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The ontogeny of personality: Repeatability of social and escape behaviors across developmental stages in Siberian hamsters (*Phodopus sungorus*)

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Abstract

Animal personality is defined as behavioral tendencies that are consistent across time and contexts within an individual, but differ across individuals. Studies investigating personality typically examine individuals across short time periods or within a single life stage. Growing evidence suggests that personality may be less stable across life stages, highlighting the need to consider the effects of ontogeny on the expression of consistent behavioral traits. We investigated individual consistency in social and escape behaviors across developmental stages using Siberian hamsters (*Phodopus sungorus*). To determine whether individuals were consistent in these behaviors as juveniles and across developmental stages, we measured male and female social and escape behaviors twice as juveniles and once as adults. Individuals' social scores were significantly repeatable within the juvenile stage, but not across developmental stages. In contrast, escape scores were highly repeatable across developmental stages, with males' scores being more repeatable than females' scores. Our results support previous findings that personality traits, especially those associated with social behavior, are less stable across development, whereas behaviors associated with stress or coping may represent a more permanent feature of an individual's phenotype. Our results also indicate potential sex differences in long-term repeatability of personality. Considering how ontogeny affects animal personality for males and females can provide insight into the evolution and mechanisms that maintain animal personality.

KEYWORDS
aggression, animal personality, avoidance, behavioral consistency, escape, investigation

1 | INTRODUCTION

Animal personality refers to behavioral tendencies that remain consistent across time and context within individuals, but differ across individuals (Cabrera et al., 2021; Réale et al., 2007). Animal personality has been documented across taxa, including mammals (e.g., Koolhaas et al., 1999; Reale et al., 2000), birds (e.g., Groothuis & Carere, 2005; Jacobs et al., 2014), amphibians (e.g., Hedrick & Kortet, 2011; Kelleher et al., 2018), and fish (e.g., Bell & Sih, 2007; Le Vin et al., 2011). Recently, research on animal personality has shifted from documenting its occurrence to understanding its ecological and evolutionary implications (Cabrera et al., 2021). New questions about the underlying mechanisms associated with personality, its adaptive benefits, and evolution (Rodel & Meyer, 2011) provide a more holistic approach (Tinbergen, 1963) to the study of animal personality. However, less attention has been given to ontogeny (Tinbergen, 1963), including sex differences, despite the importance of development in animal behavior (Cabrera et al., 2021; Guenther et al., 2014).

Personality is often examined across short time periods or within a single life stage (e.g., adulthood, Stamps & Groothuis, 2010). However there is growing evidence that personality may be less stable across life stages (Cabrera et al., 2021). Inconsistencies in behavioral traits after maturation have been observed across taxa, including in red junglefowl, (*Gallus gallus* Favati et al., 2016), North American red squirrels (*Tamiasciurus hudsonicus* Kelley et al., 2015), and great tits (*Parus major* Carere et al., 2005). Development is associated with morphological, physiological, and behavioral changes. For example, reaching sexual maturity (i.e., "pubertal transition" Cabrera et al., 2021) is associated with changes in physiological processes (e.g., hormones, Stamps & Groothuis, 2010), body mass, parental care and social affiliations, and new or unpredictable environments (Cabrera et al., 2021; Rodel & Meyer, 2011), which can influence the emergence or stability of personality. In eastern mosquitofish (*Gambusia holbrooki)* personality differences were not observed during early stages of life, but emerged later in development (Polverino et al., 2016), and in wild guinea pigs (*Cavia aperea*), associations between behaviors and physiological traits disappeared after maturation (Guenther et al., 2014). Although some studies have observed behavioral consistency across ontogeny in some traits (e.g., boldness in female cichlids, *Neolamprologus pulcher*, Schürch & Heg, 2010; docility in yellow-bellied marmots *Marmota flaviventris*, Petelle et al., 2013), few studies have investigated personality across ontogeny and of those studies, even fewer have identified consistent trends in behavioral traits across development (Cabrera et al., 2021).

