycineta bicolor*), for example, tend to fledge more young than less aggressive males (Betini and Norris, 2012), while more sociable female lizards have lower survival than asocial females but also increased reproductive success (Cote et al., 2008). Studies on sociability in animals often employ single measures (e.g. the time spent in close proximity to conspecifics or social network position) and define sociability as a unitary trait distinct from aggressiveness, such as "*an individual's tendency or propensity to associate with other individuals…not driven by reproduction or aggression*" (Gartland et al., 2022, p. 803). However, much less attention has been given to understanding personality in the more contextualized and multidimensional strategies that often mediate daily patterns of cooperation and conflict within many animal societies (Koski, 2014; Loftus et al., 2021).

Personality research on non-human primates has been an important exception in this regard, providing an essential bridge between the evolutionary literature on personality in the social behavior of humans and other animals. Using a combination of long-term focal observations, experimental assays, and observer reports in both captive and wild settings (Freeman and Gosling, 2010; Weiss, 2017; Blaszczyk, 2020), research on non-human primates has demonstrated individual differences in multidimensional traits regulating leadership, social

assertiveness, and dominance styles (Foster et al., 2009; Sapolsky and Ray, 1989; Staes et al., 2016), cooperation in collective action problems (Schneider et al., 2012), social bonding (Seyfarth et al., 2014; Ebenau et al., 2019*)*, conflict management and resolution (Webb et al., 2014), affiliation and play (Koski, 2011; Martin and Suarez, 2017), consolation (Webb et al., 2017), infant-directed communication (Fröhlich et al., 2022), and social learning strategies (Watson et al., 2018), among others. These multifaceted social traits require greater theoretical attention in the animal personality literature, as they challenge assumptions from simpler models focusing on association-based measures of sociability. For instance, Gartland et al. (2022) suggest that personality in aggressiveness may often be negatively correlated with personality in sociability, due to tradeoffs between the expression of aggressive behaviors that decrease association with conspecifics and sociable behaviors that increase association. However, for many obligately social species living in stable social groups, aggressive and affiliative behaviors are interdependent rather than opposing expressions of an individual's social strategy, functioning to solidify dominance and status while also facilitating reconciliation and maintaining tolerance within groups (De Waal, 1986).

It is generally difficult to disentangle the functional consequences of such strategies from consideration of association measures or social network metrics alone. In Hamadryas baboons (*Papio hamadryas*), for example, males often corral and maintain the spatial cohesion of females within their social units using targeted forms of harassment such as neck biting (Swedell and Schreier, 2009). Recent work suggests that aggression of male group leaders toward females tends to *increase* rather than decrease both sexual interaction and nonsexual affiliation (Baniel et al., 2021). Yet leader males who are indiscriminately aggressive may suffer from reduced fitness by suppressing female reproduction, as well as by reducing their ability to defend females due to eviction of other follower males from the group (Evans et al., 2022). It may thus matter more how, when, and to whom a male shows aggression than his overall level of aggressiveness per se. Similarly, wild female chacma baboons (*Papio ursinus*) have been found to exhibit personality in three distinct dimensions, independent of dominance and kin support, capturing interrelated patterns of touching and embracing, vocal communication, social proximity, and aggression, each of which showed distinct effects on proxies of longevity and offspring survival (Seyfarth et al., 2012). Such multifaceted social strategies are widespread across taxa, challenging simple definitional distinctions between sociability and aggression.

Individual differences in association, proximity, and network position measures have been repeatedly identified as targets of selection across a diverse range of social systems. For instance, among feral horses (*Equus caballus*), the number of associates a female maintains in her network can predict her probability of survival as a juvenile following a major decline (Nuñez et al., 2015), as well as her birth rate and survival into adulthood (Cameron, Setsaas, and Linklater, 2009). For female white-faced capuchins (*Cebus capucinus*), greater affiliation and proximity to other females is also associated with a greater probability of survival (Kajokaite et al., 2022). More generally, these findings are consistent with a large body of work demonstrating the fitness and health consequences of social rank and status in stable social groups (e.g. von Rueden and Jaeggi, 2016; Alberts, 2019; Snyder-Mackler et al., 2020; Turner et al., 2021). Recent work in fungal beetles (*Bolitotherus cornutus*) has also demonstrated variable selection on network centrality across males' reproductive careers, with more central males having higher mating success in some but lower success in other networks (Formica et al., 2021). Such fluctuating selection on network position is likely to be an important mechanism for the maintenance of adaptive personality. In some systems, selection may also lead to the evolution of developmentally plastic traits promoting social competence across multiple domains (Varela et al., 2020; Taborsky, 2021). Nevertheless, much remains unknown about how and why personality persists in the multifaceted behavioral strategies that mediate these social

competencies and network effects across taxa.

### 2.2.2. Standardized assays versus contextualized measures

A common approach in animal personality research has been to isolate individuals and measure their behavior in response to controlled social stimuli, with the goal of reducing the impact of the social environment on the expression of individual differences. For instance, Bevan et al. (2018) assessed sociability in three-spined sticklebacks (*Gasterosteus aculeatus*) by separating and then measuring individuals' repeatable distance from a randomly selected conspecific placed in a plastic cup. They found that a positive association between boldness and leadership behavior only emerged among fish of low sociability, consistent with a tendency for more sociable individuals to conform toward group members, inhibiting the effect of their boldness on the probability of leading group movement. Revealing these intricate dynamics can be difficult in observational research on personality, which requires greater attention to measuring and adjusting for environmental heterogeneity or unbalanced sampling across time. This has led to an emphasis on the limitations of using naturally occurring behaviors to measure personality, as observed differences are often due to heterogeneous motivations and environmental states (Réale et al., 2007; Stamps and Groothuis, 2010). However, observational studies using dense and long-term focal data can provide the ability to measure social behavior more directly in the developmental conditions and ecological contexts of greatest relevance to evolutionary research, for studies of both historic and contemporary adaptation. While an emphasis on experimental control is essential for establishing causal effects on fitness and behavior, more direct and ecologically valid measures of personality also remain crucial for understanding social interactions that are difficult to recreate in the lab or measure within the scope of standard sociability assays. For instance, in many long-lived and large-bodied taxa, it will be difficult to experimentally standardize individuals' stable partner choices and social bonds, or their engagement in the biological markets that structure reproduction and resource exchange in human and animal societies (Hammerstein and Noë, 2016; Jaeggi et al., 2016; Grinsted and Field, 2017).

It is also important that individual differences in behaviors expressed in isolation or other artificial conditions are not assumed to be more informative of an individual's 'true' sociability as compared to more contextualized measures. Gartland et al. (2022) argue that a failure to control free interactions among individuals can lead to less sociable individuals appearing sociable due to the presence of other, more intrinsically sociable group members. However, this assumes that personality in the behavior animals express in an artificial environment (e. g. distance to a conspecific stimuli) is due to a sociability trait that also causes functionally similar (sociable) behaviors in more naturally occurring interactions. If the mechanisms underlying behavior diverge in their expression across contexts, personality in artificial settings may provide very limited information about adaptation of personality in naturally occurring social environments (Niemelä and Dingemanse, 2014). Consider recent work in wild great tits (*Parus major*), which found that individual differences measured in field and laboratory-based assays of exploratory behavior were not genetically correlated among individuals (Mouchet and Dingemanse, 2021). This suggests that distinct behavioral mechanisms were expressed when these animals were measured in what were designed to be functionally equivalent contexts. As previously noted by Carter et al. (2013), this is a more general issue for standardized assays of personality, such as open-field or novel object tests, which tend to capture behavioral variation caused by many distinct proximate mechanisms and psychological processes across individuals and taxa, such as fear, anxiety, impulsivity, and curiosity.

Standardized assays may additionally fail to capture heritable variation in social behavior that is of potentially equal or greater importance for explaining ongoing adaptive evolution. Pike cichlids (*Crenicichla frenata*), for instance, exhibit personality in their predatory behavior

toward guppy shoals that is independent of personality in behavior expressed during assays of boldness and neophobia (Szopa-Comley et al., 2020). Consider further that among marital pairs in a small-scale human society, evolutionary anthropologists have quantified variation in over ninety cooperative activities across nine categories of direct and indirect production (e.g. wage labor, childcare, hunting, fishing, food processing; Gurven et al., 2009). Approximately 50% of these activities are not exclusive to men or women, and most activities are not exclusive to particular age classes past sexual maturity. Large cross-cultural studies on cooperative hunting further suggest ample but unexplained individual variation within more sex-specific modes of production (Koster et al., 2020). Individual differences in hunting success, intra-marital cooperation, and alloparental care, among other domains of production, are also well-established predictors of fitness variation in non-industrialized societies (e.g. Kaplan and Hill, 1985; Sear and Mace, 2008; Gurven et al., 2009; von Rueden and Jaeggi, 2016). These differences are often only modestly predicted by the Big Five and other major factor dimensions. For instance, among the Tsimane, conscientiousness and industriousness have together been found to predict ~27% of variance among men in their average time spent working, while extraversion, agreeableness, industriousness, and openness to experience predict ~35% of variance in the average time men spent socializing (Gurven et al., 2014). Each of these fitness-relevant behaviors thus provides a potential source of personality and heritable variation within a given environment, independently of the Big Five and other generalized trait measures, that can facilitate further adaptive evolution of the phenotype.

Finally, it is important to emphasize that integrative frameworks are essential for explaining patterns of adaptation and constraint in social behavior (Tinbergen, 1963; Arnold, 1992; Konner, 2011; Bergman and Beehner, 2022; Chenard and Duckworth, 2021; McNamara, 2021). Comparative research on personality thus requires clear distinctions between terms used to describe individual differences in social behavior and the proximate mechanisms (e.g. genes, hormones, emotions, motivations and goals) that have causal effects on these behaviors in specific environments. Much confusion and theoretical ambiguity can arise (MacCorquodale and Meehl, 1948; Hinde, 1956; Boag, 2011) from failing to distinguish between personality as a repeatable behavioral phenomenon, caused by the interaction between individuals and their social environments (Fig. 1), and personality as a set of hypothesized mechanisms or processes within individuals, constraining and generalizing behavior across social environments (e.g. McCrae and Costa, 1995; Dubois et al., 2020). For plastic behavioral traits, individuals are not simply characterized by a single level or type of sociability in behavior across all environments. Instead, personality can be better understood as an inherently context-specific developmental process with individual-specific parameters (i.e. behavioral reaction norms; Dingemanse et al., 2010; Stamps and Groothuis, 2010). This means that the magnitude of personality–i.e. repeatable individual differences in behavior–may change within the same traits and among the same individuals across different environments (see Box 1). From this perspective, it is generally not important to determine whether an individual is truly sociable, as measured in an artificial environment, or merely appearing sociable due to naturally occurring interactions. Individuals' repeatable tendencies to express sociable behavior may simply differ between these contexts, due to the differential activation of the mechanisms regulating their behavior. The more important task is to understand the developmental processes and fitness consequences of personality in the ecological conditions for which behavioral adaptation is most likely to have occurred or be ongoing.

### 2.3. Rating methods in humans and other animals: benefits and limitations

#### 2.3.1. Ratings as measurements of person perception

Many of the measurement issues faced in the animal personality literature have long been appreciated by personality psychologists, as much of the history of this field has been characterized by debates over the importance of measuring and defining human personality in relation to broad or narrow traits, mechanistic or dispositional models, and specific situations or aggregated experiences (Kenrick and Funder, 1988). Repeated efforts have thus been made to better integrate evolutionary research on human and animal personality (Gosling and Vazire, 2002; Uher, 2008; Nettle and Penke, 2010; Carter et al., 2013; Weiss and Adams, 2013; Hengartner, 2017). However, the behavioral methods often used for measuring personality in other animals have not been as widely applied in human personality research, despite early efforts to introduce behavioral studies of personality into evolutionary psychology (Buss and Craik, 1983). Instead, with growing interest in the discovery of 'global' and putatively universal traits (Funder, 1991), such as the Big Five or HEXACO, personality psychologists have largely moved away from using experimentally and behaviorally oriented measures (Baumeister et al., 2007). Greater emphasis has instead been placed on the holistic and qualitative insights provided by subjective ratings of personality, where an individual and/or their close associates judge their level of expression on a typically large inventory of trait terms. These ratings fundamentally capture variation in person perception, which refers to the subjective processes by which humans use concepts such as "amiability", "boisterousness", or "rebelliousness" (Goldberg, 1990) to represent, categorize, and form judgements about one another (Funder, 1995; Srivastava, 2010; Lukaszewski et al., 2020).

