ethology
international journal of behavioural biology

Ethology

CURRENT ISSUES - PERSPECTIVES AND REVIEWS

Evolutionary Perspective on the Interplay Between Family Life, and Parent and Offspring Personality

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(Invited Review)

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Received: January 12, 2010
Initial acceptance: March 10, 2010
Final acceptance: April 25, 2010
(J. Schneider)

doi: 10.1111/j.1439-0310.2010.01793.x

Abstract

Consistent inter-individual variation in behaviour over time and across contexts has been reported for a wide variety of animals, a phenomenon commonly referred to as personality. As behavioural patterns develop inside families, rearing conditions could have lasting effects on the expression of adult personality. In species with parental care, conflicts among family members impose selection on parental and offspring behaviour through coadaptation. Here, we argue that the interplay between the evolution of personality traits (i.e. boldness, exploration, activity, aggressiveness and sociability) expressed outside the family context and the specialized behaviours expressed inside families (i.e. offspring begging behaviour and parental response to offspring solicitations) can have important evolutionary consequences. Personality differences between parents may relate to the typically observed variation in the way they respond to offspring demand, and dependent offspring may already express personality differences, which may relate to the way they communicate with their parents and siblings. However, there has been little research on how personality relates to parental and offspring behaviours. Future research should thus focus on how and why personality may be related to the specialized parent and offspring behaviour that evolved as adaptations to family life.

Introduction

Across the animal kingdom, individuals of the same species differ in their propensity to take risks, explore new environments, and to be active, aggressive or sociable; these behaviours are often correlated across individuals. Behaviours showing inter-individual variation but are consistent within individuals through time and across contexts are coined ‘personality’. When different personality traits are correlated across individuals, they are considered ‘behavioural syndromes’ (Sih et al. 2004; Réale et al. 2007; Biro & Stamps 2008; Sih & Bell 2008). Thus, while personality might exist in many populations, syndromes are often environment specific (e.g. Bell 2005; Dingemanse et al. 2007). Among the main research questions raised by this expanding field are how the covariances in behavioural traits are genetically and environmentally generated, how they are maintained evolutionarily, and what is their selective value under different ecological and social contexts (Dall et al. 2004; Sih et al. 2004; Réale et al. 2007; Sih & Bell 2008; Dingemanse et al. 2010; Schuett et al. 2010; Stamps & Groothuis 2010). Considering the family context, both as a potential source of (co) variation in behaviours and as a source of selection for combinations of behaviours expressed inside and outside the family context (i.e., ‘correlational selection’; e.g., Brodie 1992) should shed new light on these three main questions.

Research on personality aims at conceptualizing from an evolutionary perspective, the common phenomenon that individuals differ markedly and consistently in behaviour. This implies that individuals are less flexible than would be expected under optimality and game-theoretical models (e.g. Arnqvist & Henriksson 1997). Surprisingly, the link between personality expressed outside the family context and behaviours expressed during parent–offspring and sib–sib interactions have rarely been considered from an evolutionary viewpoint (but see Sih & Bell 2008). There are studies from a proximate viewpoint in humans focussing on social and psychological impacts of family life on the development of personality (e.g. Belsky 1984; Denissen et al. 2009; Prinzie et al. 2009).

Behaviours expressed inside families such as offspring begging and parental responsiveness to these signals represent specialized adaptations to family life, which have (co)evolved through conflict and coadaptation (Trivers 1974; Godfray 1995; Mock & Parker 1997; Moore et al. 1997; Kölliker et al. 2005, 2010). Even though the family is a particular environment of interacting individuals, it is analogous to the ecological environment, and the specialized behaviours inside and outside the family context are not necessarily independent. For instance, the analogy of offspring begging to a foraging task has been pointed out repeatedly, in particular with regard to the competition among bird nestlings for favourable positions in the nest (Slagsvold 1997; Kölliker et al. 1998). Given the contextual analogy, one may expect selection to favour particular physiological and behavioural mechanisms to be at least partly shared across these environments, although the expressed behaviours can be specialized to foraging tasks within (i.e. begging) or outside (i.e. foraging) the family context. Hence, bold and shy individuals may differ as offspring in terms of their begging (a form of foraging for parental provisioning) and as adults in both their provisioning effort and the usual foraging tasks (e.g. Michelena et al. 2009). Furthermore, because bold parents and shy parents differ in risk-taking behaviour to find food, which in turn can affect the amount of food provided to offspring, selection is expected to favour particular combinations of personality and provisioning effort. This would generate correlational selection (Brodie 1992) on personality and parental provisioning. Such correlational selection would select for phenotypic or genetic correlations between personality and parental provisioning.

