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Individual behavioural variation does not affect social organization or reproductive success in a cooperative small mammal

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Abstract

Recent evidence indicates that individual behavioural variation in animals, defined as consistent individual differences in behaviour across contexts and time, influence ecological and evolutionary processes, and a growing number of studies demonstrate that individual behavioural variation can play a large role in shaping grouping dynamics among social animals. We studied the common degu, *Octodon degus*, a social rodent, to evaluate whether individual behavioural variation underlies social organization and the reproductive success of individuals within groups. We examined social groups in a population in central-north Chile during one breeding season, tested 67 adults in an open field test (i.e., the propensity to explore an unfamiliar environment) and 62 adults in a poke test (i.e., the propensity to charge an object) to quantify individual behavioural variation, determined assortment based on individual behavioural differences across 19 social groups, and

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performed genetic analyses to assess reproductive success. We found that the response to the poke test was repeatable, while none of the behaviours from an open field test were. The repeatable behaviour during the poke test was not associated to components of social organization (group composition), or to reproductive success. These findings imply that individual behavioural variation did not affect grouping patterns or direct fitness in this degu population.

Keywords
animal personality, repeatability, rodent, sociality, phenotype assortment.

1. Introduction

Individual personalities (individual behavioural variation; (Laskowski et al., 2022), i.e., differences in behaviour that are consistent over time and contexts (Gosling, 2001; Réale et al., 2007), can shape the costs and benefits of group living. Individual behavioural variation can influence the competitive ability of individuals and provide an advantage in resource acquisition (Webster & Ward, 2010; Briffa et al., 2015), leading to within-group differences in reproductive success (Dingemanse et al., 2020; Eccard et al., 2022). Based on the expected trade-off between current and future reproductive investment (Stearns, 1983; Dobson & Oli, 2007), risk prone individuals are expected to reproduce rapidly but exhibit a relatively low survival, implying a pace-of-life syndrome (Ricklefs & Wikelski, 2002; Dammhahn et al., 2018). However, this relationship is often not detected (Bijleveld et al., 2014; Piquet et al., 2018; Royauté et al., 2018; Moiron et al., 2020; Godin et al., 2022). Instead, individual differences in behaviour may be associated with competitive ability and/or reproductive success (Webster & Ward, 2010; Farine et al., 2015), and behavioural correlations may be influenced by trade-offs and feedbacks (Dochtermann, 2023). Individuals in group-living species may adjust their behaviour to minimize the cost of competition or increase reproductive success, or they may associate with (dis)similar individuals to achieve the same result (Webster & Ward, 2010; Farine et al., 2015).

The social niche specialization hypothesis posits that individuals limit within-group competition by behaving differently than other group members (Bergmüller & Taborsky, 2010; Montiglio et al., 2013); also, negative assortment (Dyer et al., 2009). Reduction in competition afforded through social niche specialization could result in positive feedback leading to the formation and maintenance of individual behavioural variation, and to fitness benefits whenever individuals negatively assort by behavioural variation within groups (Bergmüller & Taborsky, 2010; Wolf & Weissing, 2010). For

instance, colony growth, larvae survival, queen and worker production in gypsy ants (*Aphaenogaster senilis*) are positively associated with differences in individual behavioural variation (Blight et al., 2016). Benefits gained from associating with dissimilar individuals may stem from the advantages each individual acquires from their dissimilar group members and could reduce indirect competition for resources (Farine, 2014).

Alternatively, competition may be mitigated by individuals behaving similarly to others in their group (positive assortment), a mechanism referred to as the conformity hypothesis (McCune et al., 2018). This possibility is supported by studies reporting strong social bonds among individuals with similar behaviour in a variety of taxa, including three-spined sticklebacks *Gasterosteus aculeatus* (Pike et al., 2008), great tits *Parus major* (Aplin et al., 2013; Johnson et al., 2017), Mexican Jays *Aphelocoma wollweberi*, California Scrub-Jays *Aphelocoma californica* (McCune et al., 2018), feral horses *Equus caballus*, and chimpanzees *Pan troglodytes* (Massen & Koski, 2014; Briard et al., 2015). Selection may favour behaviourally similar groups due to negative consequences associated with within-group conflicts driven by interactions among individuals with dissimilar behaviour or due to increased benefits accrued by individuals grouping with other behaviourally similar individuals (Oliveira et al., 2001). This possibility is supported by studies on mating pairs and where individuals that associate with opposite sex but behaviourally similar individuals increase the probability of mating and fertilization, and results in higher reproductive success (Sinn et al., 2006; Gabriel & Black, 2012; Rangassamy et al., 2015; Pogány et al., 2018). In general, associating with conspecifics based on similar traits can improve group performance and can attain fitness benefits from group living. Thus, determining how individual behavioural variation and how individuals with specific behavioural variation assort into a social unit influence individual fitness can yield insights into the evolutionary significance of social complexity (Kappeler, 2019).