Rating methods generally capture a very broad range of potentially relevant traits (Wilt and Revelle, 2015) that are often challenging to measure quantitatively with observable social behaviors or actions. Most published ratings are also retrospective perceptions of personality, where an ordinal response is made to a general question about an individual's typical way of being. Person perception as measured by such retrospective reports is often reliable across raters and temporally repeatable, with self- and other-ratings tending to exhibit modest correlations (Connelly and Ones, 2010) as well as moderate rank-order consistency and stability across the lifespan (Roberts and DelVecchio, 2000; Kandler and Papendick, 2017). Both quantitative and molecular genetics studies have also shown that average differences in the personality factors emerging from subjective ratings are moderately to highly heritable (Briley and Tucker-Drob, 2014; Polderman et al., 2015; Kandler and Papendick, 2017). However, a major limitation of rating methods is their emphasis on the structure of person perception rather than behavioral expression per se. Retrospective rating methods in particular are limited in their ability to accurately capture the relationship between behavioral plasticity and personality, due to the aggregation of raters' many unique memories and perceptions of an individual, made directly or indirectly across a heterogeneous set of unmeasured and often unbalanced environments.

While rating methods consistently predict important life outcomes (e.g. Ozer and Benet-Martinez, 2006; Roberts et al., 2007) and aggregate behavioral patterns (e.g. Epstein, 1979; Wu and Clark, 2003; Fleeson and Gallagher, 2009), their primary application has been to measure latent psychological traits and linguistic concepts, rather than contextualized actions. Indeed, many researchers have emphasized that specific items and facets of the major factor scales are semi-arbitrary, as the internal psychological processes regulating human personality are expected to be very broad and dynamic in their effects while also retaining a developmentally canalized structure across societies (Costa and McCrae, 1995; DeYoung et al., 2007). In this way, a theoretical effort is made to distinguish between so-called "characteristic adaptations" of an individual, reflecting individual differences in contextualized motivations and behaviors relevant to specific situations and life circumstances, and the latent factors that organize these observable responses across societies (McCrae and Costa, 2003; McAdams and Pals, 2006; DeYoung, 2015; Nguyen et al., 2021). This decontextualized approach to measurement has made it challenging to know whether the structure and variation of subjective ratings is caused by environmental
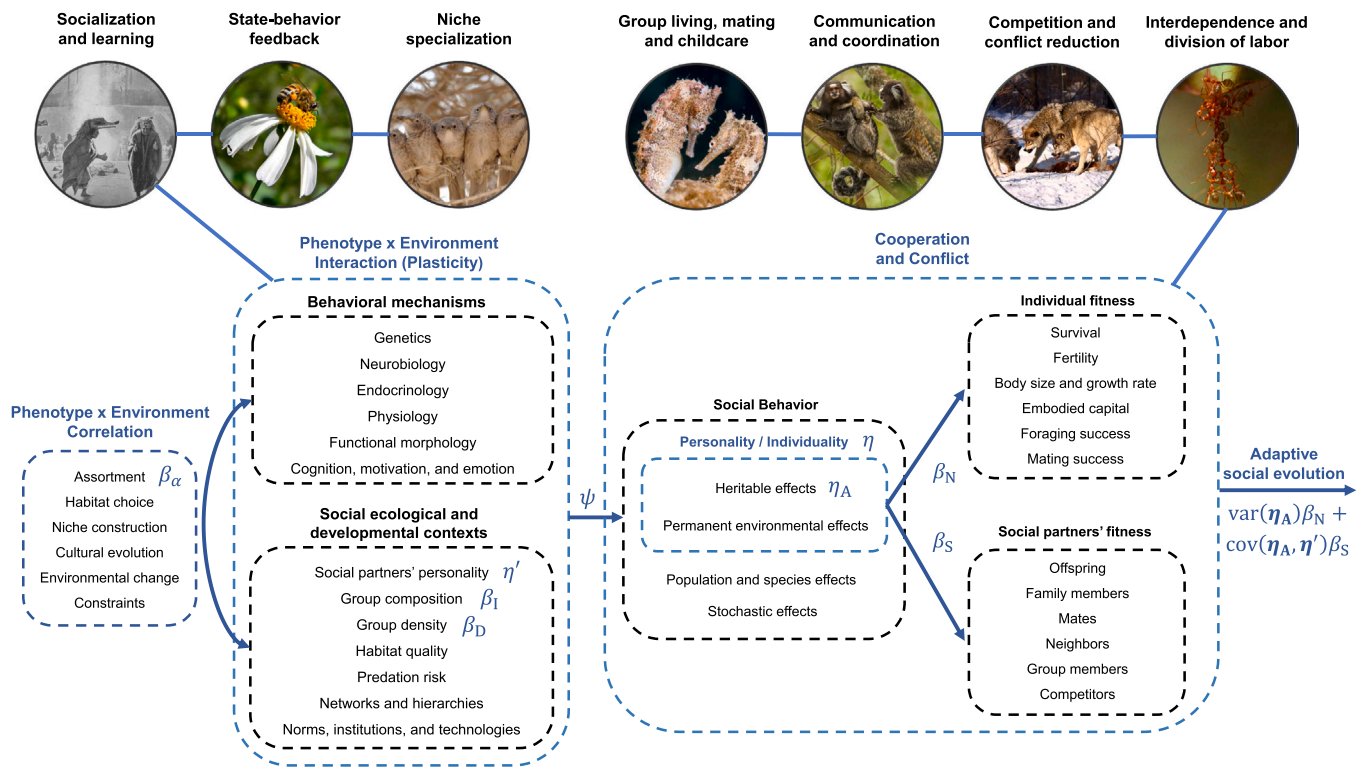
**Fig. 1.** *A social evolutionary approach to personality science*. The diagram provides a conceptual overview of the major arguments elaborated throughout this perspective, synthesizing research on the proximate causes (left side) and evolutionary consequences (right side) of personality in social behavior. We argue for greater emphasis on explaining personality/individuality $\eta$ in contextualized behaviors, as hypothetical latent traits tend to obscure causal processes due to the local environment and the biological mechanisms regulating behavior (i.e. phenotype x environment correlations and interactions). Group living, mating, and childcare, communication and coordination, competition and conflict reduction, and interdependence and division of labor are contexts of particular relevance for social evolutionary research. Socialization and learning, state-behavior feedback, and niche specialization are three key processes of phenotype x environment interaction that may cause personality in these contexts across taxa. The reaction norms underlying proximate effects on personality are crucial to understand because of their downstream consequences for adaptive social evolution, via the magnitude of assortment $\beta_\alpha$ and social plasticity $\psi$ between the personality of individuals $\eta$ and their social partner(s) $\eta'$. These parameters influence the magnitude of heritable effects on personality $\eta_A$ and the heritable covariance among social partners' personalities $\text{cov}(\eta_A,\eta')$(Eq. 4). Phenotype x environment interactions also determine the context-specific magnitude of non-social $\beta_N$ and social selection $\beta_S$ on behavior, which are likely to vary in response to density- $\beta_D$ and frequency-dependent $\beta_I$ effects across space and time (Eqs. 7–8). Collectively, these effects determine the rate and direction of adaptive social evolution $\text{var}(\eta)\beta_N + \text{cov}(\eta_A,\eta')\beta_S$ possible within a given environment. Photos are used with permission under Creative Commons and United States public domain restrictions for non-commercial purposes. Credits from left to right: painter Wilhelm Kuhnert (*The Walas'axa*; Boaz, 1897) Flickr photographer Bob Peterson, Dr. Yitzchak Ben Mocha (Harold et al., 2013), and Flickr photographers John Turnbull, Francesco Veronesi, Martin Cathrae, and Kasi Metcalfe.

heterogeneity among individuals or raters, repeatable differences in the mechanisms of behavioral consistency or plasticity expressed across these environments, the sociocultural and cognitive linguistic processes influencing person perception, and/or their interaction (Stamps et al., 2010; Uher, 2013; Lukaszewski et al., 2020).

### 2.3.2. Comparing ratings across species and societies

Comparative psychologists have also been interested in understanding the phylogenetic history of human personality factors, leading to the development of similarly standardized psychometric methods for quantifying subjective impressions of personality in animals (Gosling and John, 1999; Weiss, 2018). These rating methods have been particularly widely applied in primates, uncovering factor structures across a diverse range of species that are often highly similar to those observed in human personality research (Gosling and Vazire, 2002; Weiss, 2017, 2021). In conjunction with behavioral studies, such findings have drawn attention to the many highly conserved mechanisms that can constrain the structure of individual differences in social behavior among humans and other animals. For instance, oxytocin, vasopressin, and other homologous peptides are known to be important regulators of vertebrate social behavior (Caldwell, 2017; Johnson and Young, 2017; Ziegler and Crockford, 2017), and monoamine transporter systems are likely to have evolved very early among animals, with potentially widely conserved

behavioral functions despite complex patterns of gene duplication and loss across lineages (Gruber, 2014; Edsinger and Dölen, 2018; Bubak et al., 2020). Accordingly, individual variation in the organization of these neurotransmitter and endocrine systems is expected to be an important cause of personality (Duckworth, 2015), as has been found in diverse species from bonobos (*Pan paniscus*; Staes et al., 2016) and rhesus macaques (*Macaca mulatta*; McCormack et al., 2009) to southern field crickets (*Gryllus bimaculatus*; Abbey-Lee et al., 2018) and sticklebacks (Abbey-Lee et al., 2019). Similarly, differences in the physiological regulation of stress have been linked to common patterns of personality in numerous species (Carere et al., 2010; Koolhaas et al., 2010; Raulo and Dantzer, 2018).

As with human studies, retrospective ratings of animal personality are often able to predict aggregate behavioral patterns (e.g. Konecná et al., 2008; Morton et al., 2013; Eckardt et al., 2015) and important outcomes such as longevity (Weiss et al., 2013; Altschul et al., 2018), but they are not strongly suited to explaining the mechanisms of consistency and plasticity in animals' social behavior. The use of rating methods in comparative studies can also lead to so-called jingle fallacies in theoretical models, where the same trait term is used to describe two mechanistically and functionally distinct phenotypes (Block, 1995). For instance, the label 'extraversion' has been given to heterogeneous latent factors across the great apes, capturing partially overlapping but distinct

behavioral traits, and thus increasing the risk of confounding distinct phenotypes. Impulsivity has been argued to reflect extraversion in humans, but to reflect low conscientiousness in chimpanzees (*Pan troglodytes*) and high neuroticism in orangutans (*Pongo spp.*); friendliness is as an indicator of extraversion in chimpanzees but agreeableness in humans and orangutans; and curiosity is associated with extraversion in orangutans but openness in humans and chimpanzees (Weiss et al., 2012).

Without an a priori, functional basis for labeling these syndromes, attempting to reconstruct the evolution of human or animal personality structure through rating methods alone remains challenging, leaving studies in any particular species prone to the idiosyncratic interpretations and biases of raters. For instance, Uher et al. (2013) found that even experts' impressions of long-tailed macaque (*Macaca fascicularis*) personality were biased by socio-cultural stereotypes related to sex and age, such that their ratings of various traits poorly predicted objective behavioral measures. Uher and Visalberghi (2016) also demonstrated that raters tend to exhibit idiosyncratic interpretations of personality assessment items, which suggests that attempts to standardize trait terms may also not be a panacea for the ambiguity present in subjective assessments of traits such as "conventional" and "inventive" in animals. The absence of consistent mechanistic or functional definitions for these trait labels, as well as the inherent role of person perception in retrospective ratings, present challenges for the application of this method to describe and explain personality in highly plastic social behaviors.