If such dependencies evolve, individual personalities may play a role in how parent–offspring conflicts are resolved as a constraint because they represent a component of the expressed phenotypic variance on which selection from this conflict acts. On the other hand, parent–offspring conflict resolution may alter the development of personality expressed at adulthood (Loehlin 1992). This argument is of potentially great importance because currently the evolution of personality and family interactions are largely studied separately.

In this article, we develop the hypothesis that personality expressed in parents and their offspring influences the evolution and resolution of conflicts occurring among family members, resulting in adaptive integration of behaviours expressed during and outside family life. As parents can vary in their sensitivity to offspring begging signals (Kölliker & Richner 2001), we discuss the hypothesis that personality expressed outside family life relate to or influence parental care styles (Wilson et al. 1994; Roney et al. 2006), thereby exerting selection on the behavioural and evolutionary dynamics of family interactions. We thus expect coevolution between the usual personality traits (boldness, exploration, activity, aggressiveness and sociability) and behaviours occurring in the family context (i.e. offspring begging signals and competitive behaviour and parental effort and response to begging). To illustrate our arguments, we review the literature on the link between parent–offspring conflict and personality.

Personality in the Context of Interactions among Family Members

In humans, personality is usually considered as a relatively consistent disposition inherent in the individual that regulates the expression of activity, reactivity, emotionality and sociability. The key feature of personality, whether it first appears at a young age or at adulthood, is that although the environment and social contexts can modulate personality (which could be sensitive to age, size, sex and condition), individual differences persist across situations and through time (e.g. Kagan et al. 1988; Johnson & Sih 2007). To obtain a multi-dimensional measure of personality, five categories have been defined including an axis ‘shyness–boldness’ (i.e. reaction to risky situations), ‘exploration–avoidance’ (i.e. reaction to a new situation), ‘activity’ (i.e. in a non-risky and a non-novel environment), ‘aggressiveness’ (i.e. level of agonistic reaction to conspecifics) and ‘sociability’ (i.e. tendency to seek out social interactions) (Réale et al. 2007).

We do not claim that offspring begging behaviour and the associated parental response are personality traits. Instead, we argue that the aforementioned personality traits are expected to be functionally related to specialized behaviours expressed in the family, and thereby have the potential to influence (and be influenced by) the evolution and resolution of family conflicts. Of particular importance is to determine whether parent and offspring personality determines parental effort to broods/litters and food distribution among the progeny, and whether family interactions influence the ontogeny of personality. In the following, we propose a non-exhaustive list of personality traits for dependent offspring and their parents that might interact with offspring begging behaviour and parental response to offspring solicitations.

Personality in Dependent Offspring

Aggressiveness is well known to influence the outcome of sibling competition over resources. Aggressive individuals may compete physically to monopolize parental attention, while subordinate siblings may adopt sneaky behaviour to obtain food without being physically aggressed (Drummond 2006). These two strategies may coexist within the same family in species where dependent offspring possess armaments (claws, sharp bill or powerful jaws), and where parents do not have full control over within-family food allocation.

Siblings may also vary in their level of activity, a behaviour that could affect sib–sib interactions, with active individuals moving more often than less active siblings. Active individuals may prevent siblings to rest because of disturbance and they may also be more vigilant by watching out for their parent's return. This behaviour, independently of the specialized begging behaviours, may increase the probability of being fed before nest-mates at the cost of enhanced alertness (Roulin 2001). In birds, nestlings compete by jostling for the nest position where parents predictably deliver food (e.g. Kölliker et al. 1998). Active individuals may thus be more prone to reach better nest position than passive siblings. Alternatively, the level of activity may be traded off against signalling as these two activities may be energetically costly.

