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The ontogeny of personality in the wild guinea pig

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The role of ontogenetic processes for the emergence of personality has received only little attention in the past. One reason for the lack of experimental studies on personality development may be that trait consistency over time is one of the cornerstones of the definition of animal personality, whereas, also by definition, ontogeny deals with change over time. Single traits or correlations between traits may be consistent or inconsistent throughout ontogeny; however, the proximate and ultimate causes are not well understood. Environmental factors acting upon individuals during early ontogeny potentially influence personality development substantially. Early environments may severely constrain but also adaptively shape individuals. We examined the personality development of cavies, *Cavia aperea*, when exposed to increasing and decreasing photoperiod before and after birth. We determined how these predictive environmental cues influenced the development of three behavioural and two physiological traits, their temporal consistency and the correlations between them. We found remarkable plasticity in the development of personality in the cavy, despite a relatively high degree of temporal consistency in most traits. There were stable correlations, some of which became tighter over time, between basal cortisol levels, resting metabolic rate and fearlessness across two different ontogenetic stages. However, we also found that some correlations emerged only after maturation or disappeared over time. Whereas exploration behaviour was tightly correlated with basal cortisol and boldness was correlated with resting metabolic rate, both correlations disappeared in mature animals. Instead, a correlation between exploration and boldness was evident in mature animals. These results call for a broader incorporation of developmental aspects into personality research.

The study of animal personality, that is consistent individual differences that are stable over time and contexts (Réale & Dingemanse, 2012), has rapidly grown over the last few decades as scientists recognized that consistent differences between individuals have important implications for ecology and evolution. Interindividual variation in personality traits has been found to predict dispersal and space use, social and parental behaviour, sexual selection and life history strategies (Réale & Dingemanse, 2012). However, the role of ontogeny for the emergence of personality has received relatively little attention, at least in vertebrates (Stamps & Groothuis, 2010a, 2010b; Trillmich & Hudson, 2011). Recent studies in field crickets, *Gryllus integer*, revealed a strong influence of the rearing density on the development of correlations between personality traits such as aggressiveness and boldness in adult individuals (Niemelä, Vainikka, Lahdenperä, & Kortet, 2012), and they showed a life history-associated difference in the temporal consistency of boldness across two different ontogenetic stages (Hedrick & Kortet, 2012). Better knowledge of the development of personality may enhance our understanding of the ecology and evolution of animal personalities by revealing developmental constraints and possible life history-dependent changes (Groothuis & Maestripieri, 2013). A developmental perspective may also provide cues to underlying proximate, and perhaps age-specific, mechanisms generating personality (Stamps & Groothuis, 2010b; Trillmich & Hudson, 2011).

One main reason for the obvious lack of experimental studies on personality development may be that trait consistency over time is one of the cornerstones of the concept of animal personality, whereas, by definition, ontogeny deals with change over time (West-Eberhard, 2003). To study ontogenetic processes in personality, several personality traits need to be measured in the same individual across different ontogenetic stages and the relations between those traits need to be assessed at each of these stages (Groothuis & Trillmich, 2011). Single traits may be consistent over time if differences between individuals account for a significant proportion of the total variance in a trait (Sokal & Rohlf, 1995). This does not mean that the absolute value of a trait cannot change over time but rather that an individual that expresses a relatively high

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trait value at one age also expresses a relatively high value at a later age (Hinde & Bateson, 1984). Examples of consistent individual differences across ontogenetic stages include aggression in sticklebacks, *Gasterosteus aculeatus* (Bell & Sih, 2007), exploration behaviour in great tits, *Parus major* (Dingemanse, Both, Drent, Van Oers, & Van Noordwijk, 2002), boldness in rats, *Rattus norvegicus* (Roedel & Meyer, 2011) and aggressiveness in European rabbits, *Oryctolagus cuniculus* (Eccard & Rödel, 2011). Just like single traits, correlations between traits may be consistent or inconsistent throughout ontogeny. Correlations between traits may persist across ontogenetic stages even if the traits involved are inconsistent, although it may not necessarily be the same individuals that are more active and more explorative at different ages. If, for example, in two age classes individuals that are more active are also more explorative, we would find a cross-context correlation between these two traits across both ages. However, this will still be the case if an individual that was highly active at one age is less active at another age as long as its exploration behaviour changes accordingly.

If both single traits and correlations between traits are stable across ontogeny, then personality might impose a developmental constraint on the evolution of different personality types (Bell & Stamps, 2004). A tight connection between two temporally consistent traits early in life then limits the extent to which an individual can change its level of trait expression later during ontogeny without simultaneously changing the corresponding trait expression. In addition, this consistent connection between traits may have severe implications for selective processes if selection at one ontogenetic stage produces changes in a different, but correlated, trait later in life. Thus, selection on a particular trait early in life might affect the population wide variation in trait expression of a correlated trait later in life (Bell & Stamps, 2004).