### 2.3.3. The evolutionary ecology of human personality

Despite their limitations, rating methods have consistently provided evidence for five or six factor models of human personality in many countries and cultures (McCrae et al., 2005; Schmitt et al., 2007; Kajonius and Mac Giolla, 2017), as well as evidence of common genetic elements underlying these personality traits across populations (Jang et al., 2002; Yamagata et al., 2006).Yet most of this research has been done in rich and highly industrialized societies, with social ecologies marked by high levels of urbanization, market integration, formal education, and competitive labor markets that prioritize occupational specialization (Heine and Buchtel, 2009; Lukaszewski et al., 2017; Gurven, 2018). Studies outside of these contexts have begun to challenge the universality of the Big Five. For instance, among the Tsimane forager-horticulturalists of Bolivia, support has been found for a two rather than five factor personality structure, capturing prosocial leadership and industriousness dimensions that integrate phenotypes across the Big Five (Gurven et al., 2013). More generally, country-level variation in social and economic niches has been linked to differences in the structure of personality across societies, with more differentiated social niches leading to the expression of less integrated and higher dimensional factor structures (Lukaszewski et al., 2017; Smaldino et al., 2019). The Big Five also replicates poorly across multiple low- to middle-income countries (Laajaj et al., 2019). Even within American and Western European samples, behavioral genetic studies have failed to support common, developmentally integrated genetic factors underlying the Big Five (Briley and Tucker-Drob, 2012; Franić et al., 2014).

These findings suggest that there are not five or six universal psychological adaptations underpinning all human personality, nor are there five or six universal domains of gene-by-environment interaction in personality development. Instead, these latent traits are causally heterogeneous but predictively useful constructs, which emerge from the expression of numerous behavioral mechanisms under very specific developmental conditions within particular societies. The conditions under which the big five is most robustly observed are also uncharacteristic of many contemporary societies and are relatively recent in human history (Henrich et al., 2010), challenging the ability of current latent trait theories to explain how environmental conditions have

shaped personality development and evolution. However, doing so will be necessary to effectively integrate the evolutionary study of human personality and social behavior, as extensive behavioral plasticity and sociocultural variation are defining features of our species, as well as key drivers of our ecological and demographic success (Boyd et al., 2011; Henrich and Muthukrishna, 2021).

A clear direction for future research will, therefore, be to better synthesize mechanistic research on personality factors with socio-ecological theory of behavioral plasticity (Lukaszewski et al., 2017; Gurven, 2018; Smaldino et al., 2019). While personality traits are not as universal as once expected, socioecological theories without sufficient developmental constraints have also failed to predict the recurrence of a small number of latent dimensions–generally 2–6–across human societies. In the simulations of Smaldino et al. (2019), for example, societies with high levels of niche complexity are expected to show proportionally higher factor complexity. Yet average empirical correlations between Big Five dimensions tend not to be lower than 0.10 even in highly industrialized societies (Lukaszewski et al., 2017). This suggests that shared mechanisms likely constrain developmental plasticity and thus the overall dimensionality of personality structure. The field will benefit from quantitative models of the key phenotype x environment interactions (Fig. 1) that explain both the consistently low dimensionality but also extensive cross-cultural variability observed in human personality structure.

Testing these formal models with ethnographically and ecologically contextualized methods will also be crucial for reducing bias in comparative research (Gurven, 2018; Muthukrishna and Henrich, 2019; Lukaszewski et al., 2020). A principal challenge in comparing global personality traits across societies is to ensure that variation in ratings also reflect changes in the underlying populations means and (co)variances of behavior, rather than measurement error caused by cognitive heuristics such as reference group effects (Heine et al., 2008) or differential interpretations and engagement with rated items (Poortinga et al., 2002). Fortunately, evolutionary social scientists have increasingly begun to develop ecologically motivated measures of personality, which can more effectively capture the roles of socialization, individual learning, and the local environment in personality development. Koster and McElreath (2017), for example, provide a statistical method for measuring personality from focal samples of daily behavior, which they use to describe individual differences in activities such as agricultural work, hunting and fishing, domestic chores, and community errands among indigenous Nicaraguan men. Locally adapted behavioral experiments can also be a powerful tool for studying individual differences in the mechanisms causing personality, such as consistent moods and social preferences or learning strategies (Gervais, 2017; Pisor et al., 2020). Psychologists have also become increasingly interested in using item- rather than factor-level analyses to understand personality independent of the Big Five in the plastic behaviors and context-specific interactions of everyday life (often termed 'nuances', Mõttus et al., 2017, 2019). Analyses from large samples of German twins, for instance, have found that substantial heritable variation remained in over a hundred specific traits after adjusting for Big Five scores, which further predicted independent variation in personal interests and body mass (Mõttus et al., 2019). In addition, so-called experience sampling methods have grown steadily in their application, moving researchers toward trait models emphasizing repeated sampling of behavioral states across measurable environments (Jayawickreme et al., 2019).

Greater application of reaction norm models (Box 1) to these contextualized sampling methods is another clear avenue for future evolutionary research on human personality. Although reaction norm models have often been conceptually emphasized in this literature (e.g. Penke et al., 2007; Denissen and Penke, 2008; Nettle and Penke, 2010), they are rarely used as formal statistical tools in empirical research (see Nussey et al., 2007; Dochtermann and Dingemanse, 2013; O'Dea et al.,

2022; Martin and Jaeggi, 2022 for detailed discussions and tutorials). Doing so will help evolutionary social scientists to better formalize the interaction between personality, plasticity, and processes of cultural evolution and ecological change across human societies. It will also make it easier to synthesize quantitative research across human and animal studies, which will be important for increasing empirical interest in the evolutionary causes and consequences of personality in human behavioral plasticity.

## 2.4. Interim summary and conclusion

Both behavioral and rating methods have played an important and often mutually enriching role in personality research, with each being subject to unique pragmatic considerations contingent on the goals of a researcher and the system under investigation. However, despite predicting important behavioral patterns and life outcomes, retrospective rating methods in particular are poorly suited for comparative research

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**Box 1**
Using behavioral reaction norms to model personality.

Reaction norms provide a quantitative, evolutionary approach to describing the interaction between individuals (or genes) and the environments in which their phenotypes are expressed (Gomulkiewicz and Kirkpatrick, 1992; Dingemanse et al., 2010; Hutchings, 2011; Stamps, 2016; Gomulkiewicz et al., 2018). Longitudinal, repeated measures of the same individuals across different environments are essential for effectively estimating behavioral reaction norms with empirical data (Dingemanse and Wright, 2020). Reaction norms will often be dynamic and nonlinear in nature, requiring appropriate statistical techniques to separate repeatable individual variation from changes due to stochastic environmental effects (Dingemanse and Dochtermann, 2013; Gomulkiewicz et al., 2018; Martin and Jaeggi, 2022). Understanding the properties of simple linear reaction norms is nonetheless helpful for making theoretical generalizations about the relationship between personality, plasticity, and social behavior. Appropriate transformations can also be used to describe nonlinear reaction norms with generalized mixed effects models (Dingemanse and Dochtermann, 2013; Martin, 2021).

Consider a linear reaction norm of behavior $z$ measured repeatedly among individuals across some environmental factor $x$, such as resource availability, the density of local neighbors, risk of predation, or spatial proximity to potential mates. Reaction norms can also be defined over any environmental state that leads to learning in behavior (Wright et al., 2022). These differing environments may also be artificially versus naturally occurring conditions, and any other discrete or continuous factor. For each observation, measured behavior is a function of parameters regulating behavior in the average environment or in the absence of the environment (intercepts $\mu$), plasticity in behavior across environments (slopes $\beta$), and stochastic effects within each state of the environment (residuals $\varepsilon$). For measurement $i$ of individual $j$ in environment $x_{ij}$, observed behavior is predicted by

$$z_{ij} = \mu + \mu_j + (\beta + \beta_j)x_{ij} + \epsilon_{ij} \tag{B1}$$

where parameters $\mu_j$ and $\beta_j$ capture individual differences in the expression of mean behavior and plasticity relative to the population average values $\mu$ and $\beta$. In empirical studies, further effects due to age, sex, size, etc. should also be considered and potentially adjusted for as predictors of phenotypic means and variances (Bolnick et al., 2003; Dochtermann and Dingemanse, 2013), contingent on the research question (Westneat et al., 2020). Extensive comparative research has documented individual differences in both mean behavior (intercepts) and behavioral plasticity (slopes) across environments (Dingemanse et al., 2010; Stamps, 2016). Individual differences in residuals, reflecting personality in the variability or predictability of behavior, are also commonly observed (Biro and Adriaenssens, 2013; Westneat et al., 2015) and can be further included in the reaction norm model (O'Dea et al., 2022).

The repeatable, individual-specific component of measurement $z_{ij}$ in environment $x_{ij}$ can be represented by the population-relative reaction norm trait value

$$\eta_{ij} = \mu_j + \beta_j x_{ij} \tag{B2}$$

which provides a context-specific measure of individuality in behavior. Assuming that environmental states are mean-centered and independently distributed across individuals (Schielzeth and Nakagawa, 2022), the total amount of temporally consistent, among-individual variation in behavior is given by

$$\mathrm{var}(\boldsymbol{\eta}) = \mathrm{var}(\boldsymbol{\mu}) + \mathrm{var}(\boldsymbol{\beta})\mathrm{var}(\mathbf{x}) \tag{B3}$$

when intercepts and slopes are uncorrelated among individuals. Bolded symbols are used here and below to denote population vectors and matrices. Greater bias, proportional to $2\mathrm{cov}(\boldsymbol{\mu}, \boldsymbol{\beta})$, is expected in the presence of correlated mean behavior and plasticity. Empirical studies ignoring personality *in* plasticity $\mathrm{var}(\boldsymbol{\beta})$ thus risk missing a sizable component of the total repeatable individual variation in behavior $\mathrm{var}(\boldsymbol{\eta})$. For this reason, we refer to $\mathrm{var}(\boldsymbol{\eta})$, rather than $\mathrm{var}(\boldsymbol{\mu})$ specifically, as measuring personality, consistent with common theoretical definitions in both the human (Roberts, 2009) and animal literature (Sánchez-Tójar et al., 2022) emphasizing that personality describes temporally repeatable individual differences in behavior.

Decomposing the degree of personality in behavior due to RN intercepts $\mathrm{var}(\boldsymbol{\mu})$ or slopes $\mathrm{var}(\boldsymbol{\beta})$ is often crucial for functional interpretation of ongoing selection on behavioral consistency and plasticity across environments (Dingemanse et al., 2010; Dingemanse and Araya-Ajoy, 2015; Martin and Jaeggi, 2022). Nevertheless, the total **heritable variance** $\mathrm{var}(\boldsymbol{\eta}_A)$ underlying personality $\mathrm{var}(\boldsymbol{\eta})$, which combines heritable effects across all RN parameters influencing trait expression, will determine the adaptive potential of behavior (see Eqs. 2–5, B7a-b below). Estimating and comparing $\mathrm{var}(\boldsymbol{\eta})$ and $\mathrm{var}(\boldsymbol{\eta}_A)$ is, therefore, an essential tool for explaining variable rates of adaptation within and across social systems. Personality research will also benefit from greater emphasis on estimating $\mathrm{var}(\boldsymbol{\eta})$ because interpretation of the variance attributable to RN intercepts $\mathrm{var}(\boldsymbol{\mu})$ can be highly sensitive to centering of measurements and the overall shape of the RN (Schielzeth and Nakagawa, 2022). Given that the magnitude of environmental variation $\mathrm{var}(\boldsymbol{x})$ and repeatable behavioral effects $\mathrm{var}(\boldsymbol{\mu})$ and $\mathrm{var}(\boldsymbol{\beta})$ may also change across measurement contexts (e.g. through experimental manipulation, developmental effects, or ecological change), the total magnitude of personality $\mathrm{var}(\boldsymbol{\eta})$ in behavior may also differ within the same (sub)populations of individuals across space and time. Similar considerations apply to the context-specific heritable variance $\mathrm{var}(\boldsymbol{\eta}_A)$ of reaction norms (Eq. 2).

on highly plastic social behaviors. We have also argued throughout this section that, irrespective of methodology, greater attention is needed to the interplay between personality and plasticity in contextualized behaviors expressed during fitness-relevant social interactions. The individual differences captured by standard sociability assays or Big Five measures are clearly important for investigating common mechanisms of behavior across species and societies. However, they are also likely to miss much of the heritable variation available to selection on naturally occurring behaviors expressed during mating, predation, offspring care, and other fitness-relevant social contexts. Developing causal models that explain adaptive individual differences directly in these behaviors, rather than merely predicting them with standard personality trait scores, is thus a crucial target for future research.