Dependent offspring are not always confined to a limited space where parents deliver resources, that is, a nest or cavity. Species where offspring are not confined in a nest have been referred to as 'mobile feeding systems' (Manser et al. 2008) and display different behavioural dynamics than species or situations where offspring are forced to compete over parental resources in a limited space. Explorative offspring may obtain more resources either because parents are unpredictable in the location where they give food or because offspring can obtain resources from alien parents that are widely dispersed. A similar situation occurs in altricial birds after young have taken their first flight (e.g. Redondo et al. 1995; Roulin 1999), in mammals (Roulin 2002), and in sub-social insects where offspring can leave their nest burrow and forage independently or join other family groups (Smiseth et al. 2003; Kölliker & Vancassel 2007). As shown in the great tit (*Parus major*), offspring born from explorative parents moved longer distances between nest of fledging and nest of first breeding (Dingemanse et al. 2003). It would be interesting to investigate whether personality of parents is associated with the duration of parental care (Nilsson & Svensson 1993), which should affect the strength of selection from the interaction with the parents on the specialized begging behaviours.

Personality in Parents

Inter-individual differences in parental effort are commonplace, and evidence for inter-individual differences in parental responsiveness to offspring signals of need are accumulating (Kölliker & Richner 2001). Recent studies suggest that these differences may be associated with personality traits. In the great tit, parents who quickly and superficially explore a novel environment take more risk to protect their offspring than parents who explore the same environment slowly but thoroughly (Hollander et al. 2008). Pairs composed of slow- or fast-exploring mates produced fledglings in better condition than when one parent was fast-exploring and its mate slow-exploring (Both et al. 2005). This observation is interesting because if dependent offspring have to adjust begging behaviour to the personality of their parents, offspring may more easily adopt the correct behaviour if both parents display similar personality. Possibly, this may explain why assortative pairing with respect to personality is expected to have a selective advantage over disassortative pairing. In laboratory mice (*Mus musculus*), individuals selected for aggression nursed and groomed their pups more, and rested less alone, than mothers selected for non-aggressive behaviour (Benus & Röndigs 1996). In the convict cichlid (*Cichlasoma nigrofasciatum*), behavioural inhibition (i.e. shyness) is associated with low levels of parental care (Budaev et al. 1999). Thus, aggressive, bold and less explorative parents appear to give higher weight to the survival of the current offspring than to future reproduction (i.e. the parents' own survival), and they would be expected to be more sensitive to offspring signals of need. This is consistent with a recent model on the evolution of personality through variation in life-history trade-offs (Wolf et al. 2007) and with a meta-analysis showing that bolder animals have increased reproductive success at a survival cost (Smith & Blumstein 2008 but see Dingemanse et al. 2004; Boon et al. 2007 and Cote et al. 2008 showing that in natural populations, there is ample spatio-temporal fluctuations on the fitness consequences of personality). Further studies are needed to examine whether bold, aggressive, social, active and less explorative parents finely adjust feeding rate in relation to variation in offspring need while other parents adopt a more rigid care provisioning system by feeding their offspring at a baseline level independently of offspring need (e.g. Smiseth et al. 2008; Grodzinski et al. 2009; Kölliker et al. 2010). Another interesting aspect to tackle is whether personality differences in the propensity to be aggressive towards family and non-family members are positively (e.g. Maestripieri 1998) or negatively correlated. Parents can be aggressive towards dependent young that persistently beg for food (Horsfall 1984), a property that may vary between parents (e.g. Raihani & Ridley 2008); this parental behaviour would be associated with a tendency for low investment in current reproduction. Conversely, parents can also be aggressive towards unrelated adult competitors and predators; in this case, parental aggressiveness directed against non-family members would be positively associated with the level of investment in current reproduction.