Whether certain personality traits are repeatable across ontogeny could depend on the mechanisms and environmental conditions that mediate those behaviors or could reflect different selective pressures on phenotypic variance (Bell et al., 2009). Behaviors like aggression or sociality, which may be influenced by morphological or physiological mechanisms influenced by ontogenetic changes, may be more repeatable within a life stage (i.e., adulthood) and not across life stages (Bell et al., 2009). For example, in red squirrels, individual aggressiveness was not consistent across ontogeny (Kelley et al., 2015). In zebra finches (*Taeniopygia guttata*), only female aggressiveness was repeatable (Wuerz & Kruger, 2015) while fearlessness was strongly repeatable across all life stages (Wuerz & Kruger, 2015). Differences in repeatability may even be species-specific. In some species boldness and activity tended to be consistent within, but not across life stages (Cabrera et al., 2021; Herde & Eccard, 2013), whereas in other species, activity level (Kanda et al., 2012; Schuster et al., 2017) and boldness (Schuster et al., 2017) were more consistent across development. Additional studies investigating the ontogeny of personality are necessary to identify if certain behavioral traits are more susceptible to developmental changes and to understand the evolution and maintenance of personality (Cabrera et al., 2021; Reale et al., 2000).

We investigated individual consistency in social and escape behaviors across ontogeny using Siberian hamsters (*Phodopus sungorus*), which is an ideal, non-model system in which to test individual consistency in behavioral traits across time. Social and escape behaviors have been well documented in our lab population in both juveniles (Cusick et al., in review) and adults (Cusick et al. in prep; Munley et al., 2021; Scotti et al., 2008; Sylvia et al., 2017), and are comparable to behaviors in wild populations (Ross, 1998). Social (e.g., aggressiveness, investigation) and escape behaviors are commonly measured traits in animal personality (e.g., Cabrera et al., 2021). To determine whether these behaviors were consistent across development, we measured individuals' social and escape behaviors twice as juveniles and then once after they reached adulthood (approximately 40 days later). Our main objectives were to (1) identify individual characteristics associated with differences in social and escape behavior and (2) determine whether individuals were consistent in their social and escape behavior within the juvenile stage (i.e., before the pubertal transition) and across developmental stages (i.e., from juvenile to adulthood).

2 | METHODS

2.1 | Animal housing

Individuals were housed in same-sex pairs in polypropylene cages (28 × 17 × 12 cm) in a 16:8 light:dark photoperiod (light on at 1:00 a.m. EST), with an ambient temperature of 22 ± 2°C and a relative humidity of 55 ± 5%. To identify each individual within a cage, a small patch of fur was shaved on either the right or left side of the hamster. Hamsters had ad libitum access to laboratory rodent chow (Envigo Teklad Global Diets 18% Rodent Diet) and water. All procedures adhered to the National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by the Bloomington Institution Animal Care and Use Committee (BIACUC) at Indiana University.

2.2 | Behavioral trials

Social behavior of both males and females was assessed using a 15-min resident-intruder trial. For each individual ($n = 8$ females, $n = 11$ males), we conducted two "juvenile trials" when the focal individuals were 51–56 days old; juvenile trials were separated by one to three days. The third trial occurred after the pubertal transition had begun when individuals were 98–101 days old (pubertal transition begins at approximately 60 days old; $n = 7$ females, $n = 8$ males).

Trials occurred within the first three hours of the dark–light period under low, red-light illumination and were video recorded. Staged interactions consisted of the "intruder," which was the focal animal in this study and the "resident" individual (non-focal individual). For each trial, the focal animal was placed into the resident's cage for 15 min, then returned to its home cage.

Resident-intruder pairs were matched by sex, weight (±3 g), age, and had different parental lines. The residents' cages were not changed for at least three days before the trials and individuals were weighed the day before the trial.

2.3 | Video scoring and behavioral analyses

Behaviors from video recordings were scored using BORIS v 7.9.6 (Friard & Gamba, 2016) by one unbiased observer (C.H.A.). Duration of behaviors performed by the focal individual during the first 5 min of the trial were scored, following standard procedure in our lab. Behaviors scored included aggression, investigation, run, jump, and received aggression (defined in Table S1).

For each trial, we calculated the focal individual's "social score" and "escape score." An individual's social score was defined as the total amount of time the focal individual interacted with the resident (e.g., attacked or investigated). An individual's escape score was defined as the total amount of time the focal individual spent evading the resident (e.g., ran away or jumping at cage wall).