Studying the evolution of personality in multifaceted and ecologically relevant social behaviors, whether in humans or animals, is of course a challenging enterprise; not least because variation in and correlations between social behaviors are modified across organisms' lifespans by plasticity in response to local social environments (Bergmüller and Taborsky, 2010; Smaldino et al., 2019). Plasticity in social behavior can thus make it particularly challenging to differentiate the evolution of personality from developmental variation caused by heterogeneity in social environments (van Leeuwen et al., 2018; Mitchell and Houslay, 2021). The fitness consequences of personality in social behavior are in turn predicted to be contingent on the current state of the environment, including the personalities of social partners, generating nonlinear patterns of frequency- and density-dependent selection across space and time (Araya-Ajoy et al., 2020; McNamara and Leimar, 2020; Wright et al., 2018). Social interactions can even alter the rate and direction of adaptive behavioral evolution across generations (McGlothlin et al., 2010; Bijma, 2011). These challenges make it particularly difficult to accurately measure the underlying causal structure of and heritable variation in traits that are highly responsive to social interactions (Bijma, 2014; Hadfield and Thomson, 2017; Martin and Jaeggi, 2022).

Thus, despite a strong theoretical emphasis on the role of social environments in generating, modifying, and maintaining personality (Webster and Ward, 2011; Montiglio et al., 2013; Dingemanse and Araya-Ajoy, 2015), much is currently unknown about the adaptive evolution of personality in social behavior, particularly for species such as humans and other primates with multifaceted and developmentally plastic personality structures. As argued above, ecologically grounded behavioral methods and behavioral reaction norm models will be crucial for effectively addressing the limitations of standard sociability assays and subjective rating methods, as well as for distinguishing between personality, person perception, and the underlying mechanisms of social behavior. However, personality scientists will also need to adopt a more general evolutionary theory of social behavior to effectively compare findings across social systems, as well as to account for the role of plasticity in shaping personality development and evolution in human societies. We describe such a theory–the theory of social evolution–in the following section and consider its general application to understanding personality evolution (Fig. 1).

## 3. Social evolution of personality

### 3.1. Explaining personality in cooperation and conflict

#### 3.1.1. Adaptation of social interactions

The field of social evolution has made major advancements in our understanding of how and why complex social interactions have evolved. It should, therefore, be crucial for understanding why personality persists in human and animal social behavior. Classical models in evolutionary biology did not account for the effects of social interactions on adaptation, often assuming that mating is random, social partners are unrelated, and phenotypes are unaffected by the social environment. As a consequence, they failed to explain how costly social behaviors (e.g. food and information sharing, alloparenting and reciprocity, teaching and cultural learning, alarm calling and collective defense, division of labor and leadership) could evolve by natural selection. These issues have been addressed by models and theory of social evolution (Hamilton, 1964; Frank, 1998; Okasha, 2006; Bourke, 2011; Marshall, 2015; Rubenstein and Abbot, 2017; West et al., 2021).

Recent social evolutionary models of quantitative traits (Box 2) emphasize the importance of measuring four key parameters in social interactions to understand population adaptation: the heritable association between individuals and their social partners (often termed *relatedness* or *assortment*), their mutual effects on one another's behavior (*social plasticity* or *responsiveness*), and the effects of personality on an individual's fitness (*non-social selection*) and on the fitness of their social partners (*social selection*; Bijma and Wade, 2008; McGlothlin et al., 2010). From a variety of modeling frameworks (Marshall, 2015; Kay et al., 2020; McGlothlin et al., 2022), these parameters have been used to make powerful theoretical generalizations and empirical predictions of adaptation in social behavior, which have found strong empirical support across all domains of life (Rubenstein and Abbot, 2017; West et al., 2021), uncovering general principles governing the formation, maintenance, and transformation of social groups (Bourke, 2011). A once narrower focus on the evolution of kin-based interactions has also expanded to account for the many alternative pathways by which organisms' phenotypes and fitness can become associated in social environments (Queller, 2011), including by behavioral plasticity (Moore et al., 1997; Wolf et al., 1998; Bijma and Wade, 2008; McGlothlin et al., 2010; Dingemanse and Araya-Ajoy, 2015; Bailey et al., 2018; Araya-Ajoy et al., 2020).

Explaining the adaptation of personality in social behavior requires quantifying how behavior affects individual fitness in a particular environment, represented by the non-social selection gradient $\beta_N$, as well as how it affects the fitness of social partners in that environment, represented by the social selection gradient $\beta_S$ (see Box 2). These quantities provide an evolutionary basis for functional descriptions of social behavior, which can be meaningfully compared across humans and other animals and used to test theory of convergent evolution in personality. In particular, a social behavior is *cooperative* in a particular environment if it enhances the fitness of social partners ($\beta_S > 0$), either in an altruistic ($\beta_N < 0$) or mutually beneficial ($\beta_N > 0$) manner, or *conflictual* if it decreases the fitness of social partners ($\beta_S < 0$), either in a spiteful ($\beta_N < 0$) or selfish ($\beta_N > 0$) manner. Of course, we will often not be able to directly measure lifetime fitness consequences of a behavior in the wild across multiple developmental environments, hindering accurate predictions of microevolutionary change (Franklin and Morrissey, 2017). Nevertheless, in the absence of such long-term fitness data, proxies and short-term approximations of $\beta_N$ and $\beta_S$ are often useful for organizing and testing models in comparative research, e.g. by defining context-specific cooperation operationally through rewards provisioned in an ecologically valid experimental game, or through predicted short-term energetic or thermoregulatory effects observed in the field. The fitness consequences of behavior may also repeatedly vary spatially and temporally across social environments within individuals' lifetimes, so that behavioral reaction norms evolve to express plasticity in specific cooperative and conflictual behaviors across different environments (Wright et al., 2019; de Villemereuil et al., 2020; Haaland et al., 2021). Therefore, similar to sociability, generalized cooperativeness and conflictualness may not be underpinned by the same mechanistically or developmentally integrated traits within individuals across time. However, this will generally not be an issue for comparative research on adaptive personality in social behavior, as adaptive explanations are principally concerned with the fitness consequences rather than the mechanistic causes of personality in particular environments.

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**Box 2**
The social evolution of complex behaviors.

Behaviors are said to be genetically 'complex' when they are responsive to the environment and regulated by a large number of genes, complicating simple population genetic models based on a few alleles (Hill, 2010). Many social behaviors are highly complex in this sense, with recent genome-wide association studies confirming the long-held expectation that most human traits are influenced by direct and indirect effects from thousands of alleles, each of which tends to have an extremely small and indiscernible effect on observable outcomes in any particular environment (Visscher et al., 2017; Mathieson, 2021). Evolutionary quantitative genetics provides a framework for modeling the microevolution of such complex traits as a continuous stochastic process, where patterns of inheritance and adaptation can be effectively described using simple population parameters such as additive genetic means and (co)variances and phenotypic selection gradients (Walsh and Lynch, 2018; Walsh and Morrissey, 2019). These parameters can be estimated empirically and used with theorems of social evolution to make predictions about the adaptive evolution of any social behavior (McGlothlin et al., 2010; Queller, 2011).

The Price equation, perhaps the most fundamental theorem in evolutionary biology (Queller, 2017), provides very general insights into the evolution of complex social behaviors. For simplicity, we ignore any nonrandom environmental change ("transmission bias") between generations, focusing attention solely on the consequences of natural selection for evolution of the mean phenotype in a population over time (see Frank, 2012; Okasha and Otsuka, 2020 for more thorough treatments). In this case, the mean change in some behavior $z$ is a function of the covariance between heritable effects on this trait $z_A$ and individuals' relative fitness $w$ within the population.

$$\Delta \bar{z} = \text{cov}(z_A, w) = \frac{\text{var}(z_A)}{\text{var}(z)} \text{cov}(z, w) = h^2 s \tag{B4}$$

For complex traits with highly polygenic underpinnings, we will generally not be in a position to measure selection directly on heritable variation but will instead measure selection on phenotypes and assume that genetic effects on fitness are mediated through these phenotypes (Hadfield and Thomson, 2017). In this case, adaptive evolution can be decomposed into a differential $s$ capturing the strength of selection on behavior $z$ and the heritability $h^2$ of the behavior i.e. the proportion of phenotypic variance in $z$ attributable to additive genetic effects. This shows that adaptation will only occur in proportion to the amount of heritable variance underlying phenotypes experiencing selection. Understanding how environments shape genetic expression and phenotypic selection of traits are thus two distinct but highly complementary research goals in evolutionary biology.

Explaining these processes is less straightforward for social traits, as heritable variance in $z$, as well as phenotypic selection on $z$, may not be solely attributable to the direct effects of an individual's genes (or any other heritable factors due to niche construction and cultural evolution, Danchin, and Wagner, 2010; Danchin et al., 2011; Fogarty and Wade, 2022). This can be seen by using a social selection analysis (Wolf et al., 1998), where we regress the vector of individual $j$'s relative fitness $w_{jk}$ (mean-scaled so that the average fitness is 1; Lande and Arnold, 1983), on their behavior $z$ and the behavior $z_k'$ of their social partner $k$.

$$w_{jk} = 1 + \beta_N z_j + \beta_S z_k' + e_{jk} \tag{B5}$$

where $e_{jk}$ is a residual uncorrelated with $z_j$ and $z_k'$. In this case, the response to selection is given by (Wolf et al., 1998)

$$\Delta \bar{z} = \text{cov}(z_A, w) = \text{var}(z_A)\beta_N + \text{cov}(z_A, z')\beta_S \tag{B6}$$

The term $\text{cov}(z_A, z')$ quantifies the heritable association between an individual's genetic trait value and the phenotype of their social partner. If there is no heritable association among social partners' traits, i.e. $\text{cov}(z_A, z') = 0$, then social selection $\beta_S$ will have no impact on the adaptation of behavior. However, if social partners are repeatedly associated through behavioral or environmental mechanisms, then selection on social partners can magnify, inhibit, or even reverse the effects of non-social selection alone (Fisher and McAdam, 2019; McGlothlin and Fisher, 2022). The heritable association $\text{cov}(z_A, z')$ can be influenced both by assortment within the population (e.g. kin-biased interactions, spatial aggregation, or partner choice) and plasticity toward the social environment (Wade & Bijma, 2008; McGlothlin et al., 2010; Araya-Ajoy et al., 2020). Quantifying how social interactions influence selection on and expression of individual traits is, therefore, crucial for understanding the evolution of complex behaviors within a social system.

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While cooperation and conflict have received relatively less attention than sociability and aggression in the empirical literature, previous studies have found that personality in a diverse range of cooperative behaviors is widespread across animals (Bergmüller et al., 2010). For instance, long-term field research has found heritable and temporally repeatable individual differences in wild meerkats' (*Suricata suricatta*) babysitting, pup feeding, and sentinel behavior (Houslay et al., 2021), independently of well-known determinants of cooperativeness such as sex, age, and dominance status (Carter et al., 2014). Long-term studies across multiple chimpanzee (*Pan troglodytes*) populations have similarly shown personality in males' hunting behavior, with some males being highly motivated to hunt and catalyze group hunting as compared to other males of similar age (Gilby et al., 2015). Research on humans has also demonstrated the importance of personality in individuals' tendency to cooperate in daily life and experimental games (e.g. Oda et al., 2014; Schroeder et al., 2015; Thielmann et al., 2020).