Ontogeny of Personality

Expressed variation in adult personality cannot be fully understood without considering the external and social environments in which they emerged and developed. Thus, the social environmental influence can by partly heritable, generating indirect genetic and environmental effects (Moore et al. 1997) that can strongly affect the evolutionary dynamics of personality. Such effects, from a quantitative genetic perspective, can be studied as gene–environment interactions of behavioural development that are mediated by the social interactions during development (Smiseth et al. 2008; Dingemanse et al. 2010). Evidence that personality is already expressed at the time when offspring are still dependent on parents mainly comes from studies in primates (e.g. Asbury et al. 2003; Barr et al. 2003; Maestripieri et al. 2007), fish (Dingemanse et al. 2009) and one bird species (Fucikova et al. 2009). Inter-individual differences in personality are already detectable before birth (DiPietro et al. 2008) and have long-term persistence afterwards (Kagan et al. 1988) although personality can change over the lifespan (Roberts et al. 2006). Based on studies of human twin siblings, Loehlin (1992) concluded that 40% of the total variance in personality is genetic, 35% is attributable to the non-shared environment and only approx. 5% is linked to growing up in the same family. A review of the literature showed that heritability of behaviour is on average 0.31 (Stirling et al. 2002; see also Réale et al. 2007).

Human siblings often differ in personality, suggesting plastic adjustment of behavioural development to outcomes of family interactions. For instance, firstborns have slightly higher IQs than laterborn siblings suggesting that as families increase in size, parents have less time to devote to each child (Sulloway 2007). Laterborns appear to be more innovative (Saad et al. 2005) and more likely to become homosexual than their older brothers (Blanchard & Lippa 2007). In Japanese quails (*Coturnix japonica*), chicks hatched out from eggs treated with testosterone were bolder than control chicks (Daisley et al. 2005). In great tits, food deprivation applied during the nestling stage significantly altered personality traits at adulthood in individuals issued from experimental lines selected for high, but not for low rates of exploration and aggression (Carere et al. 2005). Studies in rhesus macaques (*Macaca mulatta*) showed the importance of genotype by environment interactions in the ontogeny of offspring behavioural syndromes (Barr et al. 2003); Maestripieri et al. (2007) found that behaviour of females that were cross-fostered shortly after birth was correlated with behaviour of their foster but not biological mother. In sticklebacks (G*asterosteus aculeatus*), the level of perceived predation risk in early life alters the expression of heritable variation in a suite of personality traits indicating genetic variation for behavioural plasticity (Dingemanse et al. 2009; see also Bell & Sih 2007).

In conclusion, genetic background as well as environmental and social conditions prevailing at the stage when dependent on parents can have lasting effects on personality (Arnold et al. 2007; Dingemanse et al. 2010). The environment modulates the expression of personality traits possibly through genetic (Malmkvist & Hansen 2002; Drent et al. 2003), epigenetic (Diorio & Meaney 2007; Kaminsky et al. 2008) and maternal effects (Carere et al. 2005; Daisley et al. 2005), or through the family environment (Cheverud & Moore 1994; Kölliker 2005;

Champagne & Meaney 2006). The previous examples suggest that family interaction can have long-term effect on personality.

Evolutionary Interplay Between Personality and Interactions Among Family Members

The study of animal behaviour has often reduced complex behavioural patterns to the units expressed in a particular functional context in which they evolved to study the adaptive value of traits specialized for particular functions. In contrast, research on behavioural syndromes emphasizes the role of coevolution between multiple traits of individuals during their lifetime and across functional contexts. Offspring behaviours can be partly understood as adaptation to the potentially heritable 'parental provisioning environment' and to their 'sibling behavioural environment', and parental behaviours as adaptation to the 'offspring behavioural environment' (Kölliker 2005), parental and offspring behaviours are expected to coevolve and become coadapted (Wolf et al. 1998; Kölliker et al. 2005). Accordingly, there is increasing experimental evidence for covariation between offspring and parental behaviours, which is either genetically or epigenetically coinherited (Kölliker et al. 2005; Diorio & Meaney 2007; Smiseth et al. 2008; Hinde et al. 2009, 2010).