2.4 | Statistical analyses

All statistical analyses were conducted in R v. 4.0.2 (R Core Team, 2020). We report mean±standard error of the mean unless stated otherwise.

Juvenile social scores (Shapiro-Wilk $W = 0.79$, $p < .05$) and escape scores (Shapiro-Wilk $W = 0.88$, $p = .02$) during trial one were not normally distributed. We performed a square-root transformation (social score Shapiro-Wilk $W = 0.95$, $p = .43$, escape score Shapiro-Wilk $W = 0.94$, $p = .23$) and conducted separate generalized linear models (GLMs, Gaussian, identity link) to test for an effect of sex, juvenile weight, and these terms' interaction on social and escape scores during juvenile trial one.

We conducted separate GLMs (Gaussian, identity link) to determine whether an individual's sex, weight, these two terms' interaction, or their received aggression score from juvenile trial 1 affected juvenile social scores and escape scores during the second juvenile trial. Juvenile trial two escape scores were not normally distributed (Shapiro-Wilk $W = 0.73$, $p < .01$) and were log transformed (Shapiro-Wilk $W = 0.95$, $p = .46$) before analyses.

We assessed whether the interaction of sex and weight affected adult social and escape scores during the adult trials using a GLM (Gaussian, identity link). Adult escape scores were not normally distributed (Shapiro-Wilk $W = 0.88$, $p = .05$) and we performed a square-root transformation ($W = 0.96$, $p = .63$) before analyses.

We assessed repeatability ("R") of social and escape scores using the lmm method in the "rpt" function for normal distributions in rptR package (Nakagawa & Schielzeth, 2010; Stoffel et al., 2017). Repeatability values range from 0 to 1, with values ranging from 0.5 to 0.7 indicating moderate repeatability and values greater than 0.7 indicating high repeatability (Harper, 1994; Koo & Li, 2016). When data did not follow normal distributions, as described previously, we transformed the data before analysis (Nakagawa & Schielzeth, 2010). To assess the significance of repeatability estimates we calculated 95% confidence intervals using 1000 parametric bootstrapping iterations (Nakagawa & Cuthill, 2007). We also calculated the "VarW/VarA ratio," which represents the ratio of within and among variances, using the *ICCest* function in the ICC package (Wolak et al., 2012). Lower ratios are associated with higher repeatability (Réale et al., 2007). We assessed the repeatability of individuals' social scores and escape scores across the two juvenile trials and the repeatability of individuals' social and escape scores across juvenile trial one and the adult trial. To determine whether one sex displayed greater repeatability, we repeated these analyses separately for each sex.

3 | RESULTS

3.1 | Social and escape score

Juveniles' average social scores during trial one (males = 24.26 ± 7.72 s, females = 16.31 ± 4.27 s) and trial two (males = 20.50 ± 5.89 s, females = 23.67 ± 4.65 s) were unrelated to sex, weight, or their interaction (Table 1a,b). As adults, we observed a nonsignificant interactive effect of sex and weight (Table 1c): as males' weight increased their social scores (21.23 ± 5.24 s) tended to decrease whereas females' social scores (11.65 ± 1.78 s) increased with increasing weight.

We found no effect of sex, weight, or their interaction on juveniles' escape scores during trial 1 (males = 50.69 ± 10.09 s, females = 34.93 ± 6.98, Table 1a), trial two (males = 49.37 ± 15.85 s, females = 29.97 ± 5.04 s, Table 1b), or during the adult trial (males = 46.03 ± 16.46 s, females = 47.72 ± 5.30 s, Table 1c).