As argued above, while it is clearly important to understand individual differences in association, proximity, and position within social networks, neither the causes nor the fitness consequences of the various traits labeled as 'sociability' are expected to be consistent across taxa, because sociability is not a robustly defined phenomenon either functionally or mechanistically. Although the label 'sociability' is often useful for describing behavioral syndromes of taxon- or clade-specific social behaviors (e.g. Koski, 2011; Martin et al., 2019), it is difficult to see how continued emphasis on sociability as a target of comparative research can inform generalizable theories of adaptation in social behavior. However, by focusing on individual differences in cooperation and conflict, as functionally defined by their consequences, personality studies can more directly inform longstanding questions and ongoing empirical work into the social evolution of individuality in behavior (Fig. 1).

### 3.1.2. Integrating individuality and sociality

West et al. (2015) identified six organizing questions in current research on major transitions in individuality throughout the history of life, from the origins of multicellularity to the emergence of eusocial insect societies. They suggest that explaining individuality requires attention to the ecological and evolutionary drivers of cooperative group (i) formation and (ii) transformation, (iii) division of labor, (iv) communication and group-level coordination, (v) conflict reduction, and (vi) mutual dependence. All major transitions in biological individuality, from cells to animals to superorganisms, were shaped in part by adaptation of individuality within populations, as natural selection favored cooperators or cheaters and defectors (e.g. Waite and Shou, 2012; Pilakouta et al., 2018; Özkaya et al., 2018), task specialists or generalists (e.g. Kassen, 2002; Wu et al., 2018; Cooper et al., 2021), and group- or solitary-living organisms (e.g. Bilde et al., 2007; Lutermann et al., 2013; Ohkubo et al., 2018). As described above, modes of communication, coordination, competition, and task specialization can also vary extensively within populations, providing raw material for adaptive social evolution. The comparative study of personality in social behavior can thus be a crucial source of empirical evidence for understanding the ecological and evolutionary processes shaping variation among animal societies.

Based on these considerations, we suggest that the current emphasis on generalized personality traits (e.g. sociability, agreeableness, aggressiveness, and extraversion) should be supplemented by greater attention to evolutionary models of personality in context-dependent cooperation and conflict (Fig. 1). In addition to providing clearer functional definitions and theoretical predictions, social evolutionary theory can also inform the selection of fitness-relevant behavioral traits for comparative research. Synthesizing across a large body of comparative research, Rubenstein and Abbot (2017b) suggest that the evolution of animal societies can be best described along four axes of variation in group structure (solitary, pair-living, group-living), reproductive structure (single or multiple reproductives), alloparental care (presence or absence), and genetic structure (high or low relatedness). These dimensions closely mirror the four components of social organization (group size, composition, pattern), social structure (group interactions and communication), mating system (who mates and who reproduces), and care system (who cares and how much) that are used to define societies in the comparative study of social complexity (Kappeler, 2019). Synthesizing the organizing questions in the evolutionary study of individuality and sociality will provide exciting opportunities for future research, which can further develop ecological theory on the role of adaptive personality in the evolution of human and animal societies. For instance, comparative phylogenetic studies across cats and dogs (*Carnivora*; Dalerum, 2007), even-toed ungulates (*Artiodactyla*; Jaeggi et al., 2020), and primates (*Primata*; Olivier et al., 2022) have demonstrated ubiquitous intraspecific and intrapopulation variation in social organization, with differences in whether and how much individuals decide to overlap with potential mates or neighbors across space and time. This capacity for individual variation and plasticity in social organization may facilitate rapid adaptation to novel environments favoring distinct social interactions (Schradin, 2013), highlighting the importance of understanding when and why personality will be maintained in the behaviors underpinning social complexity.

Social evolutionary theory also provides important tools for theoretical inference that have been largely overlooked in the personality literature. In particular, the theory of *interacting phenotypes* (Moore et al., 1997; Wolf et al., 1998; Bijma et al., 2007; McGlothlin et al., 2010) provides so-called indirect genetic effect (IGE) models for estimating the effects of social plasticity on the inheritance and expression of phenotypes (Moore et al., 1997; McGlothlin and Brodie, 2009; Bijma, 2011, 2014; Fisher and McAdam, 2019), as well as social selection models for quantifying fitness effects caused by social interactions and predicting their evolutionary consequences (Wolf et al., 1998, 1999; Bijma and Wade, 2008; Bijma, 2010; McGlothlin et al., 2010, 2022; McGlothlin and

Fisher, 2022). These methods have been extensively reviewed elsewhere and previously introduced in the behavioral ecological literature (e.g. Dingemanse and Araya-Ajoy, 2015; Santostefano et al., 2017; Bailey et al., 2018; Araya-Ajoy et al., 2020). Nevertheless, IGE and social selection models are still rarely applied in personality research, suggesting that their theoretical importance for the field remains underappreciated. In the next sections, we review insights gained from theory of interacting phenotypes to explain the importance of IGEs and social selection for understanding the inheritance and adaptation of personality in social behavior. Along the way, we also explore the relationship between evolutionary game theory, personality, and quantitative genetics (Box 3), following recent work by McGlothlin et al. (2022), and encourage further avenues of empirical research to test adaptive theory of social niche specialization in human and animal societies.

## 3.2. Personality and social plasticity

### 3.2.1. The role of behavioral plasticity in social evolution

As is explained in Box 2, social selection $\beta_S$ will only influence adaptation if there is an association between the total heritable component of individuals' phenotype $z_A$ and the phenotype $z'$ of their social partners, so that $\text{cov}(z_A, z') \neq 0$. This reflects the fact that genetic relatedness among social partners, causing $\text{cov}(z_A, z') > 0$, is a powerful promoter and stabilizer of cooperation (Marshall, 2015; Kay et al., 2020; West et al., 2021). Heritable associations can arise in social interactions from processes of partner assortment, where individuals with similar personalities either tend to aggregate in space or non-randomly select one another as partners for interaction (e.g. Class and Dingemanse, 2022; Holtmann et al., 2022; Tamin and Doligez, 2022). Assortment may, for example, be adaptive among mates due to the benefits of behavioral similarity for compatibility, coordination, synchrony, and problem-solving in cooperative interactions (Schuett et al., 2010; Fu et al., 2012; Koski and Burkart, 2015). Consistent with this expectation, personality similarity has been repeatedly demonstrated to enhance reproductive success in monogamous pair bonds (e.g., Gabriel and Black, 2012; Harris and Siefferman, 2014; Laubu et al., 2016). Personality similarity has also been found to predict friendship among unrelated chimpanzees (Massen and Koski, 2014) and brown capuchin monkeys (*Sapajus* sp.; Morton et al., 2015), suggesting that behavioral compatibility enhances the cooperative benefits of close social bonds beyond kin and mates (Massen et al., 2010). Personality similarity has also been found to predict friendship formation in human adolescence (Borghuis et al., 2017) and friendship and romantic partnerships in adulthood (Youyou et al., 2017).

The consequences of relatedness and assortment are well appreciated by personality scientists. However, less attention has been given to the role of behavioral plasticity in generating heritable associations among group members, irrespective of kinship, partner choice, and habitat selection. Responsiveness to social environments (i.e. social plasticity) generates feedback between direct genetic effects on individuals' behavior and the indirect genetic effects (IGEs) of their behavior on the behavior of social partners (Moore et al., 1997; Bijma, 2011; Araya-Ajoy et al., 2020). As a consequence, social selection on partner behavior may influence behavioral adaptation even in random interactions with unrelated individuals, due to $\text{cov}(z_A, z') > 0$ (McGlothlin et al., 2014). This means that many mutually beneficial behaviors in humans and other animals with low average group relatedness (Clutton-Brock, 2002; Hill et al., 2011; Riehl, 2013) may not simply have byproduct social effects due to non-social selection, as has often been historically assumed (e.g. Connor, 1995); in the presence of behavioral plasticity and IGEs causing feedback in the environment, social selection can further shape personality in behavior.

### 3.2.2. Social plasticity and indirect genetic effects

The effects of social plasticity on heritable variation can be estimated using social reaction norms (Dingemanse and Araya-Ajoy, 2015;

Strickland et al., 2021; Martin and Jaeggi, 2022), which build on standard behavioral reaction norms (Box 1) to account for phenotypic and genetic feedback across repeated interactions in social environments. Social reaction norms are not only relevant for phenomenologically social behaviors, such as grooming or aggression that involve direct physical contact with others, but also for any trait that contributes to the expression of and selection on social partners' behavior. Building on Eq. (B2), consider personality in some behavior (reaction norm trait value $\eta$), modeled as a function of individuals' mean behavioral tendency (intercept $\mu$) and social plasticity (slope $\Psi$) toward the reaction norm $\eta'$ of their social partner. For simplicity, we begin by assuming that there is only personality in mean behavior $\mu$, with $\Psi$ being fixed at the population level (i.e. no personality in and thus no evolution of plasticity). In this case, the expected context-specific trait value for individual $j$ while interacting with partner $k$ is given by

$$\eta_{jk} = \mu_j + \psi\eta'_{kj} \tag{1a}$$

It is standard to scale the model so that $-1 < \psi < 1$ and to assume that $\mu$ is centered on zero. In a symmetric interaction, the same reaction norm describes the social partner's repeatable behavior such that

$$\eta'_{kj} = \mu'_k + \psi\eta_{jk} \tag{1b}$$

The social reaction norm slope $\Psi$ is often called an interaction coefficient and quantifies repeatable behavioral change in response to the social environment (Bailey and Desjonquères, 2022). The feedback effects of $\psi\eta'$ are thus referred to as indirect effects, as opposed to direct effects proportional to $\mu$ that are independent of variation in social partners (McGlothlin and Brodie, 2009). Substituting Eq. (1b) into Eq. (1a) and solving for the focal individual's trait value shows how reaction norms feedback on one another during social interactions. In particular, the repeatable behavior of individual $j$ is given by

$$\eta_{jk} = \frac{\mu_j + \psi\mu'_k}{1 - \psi^2} \tag{1c}$$

The numerator reflects the initial effect of interaction among the focal individual $j$ and social partner $k$, where each exhibits plasticity toward the other's mean behavioral tendency. The denominator quantifies how social plasticity further feeds back on the trait value: positive social plasticity ($1 > \psi > 0$; e.g. due to reciprocity, reinforcement and investment, and/or synergy), magnifies personality in due to, which is the expected behavioral tendency independent of measured variation in the social environment; negative social plasticity ($-1 < \psi < 0$; e.g. due to punishment, specialization, or diminishing returns), can also dampen or reverse personality attributable to intercepts $\mu$ by shifting individuals away from their average tendency. More specifically, the magnitude of personality within a particular social environment (i.e. the variance of reaction norm trait values var($\eta$), see Box 1) is regulated by $\psi$ such that

$$\text{var}(\boldsymbol{\eta}) = \text{var}(\boldsymbol{\mu})\frac{1 + \psi^2}{(1 - \psi^2)^2} \tag{2}$$

for randomly assorted social partners (Moore et al., 1997). This simple model can be easily extended to account for feedback within larger social groups using the average group size and trait value, as well as among multiple distinct behavioral traits (see McGlothlin et al., 2010). The reaction norm slope can also be further decomposed to investigate the consequences of individual differences in social impact versus responsiveness for observed social plasticity across environments (Araya-Ajoy et al., 2020; de Groot et al., paper in the same special issue). Empirical studies of $\psi$ will also need to use appropriate study designs and mixed effects models to account for dynamic measurement error among social partners' observed behaviors (Bijma, 2014; Koster et al., 2015; Martin and Jaeggi, 2022), which has been ignored here for theoretical clarity.