The model by Wolf et al. (2007) is particularly interesting to further understand patterns of such parent–offspring coadaptation. The model predicts that inter-individual variation in the trade-off between current and future reproduction generates selection to the extent for which individuals should be bold or shy towards predators. If current reproduction weighs more, individuals should be more risk prone, and if individuals weigh current reproduction less than future reproduction, they should take fewer risks to protect their progeny against predators. Parents who weigh current more than future reproduction may provide longer care to the progeny, exerting selection on offspring to stay in the nest for longer periods of time favouring shy and non-explorative offspring. Conversely, parents that weigh future more than current reproduction may terminate care earlier, exerting selection on offspring to leave the nest earlier, thereby favouring bold and explorative offspring. Based on variation in a life-history trade-off, coadaptation theory (Moore et al. 1997; Kölliker et al. 2005, 2010; Smiseth et al. 2008) predicts selection for compatible offspring and parents who match their personality to maximize individual lifetime reproductive success (Bateson 1994). Furthermore, as the balance between the costs and benefits of a particular personality may differ between dependent offspring and parents, parents and offspring may be in conflict over the way personality is expressed.

Stamps (2007) proposed that inter-individual differences in growth rates favour the evolution of personality traits. Compared to slow-growing individuals, faster-growing conspecifics may indeed be selected to take more risks in foraging. This hypothesis is particularly interesting because faster-growing individuals may invest more effort in conspicuous begging signals that attract predators (Haskell 1994) and increase the risk of falling out of the nest in bird species that build nests on the edge of cliffs or in trees (Bize & Roulin 2006). Thus, the hypothesis of a link between personality and life-history traits (Biro & Stamps 2008) highlights the importance of considering personality in the context of interactions between family members. This link may indeed promote the coevolution between personality and begging behaviour and in turn parental response to offspring signals.

The research on parent–offspring conflict has highlighted the importance of offspring signals of need and/or quality for parents to adjust their investment and for offspring to attract parental attention and to compete against siblings (Royle et al. 2002). For instance, avian offspring behave conspicuously when a parent is delivering food by displaying vivid gapes, extending their neck and vocalizing vigorously. These behaviours are more extravagantly expressed when hungry and they increase the likelihood of being fed (Kilner 2002). Given the increasing number of experimental studies reporting an innate, potentially genetic correlation, between offspring begging and parental care styles (Agrawal et al. 2001; Kölliker & Richner 2001; Smiseth et al. 2008), the potential is high that these individual-specific offspring competitive styles and specific parental responsive behaviour are associated with personality. Further experimental research addressing the environmental vs. genetic nature of associations between offspring/parental behaviours and personality will be crucial to test the hypothesis of an adaptive integration of behaviours expressed during family life and animal personality.

In the broad context of parent–offspring conflict, direct measurement of personality in dependent offspring is scant in non-human organisms. Therefore, we can only discuss hypothetical scenarios regarding the potential importance of offspring personality in the dynamics of family interactions and on how personality interacts with specialized begging behaviours to determine success in attracting parental attention to obtain resources. Studies on offspring begging behaviour typically consider that the most socially dominant and conspicuous offspring out-compete their subordinate and reserved siblings. What benefits can an offspring derive from being shy and neither aggressive nor social and active? Alternative personalities may be evolutionary stable if the net benefit of each strategy is the same at an equilibrium frequency achieved under frequency- or density-dependent selection (Wilson et al. 1994; Wolf et al. 2008). Shy individuals may be constantly less conspicuous than bold siblings, and pay a lower cost imposed by competitive behaviours, which require substantial energy but also specific hormones and neurotransmitters having negative side effects. Bold offspring may be pursuing a high-benefit/high-cost strategy, and shy offspring a low-benefit/low-cost strategy with similar net benefits. Because the benefit of the different offspring strategies depends on how parents respond, selection from family conflicts and parent–offspring coadaptation is expected to determine the potential for polymorphism in offspring personality to persist within and among families. A particularly relevant case favouring such polymorphism within families would be in bi-parental species where the two parents show different patterns of parental care. In birds, mothers often provide food to the smallest offspring within their brood more often than fathers (Slagsvold 1997; Lessells 2002), and different parents often vary considerably in their care behaviours.