3.2 | Repeatability of social and escape scores

Individuals' social scores were significantly repeatable across the two juvenile trials ($R = 0.55$; SE = 0.17; 95% CI = 0.14, 0.80; $p < .01$, $\mathrm{Var_W/Var_A} = 0.82$, Figure 1a). Juvenile males' social scores were highly repeatable across juvenile trials ($R = 0.64$; $SE = 0.20$; 95% CI = 0.11, 0.88; $p = .01$; $N = 11$) and juvenile females' social scores were moderately repeatable across trials ($R = 0.40$; $SE = 0.27$; 95% CI = 0, 0.81; $p = .16$; $N = 8$). Escape scores were not highly repeatable across the two juvenile trials ($R = 0.35$; SE = 0.19; 95% CI = 0,0.69; $p = .07$; $\mathrm{Var_W/Var_A} = 1.8$; Figure 1b). Juvenile females tended to exhibit slightly higher levels of repeatability in their escape scores ($R = 0.54$; SE = 0.24; 95% CI = 0, 0.86; $p = .07$; $N = 8$) compared to juvenile males ($R = 0.34$; SE = 0.23; 95% CI = 0, 0.75; $p = .15$; $N = 11$).

Social scores of females ($R = 0.29$; SE = 0.26; 95% CI = 0, 0.80; $p = .28$; $N = 7$) and males ($R = 0.21$; SE = 0.24; 95% CI = 0, 0.76; $p = .35$; $N = 8$) were not repeatable across developmental stages ($R = 0.23$; SE = 0.20; 95% CI = 0, 0.62; $p = .23$, $\mathrm{Var_W/Var_A} = 3.4$; Figure 1c). In

TABLE 1 Effects of sex and weight on social and escape scores across juvenile and adult trials

Trial	Behavioral score	Terms	Estimate ± SE	*t* value	*p* value
(a) Juvenile trial 1	Social score	Sex male versus female	12.26 ± 13.50	0.91	.38
		Weight	0.49 ± 0.35	1.42	.18
		Sex*weight	−0.41 ± 0.43	−0.94	.36
	Escape score	Sex male versus female	9.19 ± 13.50	0.68	.51
		Weight	0.15 ± 0.35	0.42	.68
		Sex*weight	−0.26 ± 0.43	−0.60	.56
(b) Juvenile trial 2	Social score	Sex male versus female	96.38 ± 116.48	0.83	.42
		Weight	3.75 ± 2.89	1.29	.22
		Received aggression trial 1	−0.37 ± 1.29	−0.29	.78
		Sex*weight	−3.45 ± 3.69	−0.94	.37
	Escape score	Sex male versus female	9.40 ± 5.26	1.79	.10
		Weight	0.13 ± 0.13	1.01	.33
		Received aggression trial 1	0.01 ± 0.06	0.24	.82
		Sex*weight	−0.29 ± 0.17	−1.73	.11
(c) Adult trial	Social score	*Sex male versus female*	*119.66 ± 57.17*	*2.09*	*.06*
		Weight	0.40 ± 1.06	0.37	.72
		*Sex*weight*	*−2.94 ± 1.57*	*−1.87*	*.08*
	Escape score	Sex male versus female	−3.12 ± 16.10	−0.19	.85
		Weight	0.16 ± 0.30	0.53	.61
		Sex*weight	0.04 ± 0.44	0.09	.93

Note: Results of GLMs (Gaussian, identity link) investigating the effects of sex, weight, their interaction, and received aggression trial 1 (for Juvenile trail 2 only) on male and female social and escape scores. The same 19 individuals were assessed during Juvenile Trial 1 and Juvenile Trial 2. Of the 19 individuals assessed as juveniles, 15 individuals were assessed a third time as an adult. Terms in italics indicate nonsignificant terms (.05 < *p* < .1) trending towards significance.

contrast, escape scores were highly repeatable across development ($R = 0.62$; SE = 0.17; 95% CI = 0.18, 0.85; $p < .01$, $\text{Var}_W/\text{Var}_A = 0.42$; Figure 1d), which was driven by the greater repeatability in males ($R = 0.70$; SE = 0.21; 95% CI = 0.03,0.93, $p = .02$; $N = 8$ individuals) compared to females ($R = 0.25$; SE = 0.25; 95% CI = 0, 0.78; $p = .32$; $N = 7$ individuals).

4 | DISCUSSION

Growing evidence suggests that personality may be less stable across life stages, highlighting the need to consider how ontogeny affects animal personality (Cabrera et al., 2021). We measured individual hamsters' social and escape behaviors as juveniles and as adults. Individuals' social scores were repeatable within the juvenile stage, but not across developmental stages. Individuals' escape scores were repeatable across developmental stages, despite not being repeatable as juveniles.