Estimating feedback effects from social plasticity is crucial for accurately testing developmental and adaptive explanations of context-specific personality. Researchers failing to account for how $\psi$ changes $\mu$

may overattribute personality to repeatable individual factors independent of variation in the social environment (i.e. direct effects). This risk is particularly high in species with high levels of social plasticity such as humans and other primates, further emphasizing the importance of distinguishing between descriptive and explanatory models of behavioral traits (Briley et al., 2019). For example, extensive but often predictable variation exists across human societies in cultural norms regulating reciprocity and punishment, marriage and childcare, collective action and production, and various other domains of social interaction (e.g. Boyd et al., 2011; Kelly, 2013; Ringen et al., 2019; Martin et al., 2020; Henrich and Muthukrishna, 2021; Boyd and Richerson, 2022; Lehmann et al., 2022). Permanent indirect effects on personality may, therefore, be caused by local heterogeneity in $\psi$, arising from cultural and ecological variation among groups within a population (e.g. Gurven et al., 2008; Leeuwen et al., 2018). Cultural evolution and niche construction can also change the institutions and norms regulating social plasticity in human societies (Powers, van Schaik, and Lehmann, 2021; Fogarty and Wade, 2022), rapidly shaping personality by modifying both selection and the magnitude and direction of feedback effects on behavior.

### 3.2.3. Heritable variance of personality due to social environments

Behavioral plasticity has long been thought to play a central role in driving evolutionary change (Mayr, 1959; Wcislo, 1989; West-Eberhard, 2003; Chenard and Duckworth, 2021; but see Huey et al., 2003; Oostra et al., 2018), such as by facilitating the colonization of new habitats (Price et al., 2003; Wang and Althoff, 2019) or accelerating reproductive isolation and speciation (Nonaka et al., 2015). When personality is underpinned by heritable effects (including those caused by non-genetic factors, Danchin and Wagner, 2010; Danchin et al., 2011; Fogarty and Wade, 2022), $\psi$ can also facilitate rapid eco-evolutionary feedback (Hendry, 2016; Lion, 2018; Govaert et al., 2019) by enhancing the adaptive potential of behavior in environments that promote social plasticity (Kazancıoğlu et al., 2012; Bailey and Kölliker, 2019; Araya-Ajoy et al., 2020; Bailey et al., 2021). Understanding the quantitative genetics of social reaction norms is thus crucial for explaining the role of social environments in the adaptation of behavior. Assuming a simple additive decomposition of personality, the total heritable trait value $\eta_A$ for individual $j$ is given by (Moore et al., 1997; Bijma, 2011)

$$\eta_{Aj} = \frac{\mu_{aj}}{1 - \psi^2} + \frac{\psi\mu_{aj}}{1 - \psi^2} = d_j + i_j \tag{3}$$

Where $\mu_{aj}$ is the heritable component of an individual's expected behavior independent of variation in the social environment (i.e. reaction norm intercept $\mu$), which interacts with local plasticity to determine an individual's total direct genetic effect $d_j = \frac{\mu_{aj}}{1 - \psi^2}$ on their own phenotype. The indirect effect $i_j = \frac{\psi\mu_{aj}}{1 - \psi^2}$ contributes to an individual's total genetic trait value $\eta_A$ because of feedback caused by plasticity in the social environment toward their trait value $\psi\mu_{aj}$, and is thus an IGE mediated by the social interaction (McGlothlin and Brodie, 2009; Bijma, 2014).

The role of $\psi$ and attendant IGEs in shaping $\boldsymbol{\eta}$ challenges perspectives that interpret personality as evidence of developmental constraints on plasticity (cf. Sih et al., 2004). In many social systems, personality may be a consequence of rather than constraint on social plasticity. Yet study designs in human behavioral genetics in particular have often focused on readily measured, high-level proxies of environmental variation, such as income, educational status, and religious background, that fail to capture more localized social interactions shaping fitness and behavior. For example, among a large Ugandan cohort, unmeasured spatial interactions were found to account for a sizable proportion of the heritability estimated in bodily condition, liver function, blood pressure, and other pertinent health traits (Heckerman et al., 2016). Evolutionary social scientists should thus take greater caution in biologically

interpreting heritability estimates of personality, particularly in models that do not account for the interaction between culturally contingent social reaction norm slopes and environmental conditions (Briley et al., 2019; Uchiyama et al., 2021). Environmental conditions are also likely to shape genetic (co)variance in personality across a much broader range of taxa (Mitchell and Houslay, 2021), warranting further comparative research on the interplay between developmental and social plasticity in shaping the heritable variance of personality.

Taking these insights together, we can finally consider the consequences of assortment, social plasticity and IGEs for adaptation via social selection (see Box 2). In particular, for a single behavior expressed in a symmetric social interaction (McGlothlin et al., 2010, 2022), we expect for phenotypic assortment $\beta_\alpha$ and social plasticity $\psi$ to each contribute to the total heritable variance in personality $\mathrm{var}(\boldsymbol{\eta}_\mathrm{A})$ as well as the association $\mathrm{cov}(\boldsymbol{\eta}_\mathrm{A}, \boldsymbol{\eta}')$ between individuals' genetic trait values for personality $\boldsymbol{\eta}_\mathrm{A}$ and the personality $\boldsymbol{\eta}'$ of their social partners, such that

$$\mathrm{var}(\boldsymbol{\eta}_\mathrm{A}) = \mathrm{var}(\boldsymbol{\mu}_a)\frac{1 + \beta_\alpha\psi}{(1 - \psi)(1 - \psi^2)} \qquad (4a)$$

$$\mathrm{cov}(\boldsymbol{\eta}_\mathrm{A}, \boldsymbol{\eta}') = \mathrm{var}(\boldsymbol{\mu}_a)\frac{\beta_\alpha + \psi}{(1 - \psi)(1 - \psi^2)} \qquad (4b)$$

under the assumption that heritable assortment or relatedness $r$ (Hamilton, 1964; Marshall, 2015) is proportional to and mediated through repeatable phenotypic assortment among social partners (Martin and Jaeggi, 2022). Substituting these quantities into Eq. (B6) in Box 2, the adaptive response to selection on personality in a given environment is then estimated by (McGlothlin et al., 2010)

$$\Delta\bar{\eta} = \mathrm{var}(\boldsymbol{\eta}_\mathrm{A})\beta_\mathrm{N} + \mathrm{cov}(\boldsymbol{\eta}_\mathrm{A}, \boldsymbol{\eta}')\beta_\mathrm{S} = \mathrm{var}(\boldsymbol{\mu}_a)\frac{(1 + \beta_\alpha\psi)\beta_\mathrm{N} + (\beta_\alpha + \psi)\beta_\mathrm{S}}{(1 - \psi)(1 - \psi^2)} \qquad (5)$$

Empirical systems will often violate the assumptions of this simple model, with social feedback being attenuated by additional factors such as the time-dependent and iterative nature of interactions, group sizes, distinct classes of social partners, and the indirect effects of other interacting behaviors (see McGlothlin et al., 2010; Bijma, 2014; Trubenová et al., 2015; Martin and Jaeggi, 2022; McGlothlin et al., 2022 for further discussion). Nevertheless, its simplicity clearly demonstrates a more general theoretical result—that assortment and social plasticity both contribute to the heritable (co)variance observed in personality, as well as the response to social selection on personality (Fig. 1; Box 3, Fig. B1), and thus determine the adaptive potential of social behavior, commonly referred to as **evolvability** (Kirschner and Gerhart, 1998; Hansen and Pélabon, 2021). Quantifying the magnitude of both $\beta_\alpha$ and $\psi$ for heritable social behaviors is thus crucial for future personality research. Currently, the evolutionary consequences of IGEs caused by $\psi$ remain largely overlooked in both the human and animal literature (see Santostefano et al., 2016; Santostefano et al., 2017 for notable exceptions). Ignoring such forms of gene-by-environment interaction can inflate estimates of direct genetic or environmental effects on behavior, depending on study design, leading to overconfidence in the consistency of behavior across social environments (Beam and Turkheimer, 2013; Briley and Tucker-Drob, 2017; Kandler et al., 2019). Failure to account for $\psi$ and its potentially non-random variation within a population may,
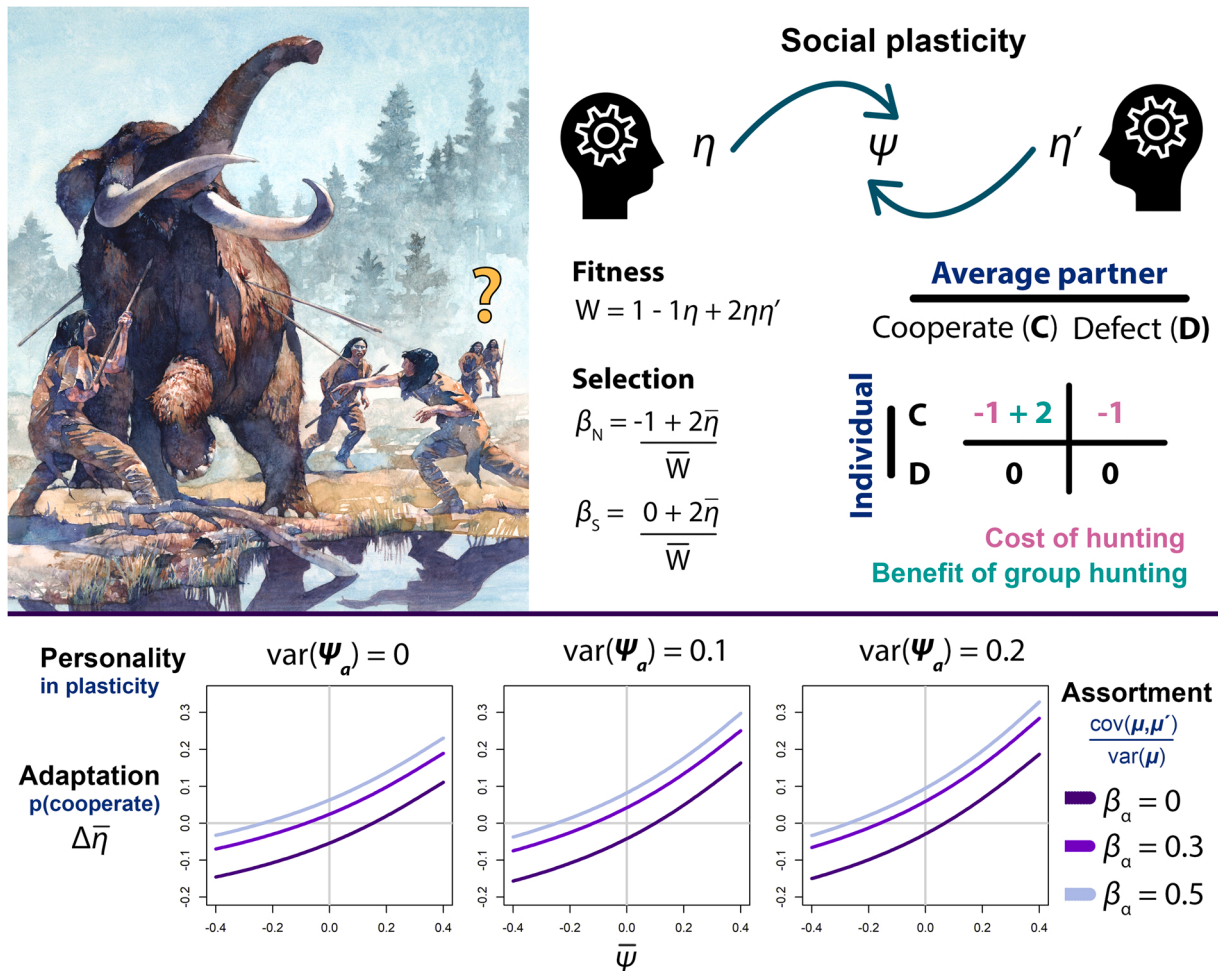


**Fig. B1.** Evolution of cooperation in costly group hunts. ***note.*** *Hunting a Mastodon* by artist Greg Harlin has been freely used and modified with written permission for non-commercial purposes.

therefore, be an important but overlooked source of bias in heritability estimates from standard quantitative genetic models of human and animal personality.