Personality in parents is not selectively neutral, and its effect on fitness can be sex-specific (Dingemanse et al. 2004; Pruitt & Riechert 2009). For example, in captive animals, bolder males achieve a higher reproductive success at a survival cost (Smith & Blumstein 2008). These relationships still need to be confirmed in natural populations (Réale et al. 2007, 2009). As fathers and mothers are often not equally responsive to offspring begging behaviour (Kölliker et al. 1998; Krebs 2001; Quillfeldt et al. 2004), future studies should test the sex-specificity of personality with respect to parental care and its evolutionary implication on the resolution of both parent–offspring and sexual conflicts. Consistency in behaviour in the two parents may facilitate negotiation over investment in parental care duties to each other's effort (McNamara et al. 1999; Hinde & Kilner 2007). In this context, it would be interesting to investigate the effect on family interactions when one sex is less consistent in behavioural patterns across contexts than the other sex (Budaev et al. 1999; Lessells et al. 2006; Nakagawa et al. 2007) and when pairing with respect to personality associated with parental care duties is not random (Both et al. 2005).

Future Research

The study of personality in the context of parent–offspring conflict necessitates an experimental approach to assess personality traits in relation to offspring begging signals, offspring need (e.g. hunger level) and quality (e.g. competitive ability), and parental effort and response to begging. Here, we propose four major research areas. First, theoretical models of family interactions should incorporate personality to examine the ecological conditions under which offspring and parental personality can emerge and be evolutionary stable. Alternatively, models for the evolution of personality like the one by Wolf et al. (2007) should incorporate family interactions as potential determinants of developmental trajectories towards adult personality. A promising way is an approach based on behavioural reaction norms, which was recently proposed for an integrated study of behavioural evolution (Smiseth et al. 2008; Dingemanse et al. 2010). Behavioural reaction norms allow us to explicitly study both theoretically and experimentally variation and covariation in behavioural phenotypes of which animal personalities may be composed, both as response slopes to social or ecological stimuli, and as intercepts of fixed baseline behaviours (Smiseth et al. 2008 and Dingemanse et al. 2010). From a theoretical perspective, it will be critical to explore the nature of correlational selection on combinations of responsive and baseline behaviours expressed within vs. outside the family context that favours coadaptation among personality and behaviours expressed in the family context. Furthermore, the impact of offspring and parental personality on the resolution of parent–offspring conflict should also be theoretically evaluated (i.e., variation in animal personalities as a constraint on conflict resolution), as well as the effect of selection from parent–offspring interactions on the evolution of personality (i.e., variation in animal personalities as evolved consequence of conflict resolution). Second, empirical studies should investigate whether dependent offspring already express a wide variety of personality traits: how this variation is related to the specialized begging behaviours; how parents respond to them; how offspring adjust the specialized begging signals of need or quality in relation to parental personality. In this context, the results reported in the great tit (Carere et al. 2005) are promising because they show a link between a personality trait and vocal signalling. Third, to test if the benefit of each personality trait depends on its frequency within a family, the proportion of the different personality types could be manipulated with cross-fostering experiments of individual young between families. Finally, a powerful approach is to select breeding lines for alternative adult personality such as boldness and shyness, explorative and non-explorative tendency. Individuals issued from these different lines could then be tested for begging behaviour and parental responses to offspring behaviour (Carere et al. 2005). This approach has already shown that great tits selected for bold personality increase the amount of androgens in eggs (Groothuis et al. 2008). These hormones affect development and begging behaviour (Muller et al. 2007). Such breeding experiments are certainly promising, and more similar studies are needed to better understand the coevolutionary dynamics of personality and parent–offspring behaviours, especially by selecting for begging behaviour.

To conclude, we suggest that the study of personality expressed during and outside family interactions, and their relation to adult personality, is a field wide open to a variety of new experiments and concepts to be developed. Most importantly, personality may be an important criterion along with need and competitive ability that determines parental effort and how resources are allocated among family members.

Acknowledgements

The Swiss National Science Foundation supported the study financially (no. 3100A0_120517 to A. Roulin; no. PP00A-119190 to M. Kölliker). We are grateful to two anonymous referees and Kathryn Hine for useful comments on a previous version of the manuscript.

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