4.1 | Social scores

Reaching sexual maturity, especially in direct-developing species, is associated with a variety of physiological, social, and environmental changes that may influence the stability of certain behavioral traits, while not affecting others (Cabrera et al., 2021). In the current study, individuals' social scores, which were comprised of aggressive and investigatory behavior, were not consistent across development in

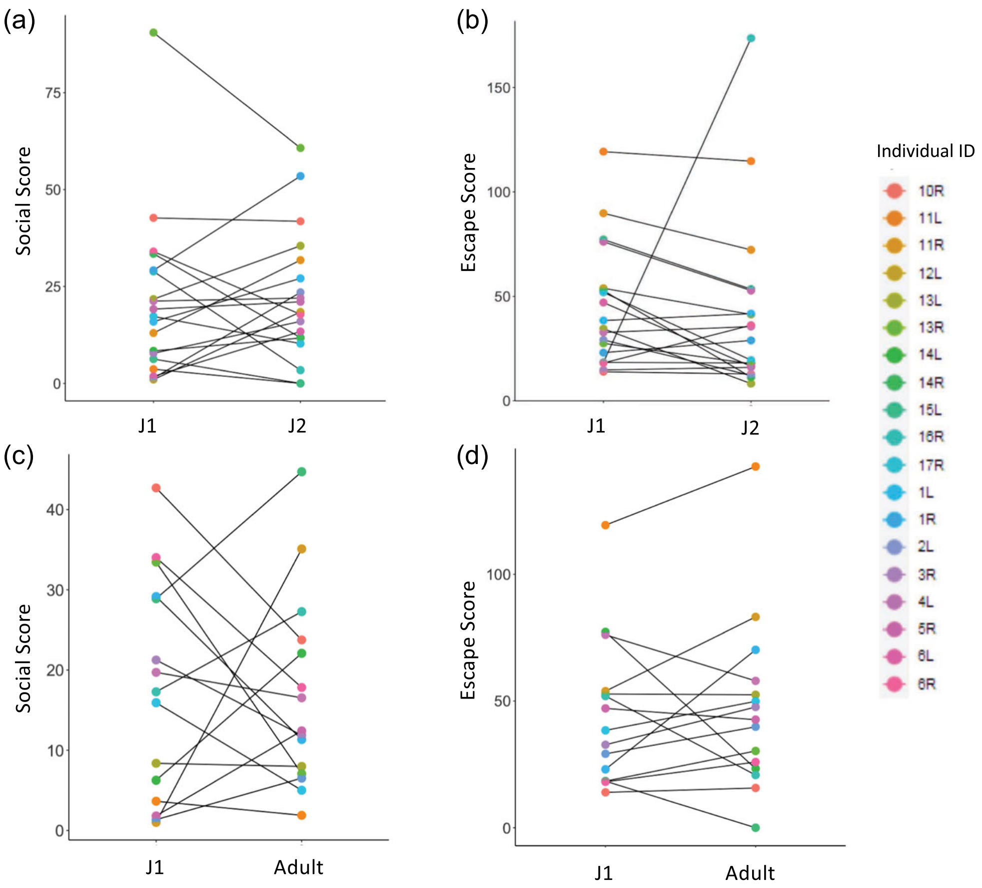

FIGURE 1 Individual repeatability of (a) social scores and (b) escape scores across juvenile trials ($n = 19$), and (c) social scores and (d) escape scores across developmental stages ($n = 15$). Trial type is listed on the x-axis: "J1" indicates juvenile trial one, "J2" indicates juvenile trial two, and "Adult" indicates adult trial. Individuals' social scores were significantly repeatable across the two juvenile trials and individuals' escape scores were significantly repeatable across developmental stages. Dots represents individual scores and solid lines connect the scores of a single individual across trials [Color figure can be viewed at wileyonlinelibrary.com]