### 3.2.4. Personality in social plasticity enhances evolvability

Finally, while we have thus far assumed social plasticity to be constant (Eqs. 1–5), individual differences have also been found in various forms of social plasticity across taxa. For instance, male water dragons (*Intellegama lesueurii*) have been found to repeatedly differ in the plasticity of their social behavior toward the local density and sex ratio of conspecifics (Strickland and Frère, 2019). Similarly, consistent individual differences have been documented in male water striders' (*Aquarius remigis*) tendency to change activity level in the presence of competitors (Montiglio et al., 2017), as well as in both male and female chimpanzees' propensity to use social information from group mates across experimental tasks (Watson et al., 2018). The social reaction norm model of context-specific personality (Eq. B2 in Box 1) can thus be expanded to account for personality in reaction norm slopes

$$\eta_{jk} = \mu_j + (\psi + \psi_j)\eta'_{kj} \tag{6}$$

where individual-specific social plasticity $\psi_j$ is expressed as a deviation from the population average slope (see Dingemanse and Araya-Ajoy, 2015; Martin and Jaeggi, 2022 for details on estimating these models with empirical data). Allowing for variation in social plasticity, i.e. $\mathrm{var}(\psi) > 0$, further modifies the total magnitude of heritable variance $\mathrm{var}(\boldsymbol{\eta_A})$ and covariance $\mathrm{cov}(\boldsymbol{\eta_A}, \eta')$ in personality, facilitating potentially even more rapid adaptation and eco-evolutionary feedback in response to social selection (Box 3). It also provides scope for selection directly on social plasticity across environments (Scheiner, 1993; Kazancıoğlu et al.,

2012). For instance, game theoretic models suggest that negative frequency-dependence between responsive ($\psi \neq 0$) and unresponsive ($\psi = 0$) strategies can lead to the maintenance of adaptive personality in social plasticity (Wolf et al., 2011). Even in conditions of positive frequency-dependence, which are expected to diminish adaptive personality, mechanisms generating personality in social plasticity can shift the direction and pace of evolutionary change (see Box 3). Evolution of $\psi$ has also been experimentally demonstrated for sexual display traits in fruit flies (*Drosophila serrata*; Chenoweth, Rundle, and Blows, 2010), motivating further attention to the role of social plasticity as a driver of eco-evolutionary feedback in social environments.

Deriving further analytic results for the heritable variance and response to selection on social reaction norms is cumbersome, due to the interaction between changes in mean behavior (intercepts $\mu$) and social plasticity (slopes $\psi$). Nevertheless, it is helpful to see that adaptation of the reaction norm with fixed social plasticity (Eq. 5) is proportional to the factor $\psi \Delta \bar{\mu}_a$, capturing heritable change in mean behavior $\Delta \bar{\mu}_a$. In turn, adaptation of the social reaction norm with personality in plasticity (Eq. 6) is further proportionally magnified by heritable changes in social plasticity $\Delta \bar{\psi}_a \bar{\mu}_a$ and their interaction with heritable changes in mean behavior $\Delta \bar{\psi}_a \Delta \mu_a$ (see Kazancıoğlu et al., 2012; Araya-Ajoy et al., 2020; Martin and Jaeggi, 2022 for details). This means that personality in social plasticity, i.e. temporally repeatable individual differences in responsiveness to social partners, can further change the evolvability of behavior. This occurs because personality in plasticity generally increases the total magnitude of heritable (co)variance in reaction norms, as compared to when plasticity is fixed in the population (see Box 3), further increasing the importance of social effects for explaining behavioral evolution. See Fig. B1 for a visual demonstration of this phenomenon in the context of a well-known evolutionary game. A

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**Box 3**
Personality and social plasticity shape behavioral adaptation.

A worked example is shown in Fig. B1 for the decision (?) to take part in or defect from costly group hunts in a human society. Individuals exhibit social plasticity $\psi$ and can adjust their probability of cooperation $\eta$ in response to the average probability of cooperation among fellow hunters $\eta'$. The fitness consequences of the decision to cooperate or defect are described by a simple payoff matrix: participation in group hunting (C) has direct costs due to energy invested and the risk of bodily injury or death ($-1$), but it also has synergistic benefits when social partners cooperate and collectively take down large prey ($+2$). Defection (D) has no direct costs but also no benefits, as the returns of dangerous hunts are not shared with defectors. Defection is adaptive in high defection social environments, while cooperation is adaptive in high cooperation environments. These payoffs introduce positive frequency-dependent dynamics, as is characteristic of stag hunt or assurance games in evolutionary game theory (Van Cleve, 2017).

Over time, adaptive personality is expected to be diminished by selection driving either cooperation or defection to fixation. However, any phenotype x environment interactions that cause personality in behavior may change the direction and rate of adaptation. This can be seen by translating the payoff matrix into a quantitative genetic model for the probability of cooperation, following McGlothlin et al. (2022). This model predicts whether adaptive social evolution will increase or diminish group hunting under specific conditions. The bottom plot of Fig. B1 demonstrates how variation in the population average social plasticity $\bar{\psi}$ (x-axis), degree of personality in plasticity $\mathrm{var}(\psi)$ (left-to-right plots), and phenotypic assortment ($\beta_\alpha$) (colored lines) influence adaptive evolution to increase ($\Delta \bar{\eta} > 0$) or decrease ($\Delta \bar{\eta} < 0$) cooperation (y-axis). The upward movement of the lines in response to increasing levels of $\beta_\alpha$ and $\mathrm{var}(\boldsymbol{\psi_a})$ demonstrates that these factors increase the range of conditions under which cooperation can evolve.

Results assume that the population begins relatively risk-averse, with an intrinsic probability of cooperation $\bar{\mu}_a = 0.4$, so that individuals have a slightly higher chance (p = 0.6) of defecting on average. Individuals are also assumed to have a moderate degree of personality in their heritable tendency to cooperate $\mathrm{var}(\mu_a) = 0.3$, independently of social plasticity. Following McGlothlin et al. (2010) for Eq. 6, the total heritable (co)variance in reaction norms with personality in plasticity is given by

$$\mathrm{var}(\boldsymbol{\eta_A}) = \mathrm{cov}\big((\mathbf{I} - \boldsymbol{\psi_a})^{-1}\boldsymbol{\mu_a}, (\mathbf{I} - \boldsymbol{\psi}\boldsymbol{\psi}')^{-1}(\boldsymbol{\mu} + \boldsymbol{\psi}\boldsymbol{\mu}')\big) \tag{B7a}$$

$$\mathrm{cov}(\boldsymbol{\eta_A}, \eta') = \mathrm{cov}\big((\mathbf{I} - \boldsymbol{\psi_a})^{-1}\boldsymbol{\mu_a}, (\mathbf{I} - \boldsymbol{\psi}\boldsymbol{\psi}')^{-1}(\boldsymbol{\mu}' + \boldsymbol{\psi}'\boldsymbol{\mu})\big) \tag{B7b}$$

for an instantaneous interaction in a single phenotype, where $\boldsymbol{\Psi}$ and $\boldsymbol{\Psi}'$ indicate diagonal matrices of individual and partner RN slopes and $(\mathbf{I} - \boldsymbol{\Psi_a})^{-1}$ is the additive genetic trait value (see Moore et al., 1997; McGlothlin et al., 2010 for further details and multivariate extensions). Exact (co)variances cannot be calculated for ratios of random variables but can be approximated with simulation. We use this approach in Figure B1, showing how personality in social plasticity further magnifies the heritable (co)variance among social partners, as compared to the evolutionary response in the presence of fixed plasticity (Eq. 5).

worked example is used to show how personality, social plasticity, and assortment influence adaptation of cooperative hunting behavior under positive frequency-dependent selection. These results emphasize that empirical studies failing to estimate among-individual variation in $\psi$ as well as direct or indirect selection on $\psi$ will often fail to accurately predict the phenotypic response to selection. Following the results of McGlothlin et al. (2022), the example also demonstrates fundamental relationships between evolutionary game theory and quantitative genetic approaches to explaining personality in social behavior.

### 3.3. Niche specialization and social selection

#### 3.3.1. Personality via social niche specialization

To explain adaptive personality in social behavior, it is necessary to know how social environments shape heritable variance in personality as well as how they affect selection on personality. As reviewed above, while extensive evidence exists of non-social selection $\beta_N$ on personality, the social selection gradient $\beta_S$ has rarely been quantified in comparative personality research. A notable exception is provided by recent work on Eastern chipmunks (*Tamias striatus*), where females of high docility have been shown to reduce the fitness of other female neighbors (i.e. negative social selection; Santostefano et al., 2020). Failure to account for social selection terms may not only lead to inaccurate estimates of the response to selection on personality as shown above (Eq. 5), but also biased estimates and interpretation of non-social selection (Morrissey et al., 2012). Evolutionary genetic models suggest that adaptive plasticity is favored when selection on behavior shifts predictably in response to environmental heterogeneity within individuals' lifetimes and the physiological costs of changing behavior are not too high (Gavrilets and Scheiner, 1993; De Jong, 1995; Haaland et al., 2021). Therefore, we should expect mechanisms of adaptive social plasticity in personality to reflect the shifting costs and benefits of social behavior in particular contexts. The evolutionary study of social plasticity and social selection are thus closely allied, with selection on $\psi$ expected to occur in response to predictable changes in $\beta_N$ and $\beta_S$ across social partners and environments. Despite a lack of attention to quantifying these parameters, evolutionary models of personality have emphasized the importance of positive feedback loops for promoting the emergence and adaptive maintenance of individual differences in behavior. Collectively, these models are referred to as state-behavior feedback models (Sih et al., 2015), also known as models of facultative calibration in the human sciences (Lukaszewski and Roney, 2011; von Rueden et al., 2015). In contrast to the typical usage of 'state' within psychology (see Steyer et al., 1999), behavioral ecologists use the term 'state' to describe any variable that alters the fitness costs and benefits of an organism's actions (Houston and McNamara, 1999). States that tend to exacerbate rather than reduce differential fitness outcomes (i.e. those that produce positive rather than negative behavioral feedback processes) should facilitate the maintenance of personality, as individuals who adaptively respond to initially differing states will develop more pronounced differences over time (McElreath et al., 2007; Sih et al., 2015).

The theory of social niche specialization predicts that the availability and fit of local niches, as well as the density and frequency of behavioral strategies within social groups, are central states moderating selection on personality in social behavior (Montiglio et al., 2013). Social niche specialization is a broad term referring to the emergence of personality by means of individuals occupying consistently distinct social roles (Bergmüller and Taborsky, 2010), thus encapsulating many specific forms of niche specialization such as reproductive and non-reproductive division of labor that have been extensively studied in the field of social evolution (e.g. Bourke, 2011; West et al., 2015; Cooper and West, 2018; McNamara and Leimar, 2020; Cooper et al., 2021). Therefore, the adaptive evolution of social roles, which are the specific tactics individuals employ in relation to social challenges, is likely to be caused by many distinct individual and group-level processes that can optimize

interactions with social partners. Social niche specialization may thus be adaptive for several reasons (Bergmüller and Taborsky, 2010; Montiglio et al., 2013; Loftus et al., 2021): because individuals benefit from focusing on tasks that are best suited to their initial traits and preferences, such as through enhanced learning or task-specific proficiency; because it reduces the costs of conflict with group members who are competing for common niches, and/or because it enhances synergies and marginal benefits between group members who specialize.

Much of the work on personality via social niche specialization has been theoretical, but a few important empirical studies have also provided direct or indirect support for the hypothesis that persistent interactions drive specialization in social behavior. For instance, among closely related species of shrew (*Neomys* and *Sorex*), group-living species have been found to exhibit a greater magnitude of personality in agonistic behavior than solitary species, suggesting that group-living promotes niche specialization in aggression (von Merten et al., 2017). Repeated interactions with conspecifics can also promote personality in aggressive behavior among southern field crickets (Jäger et al., 2019). Experimental work in primitively eusocial wasps (*Ropalidia marginata*), solitary sweat bees (*Lasioglossum spp.*), and clonal raider ants (*Ooceraea biroi*) has further shown that increasing group size can spontaneously generate non-reproductive division of labor, which can subsequently enhance nest guarding, homeostasis, and productivity (Tate Holbrook et al., 2009; Brahma et al., 2018; Ulrich et al., 2018). The process of specialization itself may also additionally function to enhance positive feedback between personality and social roles over time. In a resource-defense context, for example, with high costs for fighting, individuals are expected to also benefit from consistency in and signaling of aggressiveness toward potential competitors (Botero et al., 2010; Dall et al., 2004). These considerations can be extended to dominance hierarchies in species where the acquisition of dominance facilitates enhanced access to female sexual partners, which are often vigilantly defended from subordinates (e.g. Cornwallis and Birkhead, 2008). In domestic fowl (*Gallus gallus domesticus*), personality is exhibited across both dominant and subordinate males in their tendency to produce territorial calls. Not only do more frequent vocalizers tend to become more dominant, but the acquisition of dominance in itself increases the frequency of vocalizing, such that personality in territorial calling and attendant dominance behaviors (e.g., vigilance toward conspecifics) will tend to be enhanced across development due to positive feedback with social status (Favati et al., 2014).