Few studies investigate how correlations between different personality traits change across ontogeny (Bell & Stamps, 2004) or experimentally test how defined conditions at a given ontogenetic stage influence correlations between personality traits at a later stage in life (Bell & Sih, 2007; Dingemanse et al., 2009). Even fewer studies have considered correlated development of behavioural and physiological traits (Guenther & Trillmich, 2013; Naguib, Flörcke, & Van Oers, 2011), although the latter have frequently been shown to be connected to individual differences in behaviour (Groothuis, Müller, Von Engelhardt, Carere, & Eising, 2005; Koolhaas et al., 1999; Réale et al., 2010). The tentative consensus so far appears to be that single behavioural traits that show temporal consistency in adult individuals are not always consistent when compared across different ontogenetic stages and that some correlations between traits remain consistent across ontogeny whereas others surface only at specific ages. The proximate and ultimate reasons for these changes within and between personality traits across ontogeny are not yet well understood.

The genetic make-up of individuals and especially environmental factors acting upon individuals during early ontogeny have the potential to affect personality development substantially (Stamps & Groothuis, 2010a, 2010b). Development of a phenotype that matches specific environmental conditions may be constrained by stressful circumstances in situations in which low resource availability during early life gives rise to stunted, poorly performing individuals (Monaghan, 2008). However, early influences may also adaptively shape individuals according to the environment they are facing (Del Giudice, 2012; Kaiser & Sachser, 2005; Koolhaas, De Boer, & Buwalda, 2006). Depending on their ecological relevance, predictability and temporal consistency, different factors are expected to influence development of personality types as well as temporal consistency in different but predictable ways.

In the current study, we examined the personality development of cavies, *Cavia aperea*, experiencing two different experimental photoperiod treatments. Increasing or decreasing photoperiod, simulating spring or autumn conditions, have been shown to induce differences in the timing of maturation and hence expected life histories in this species, for females (Trillmich, Mueller, Kaiser, & Krause, 2009) and for males (Guenther, Palme, Dersen, Kaiser, & Trillmich, 2014). Individuals born into increasing photoperiod (spring) follow a fast life history strategy with early maturation and fast growth, whereas individuals born into decreasing photoperiod (autumn) delay reproduction and grow more slowly. A field study showed that indeed individuals born early in the year were able to reproduce successfully in their first summer, whereas individuals born late in the year did not start reproduction before the following spring (Kraus, Trillmich, & Künkele, 2005). An experimental study showed that prenatal photoperiodic treatment induced predictable differences in the behavioural and physiological phenotypes of offspring (Guenther & Trillmich, 2013). Offspring of mothers that experienced increasing photoperiod during pregnancy were bolder and more explorative and showed a decreased stress response, whereas offspring of mothers that experienced decreasing photoperiod were shy and nonexplorative and showed an elevated stress response. These differences disappeared after maturation if all offspring were kept under an intermediate photoperiod after birth, indicating a high degree of plasticity in the personality development of this species. In addition, this study found correlations between consistent personality traits only in juveniles but not later in life.

Seasonal environments have been shown to influence the personality type expressed in small rodents, both in the field (Eccard & Herde, 2013) and under laboratory conditions (Pyter & Nelson, 2006). Common voles, *Microtus arvalis*, caught in spring were bolder and more active than individuals caught later in the year (Eccard & Herde, 2013), and male Siberian hamsters, *Phodopus sungorus*, showed more anxiety-related behaviours in an elevated plus maze when kept under short days than when kept under long days (Pyter & Nelson, 2006). Here, we tested how increasing and decreasing photoperiod before and after birth influenced the development of three behavioural and two physiological traits, their temporal consistency and the correlations between them. In contrast to the aforementioned study, in which personality differences disappeared over time, we expected a postnatal photoperiod that exposes the individuals to continuing photoperiodic changes as expected in the natural year to amplify personality differences between juveniles born into these different photoperiods. We also tested whether the photoperiodic treatment affected the temporal consistency of traits and the development of correlations between different traits. Therefore, individuals were tested repeatedly, as juveniles and after maturation, for their exploration behaviour, fearlessness and boldness. Additionally, we measured at the same life stages individual plasma cortisol levels and resting metabolic rates (RMR). We chose these two physiological traits, as both have been shown to be tightly associated with rodent personality traits. For instance, Koolhaas et al. (1999) showed that mice artificially selected for high aggressiveness were highly active and explorative and produced little corticosterone in response to a stressful situation. Energy metabolism, most often measured as RMR, is related to cortisol or corticosterone excretion in a number of rodent species (Careau, Thomas, Humphries, & Réale, 2008) and has been shown to be associated with various personality traits (Careau et al., 2008; Careau, Bininda-Emonds, Thomas, Réale, & Humphries, 2009). For each life stage we tested whether behaviours and physiology correlated with each other. Across both life stages we assessed whether single behavioural and physiological traits were consistent over time and whether the personality structure showed temporal consistency.