males and females. Few studies have documented consistency in such behaviors across developmental stages. A recent review by Cabrera et al. (2021) revealed that none of the studies they evaluated detected consistency in sociality. Further, they found aggression to be consistent across development in only two out of the 10 studies investigating this phenomenon, and found consistency in exploration across life stages in only one of 14 studies. In our study, juveniles' social scores consisted of investigation (mean ± *SD* = 19.56 ± 18.52 s) more than aggression (mean ± *SD* = 1.35 ± 3.18 s), while adults' social scores consisted of an increase in aggression (mean ± *SD* = 7.23 ± 11.36 s) and a decrease in investigation (mean ± *SD* = 9.03 ± 5.94 s). This suggests that Siberian hamsters become more aggressive and less investigatory with age, similar to other species. For example, investigation can decrease with age (e.g., Miller et al., 2015), as exploration may be more beneficial to juveniles than adults (Sih & Del Giudice, 2012). Further, in the study species, aggression appears to be under gonadal regulation during long-day photoperiods (Munley et al., 2018), which is the condition under which this study occurred. As individuals mature, changes in gonad morphology and function as well as gonadal steroid secretion may influence individual's aggressive behavior and explain why social scores were not consistent across developmental stages. Both aggressive and investigatory behaviors may be susceptible to hormonal, social, and environmental changes associated with maturation (e.g., Kelley et al., 2015; Miller et al., 2015). Therefore, social behavior, as seen in this study, may be subject to behavioral reconstruction across development.

4.2 | Escape scores

Escape scores were highly repeatable across maturation. Escape scores were comprised of run and jump behaviors, which are associated with avoiding and escaping from an unfamiliar conspecific. In other studies, behavioral traits similar to escape behavior are repeatable across developmental stages. In Eurasian harvest mice (*Micromys minutus*), individual activity (i.e., similar to escape behavior measured in the current study) was consistent across maturation (Schuster et al., 2017). In a different population of Siberian hamsters, open field activity, a measure similar to jump behavior assessed in the current study, was highly correlated across juvenile and adult trials (Kanda et al., 2012).

Escape score repeatability across maturation was primarily driven by the high repeatability scores of males. Although sex differences in repeatability are not always reported, higher repeatability for certain behavioral traits in males has been reported (e.g., response to threat: Amy et al., 2017; aggression: Schürch & Heg, 2010). Behavioral traits associated with fearlessness, anxiety, stress, and coping mechanisms are often highly repeatable. For example, individuals' coping styles and escape attempts were consistent across time in the Senegalese sole (*Solea senegalensis*, Ibarra-Zatarain et al., 2020). Moreover, in wild guinea pigs (*Cavia aperea*), fearlessness was consistent across two distinct ontogenetic stages (Guenther et al., 2014). Individual variation in stress response, specifically baseline and stress-induced glucocorticoid levels, also tend to be repeatable across life stages (e.g., Baugh et al., 2017; Guenther et al., 2014; Rensel & Schoech, 2011; Small & Schoech, 2015). Sex differences in these physiological mechanisms, which can be the result of sex differences in prenatal programming (Seckl & Meaney, 2004), could be one aspect influencing individual variation and consistency in behavior. For example, in dark-eyed juncos (*Junco hyemalis*), circulating testosterone related to aggressiveness in males only, but neural sensitivity to testosterone (e.g., abundance of androgen receptor) related to individual variation in aggressive behavior in females and males (Rosvall et al., 2012). Sex differences in various aspects of the stress response (e.g., corticotropin-releasing hormone, Bangasser & Wiersielis, 2018) could also lead to long-lasting individual differences in behaviors. Consistent individual differences in stress response could represent a permanent feature of an individual's phenotype (Cockrem, 2013; Duckworth, 2015) and may explain why behaviors associated with this physiological system, like escape behavior measured in the current study, remain consistent across long periods of time (Baugh et al., 2017).

5 | CONCLUSION

Assessing personality within a single life stage may result in a partial view of an individual's behavioral range. Our study found individuals' social scores were repeatable within the juvenile stage while individuals' escape scores were repeatable across developmental stages. Further, we observed strong sex differences in the repeatability of certain behavioral traits, but not others. We also observed that the particular traits that were repeatable across ontogeny differed between the sexes. Our results are consistent with previous findings that sex differences in repeatability of behavioral traits are observed for some traits, but not others, and whether sex differences are observed can depend on the species (Cabrera et al., 2021). Considering how ontogeny affects animal personality for males and females can provide insight into the evolution and mechanisms that maintain animal personality (Cabrera et al., 2021).

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data from this study are available upon request.

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