#### 3.3.2. Social niche specialization in human societies

Personality psychologists have also extensively documented the importance of state-behavior feedback processes in social environments, often termed 'person-environment transactions', for maintaining the developmental stability of human personality (Caspi et al., 2005; Mõttus et al., 2017; Kandler et al., 2019). For instance, conscientiousness is a well-established predictor of academic achievement in industrialized societies, often explaining more variance in academic outcomes than general intelligence (Kappe and van der Flier, 2012). In a 12-month study of German high school students, students who graduated and began transitioning into adult life experienced appreciable increases in conscientiousness. Moreover, these gains were largest in students who invested more in their academic achievement, suggesting a positive feedback process between conscientiousness and academic achievement (Bleidorn, 2012). Evidence that conscientiousness mediates the effects of education and work experience on career success (Ng and Feldman, 2010) further indicates that such processes—particularly during major social role transitions (Bleidorn, 2015)— are likely to have long-term effects on the stability and variability of conscientiousness observed within industrialized societies. These findings are further complemented by socioecological models of human personality discussed above, which have begun to integrate the effects of niche specialization and social niche complexity to explain why personality structure varies across societies (Lukaszewski et al., 2017; Gurven, 2018; Smaldino et al., 2019).

Indirect evidence of the importance of niche specialization for human personality also comes from extensive longitudinal and behavioral genetic research in early adolescence and adulthood. These studies show steady increases in the rank-order stability of personality across early childhood and adolescence followed by a plateau in middle adulthood (Briley and Tucker-Drob, 2014; Borghuis et al., 2017). Mõttus et al. (2017) demonstrated that across both US and Russian cohorts, variance in personality increased and subsequently plateaued from early childhood into late adolescence. Similar study designs following cohorts into late adolescence and adulthood have not observed consistent differences in personality variance (Mõttus et al., 2016), suggesting that the shift from juvenile to adult social roles marks a critical transition for establishing the degree of personality within a population.

Briley and Tucker-Drob (2014) conducted a meta-analysis to evaluate the heritability and degree of genetic and environmental effects on personality development across the lifespan. Consistent with decades of research on various complex human traits (Polderman et al., 2015), the heritability of personality was found to be moderate across development, supporting the importance of genetic effects on human personality (Sanchez-Roige et al., 2018). Nonetheless, as expected by social niche specialization theory, as well as the closely related social investment theory in social psychology (Roberts et al., 2005; Bleidorn, 2015), environmental effects on personality also become more pronounced in older individuals (Briley and Tucker-Drob, 2014). Current behavioral genetics research, therefore, suggests that environmental exposures, particularly non-shared environmental exposures, are key to understanding personality development from adolescence into adulthood (Briley and Tucker-Drob, 2017). Recent studies of Norwegian twins further pinpoint the importance of gene x environment interactions in explaining these observed increases in environmental effects and the overall magnitude of personality into adulthood (Kandler et al., 2019). These interactions likely reflect the importance of social plasticity and feedback on personality during this critical period of human development.

More generally, human life history is characterized by a rare coupling of relatively short interbirth intervals, early weaning, and large birth size with slow maturation, late puberty, persistent alloparental care, and an elongated post-reproductive lifespan (Mace, 2000; Kramer, 2010; Gurven et al., 2012; Miller et al., 2019; Martin et al., 2020). These traits support a long period of somatic investment across juvenility, where individuals engage in an appreciable degree of cultural learning and complex skill acquisition (Tomasello, 2016; Legare, 2017; Del Giudice, 2018) while also undergoing extensive brain and bodily development (Blakemore, 2008; Dorn and Biro, 2011; Herting and Sowell, 2017). As expected from embodied capital theory, which extends traditional life history theory to account for somatic investments beyond body size (e.g. brain size, strength, and skills), the costs of this prolonged investment period tend to be offset by later benefits accrued through high levels of productivity in adulthood, using decades of acquired foraging knowledge to cooperatively access high-quality and difficult-to-acquire resources (Kaplan et al., 2000, 2001; Kaplan et al., 2009). In addition, investments across development in other forms of embodied capital such as physical strength, technical skill, formal education, prestige, and creativity begin to reap the benefits of social support and reproductive success across adulthood (e.g. Gurven and Von Rueden, 2006; Nettle and Clegg, 2006; von Rueden et al., 2008, 2011; Apicella, 2014; Smith et al., 2017). Human juvenility can, therefore, be seen as a period for developing the investments necessary to acquire and capitalize upon adult social roles, wherein individuals employ their skills and knowledge to produce food, acquire friends and mates, care for others, and function as a competent member of their culture and social group. Integrating this evolutionary anthropological perspective with the behavioral genetic research reviewed above suggests that social niche specialization likely plays a crucial but currently underappreciated role in the evolution of human personality (Smaldino et al., 2019; Hunt and Jaeggi, 2022). Greater emphasis on directly testing the theory

of social niche specialization within human societies is thus an important target for future empirical research.

### 3.3.3. Social selection for niche specialization

Verbal models of social niche specialization have largely emphasized direct benefits of personality for individual fitness, irrespective of its consequences for the fitness of social partners. However, as explained above, in many cases we expect that the costs and benefits of social niche specialization will be further affected by social selection, due to social plasticity in behavior as well as variation in the frequency of personalities and density of group members in the local environment. Among guppies (*Poecilia reticulata*), for example, individuals' foraging success is contingent both on their own degree of boldness and on the boldness of other fish in the shoal. Both bold and shy individuals perform better in mixed rather than highly bold or shy shoals respectively (Dyer et al., 2008), potentiating negative frequency dependent selection on this behavior. Aggressiveness among fruit flies (*Drosophila melanogaster*) has similarly been shown to experience negative frequency dependent selection, but only at medium and high group densities (Kilgour et al., 2018).

Frequency-dependent selection can be understood as a form of interaction between social and non-social selection, both in dyads such as mated pairs or larger groups such as neighborhoods, coalitions, and herds. In particular, for personality $\eta_j$ of focal individual $j$ expressed in social group $k$ with average personality $\bar{\eta}'_k$, the interactive selection gradient $\beta_I$ can be introduced to quantify how non-social and social selection shift in response to the joint trait value $\eta_j\bar{\eta}'_k$ of individuals and their average social partners within groups (Westneat, 2012; Araya-Ajoy et al., 2020; Dingemanse, 2021; Martin and Jaeggi, 2022). Modifying Eq. B5 accordingly, the social selection model for the relative fitness $w$ of individual $j$ given by

$$w_{jk} = 1 + \beta_N\eta_j + \beta_S\bar{\eta}'_k + \beta_I(\eta_j\bar{\eta}'_k) + e_{jk} \tag{7}$$

See Box 2 for further details on model assumptions. The model shows that the sign and strength of social $\beta_S\bar{\eta}'_k$ and non-social $\beta_N\eta_j$ selection can vary as a consequence of synergy (i.e. positive frequency dependence, $\beta_I > 0$) or antagonism (i.e. negative frequency dependence; $\beta_I < 0$) between the trait values of individuals and their social groups. The magnitude of these effects may also be density-dependent, further shifting patterns of selection across social environments. As previously discussed, these density-dependent effects are likely to be particularly important for explaining variation in and the emergence of non-reproductive division of labor (e.g. Tate Holbrook et al., 2009; Brahma et al., 2018; Ulrich et al., 2018), as the marginal benefits of behavioral specialization tend to increase in larger groups (Nakahashi and Feldman, 2014). Variation in density is also likely to be crucial for explaining the maintenance of life history variation within populations, including cooperative or conflictual behaviors that enhance reproductive potential or buffer environmental risk (Wright et al., 2019). These effects can be further introduced to the model with interactive density effects $\beta_D$ contingent on the density $d_k$ of the social group or local population

$$w_{jk} = 1 + \beta_N\eta_j + \beta_S\bar{\eta}'_k + \beta_I(\eta_j\bar{\eta}'_k) + \beta_{D_N}(d_k\eta_j) + \beta_{D_S}(d_k\bar{\eta}'_k) + \beta_{D_I}(d_k\eta_j\bar{\eta}'_k) + e_{jk} \tag{8}$$

Assuming $d_k \geq 0$, it can be seen that group density increases the strength of negative frequency-dependent selection when $\beta_I < 0$ and $\beta_{D_I} < 0$.

Interactive frequency- and density-dependent effects on fitness mean that selection on personality should vary in response to spatiotemporal changes in the composition of social groups across time (whether through stochastic, ecological, or evolutionary processes). This provides ample opportunity for empirical research to detect and directly test theories of frequency- and density-dependent selection within social environments. It also means that $\psi$ may often evolve to track these

changes in fitness optima and in the process promote adaptive niche specialization. Fluctuating and balancing selection on behavior, driven principally by variation in the social environment, may thus be a crucial mechanism for the maintenance of adaptive personality. While many theoretical models have suggested that negative frequency-dependence is important for the maintenance of individual differences in social behavior (Bergmüller and Taborsky, 2010; Dingemanse and Wolf, 2010; Wolf and Weissing, 2010), little to no empirical research on personality has directly measured $\beta_I$ or its interaction with $\beta_{D_I}$ across space and time. Fortunately, simulations suggest that modest sample sizes can be used to detect such interactive selection effects with sufficient repeated sampling and variability in social interactions (Martin and Jaeggi, 2022). Therefore, we end by calling for future comparative research to better integrate the quantitative study of social plasticity, niche specialization, and selection on personality, which will be crucial for more directly testing adaptive theory and accurately predicting processes of social evolution in the wild.

## 4. Conclusion

In this perspective, we critically evaluated the current state of evolutionary science on personality in social behavior. Despite great empirical success, we argued that research has been limited by a lack of integration with the broader study of social evolution in humans and other animals. This divide is exacerbated in part by unique measurement challenges and conceptual issues in comparing personality across species and societies, which have inhibited successful efforts to combine human and animal research. Animal studies have overemphasized simple and experimental measures of sociability, often failing to capture more multifaceted and ecologically valid forms of social interaction, while human studies have relied too much on subjective and retrospective ratings that easily obscure plasticity in behavior. Research in both fields has also lacked empirical attention to the role of social environments in shaping heritable variance in and the fitness consequences of personality, despite a strong theoretical foundation. This makes current methods prone to bias when estimating the heritability and response to selection on social traits.

To address these challenges, we introduced social reaction norms and applied some fundamental insights from the theory of social evolution relevant for personality research. We proposed that comparative studies should focus less on methodological standardization of personality measures, particularly for generalized latent traits such as sociability and extraversion, turning more toward the investigation of personality in contextualized forms of cooperation and conflict. Comparative research has also lacked sufficient attention to the role of social environments in shaping the inheritance and adaptation of personality. We showed how IGEs caused by social plasticity and personality in plasticity can dramatically magnify heritable variance and the evolvability of behavior, potentiating an evolutionary response to social selection even in the absence of assortment and genetic relatedness. Finally, to more directly address adaptive theory of social niche specialization in humans and other animals, we called for greater attention to quantifying variation in social selection across space and time, particularly due to frequency- and density-dependence. In summary, by focusing on the measurement of personality in ecologically relevant forms of cooperation and conflict, as well as temporal variation in IGEs and social selection on these traits, personality scientists will be positioned to make important contributions to the study of social evolution in complex behaviors more generally.

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