We aimed this study to examine the influence of individual behavioural variation on assortment and individual reproductive success in *Octodon degus*, the common degu, a social, diurnal, and semi-fossorial rodent endemic to central Chile (Woods & Boraker, 1975; Ebensperger et al., 2004; Hayes et al., 2009). The primary form of degu social organization is multi-female groups (Ebensperger et al., 2009; Hayes et al., 2019). Several observations suggest that assortment is an important factor influencing degu

sociality. Females assort into groups with similarly masculinized females and inter-female aggression is most common in groups consisting of masculinized females and when in groups including feminized and masculinized females (Correa et al., 2013). Assortment by masculinization is fitness-enhancing to females when groups consist of masculinized females (Correa et al., 2021). Three additional observations from a population in central Chile support social niche specialization: (1) the propensity to charge an object (poke test) is associated with the propensity to explore an open field test arena, (2) both measures are repeatable in male and female adults and (3) adults assort according to the social niche specialization hypothesis (assortment by dissimilar exploratory behaviour) (Chock et al., 2017).

Our objectives were to assess behavioural repeatability within a northern population, examine whether individual group composition in behaviour supports the social niche specialization or the conformity hypothesis, and investigate how individual behavioural variation correlates with reproductive success. We expected (i) degu behaviour based on exploration (open field test) and on charging an object (poke test) to exhibit repeatability, and (ii) that degus assort according to the social niche specialization hypothesis, where social groups would consist of adults with dissimilar behaviour. If degus assort by the conformity hypothesis, (iii) we expected social groups to consist of adults with similar individual behavioural variation. We predicted that (iv) degus that are bolder (responded to poke test) and/or more exploratory (moved greater distance in open field test) have higher individual reproductive success in accordance with the pace-of-life syndrome. Provided that individuals group preferentially with dissimilar individuals to reduce costs associated with competition (v) we predicted groups with more dissimilar individuals will have increased per capita offspring weaned.

2. Methods

2.1. Study site, burrow identification, trapping, and degu individual marking

We conducted live-trapping, radio-telemetry, and behavioural measurements in a 1.79 ha area in El Salitre, northern Chile (71°37′50.09″W, 30°41′29.70″S) from August to November 2017. The timing of data collection fell around the period of late gestation, parturition, and offspring rearing (Hayes et al., 2007; Ebensperger et al., 2014). We conducted trapping and night telemetry to determine the location of 32 burrow systems, defined as

a group of interconnected burrow openings from which individuals emerged during daytime and returned to at nighttime (Fulk, 1976). Following previous methods (e.g., Hayes et al., 2019), we live-trapped at each burrow system six days per week. Upon first capture, animals were fitted with ear tags (Monel 1005-1, National Band and Tag, Newport, KY, USA) for individual identification and a tissue sample was taken from one ear. On the first and all subsequent captures, we recorded animal ID, burrow number, sex, reproductive and lactation status of adult females, and body mass (g).

2.2. *Quantification of behaviour*

We quantified individual behaviour of degus when exposed to an open field test (Réale et al., 2007; Perals et al., 2017) and a poke test (Chock et al., 2017). During the open field test, we placed subjects in a closed metal shelter within the arena (89 × 89 × 142 cm, Figure A1 in the Appendix) and allowed them to acclimate for 3 min. The corner in which the hide was placed was rotated before the beginning of each trial to eliminate effects of hide placement. We then opened the shelter and recorded the degus for 7 min with observers out of view. Due to slight variations in camera placement each day, the placement of the open field box was made uniform on each video using Lightworks (EditShare). Exported files from this program were then changed to the mpeg2 video format with Any Video Converter (Anvsoft) for compatibility with EthoVision XT 14 (Noldus Information Technology). One researcher (N.E.J.) used the Ethovision program to analyse the latency (s) to emerge from the hide (all degus entered the open field test arena), the time spent moving (proportion of time spent moving by the total time spent within the arena), and total distance the degu moved within the arena (cm). Each video was checked individually to ensure that the software tracked the animal correctly. Trials involving the open field test took place during September through early October of 2017. We recorded more than one behavioural measure for 67 adult degus, including 46 females and 21 males (mean number of measures 3.67 ± 0.88 (SD), range 2–6, per individual with a total of 246 observations over 24 days).

During the poke test, one observer (S.G.) used the eraser-side of a pencil to gently poke individual hindquarters through the wire-mesh of the Tomahawk trap and recorded whether a degu turned and charged at the eraser end of a pencil that was touching its hindquarters (see Chock et al., 2017). The strength used was held constant and we limited variation in poke strength by having only one observer perform the poke test. We scored a 1 if the

degu subject turned and charged the pencil or as a 0 whenever the degu subject did not charge. Additionally, we calculated the proportion that each individual degu turned and charged the pencil across all poke trials. Adult degus were tested prior to handling each day that they were trapped from mid October to early November 2017, approximately 15 min after relocation to the processing station. We obtained more than one measure for 62 adult degus (mean ± SD = 12.95 ± 5.23, range 2–20 measures for a total of 44 females and 18 males obtained over 21 days). The identity of subjects during these trials was not known.

2.3. Social group quantification

Quantification of social groups closely followed the methods of an ongoing long-term study on degu sociality in a central Chile population (Ebensperger et al., 2011, 2014). Social group membership of 75 adult degus resulted from a combination of early daytime live trapping at burrow systems (mean ± SD = 40.4 ± 21 days) and night-time telemetry ($N = 51$ collared adults, mean ± SD = 39.98 ± 11.58 nights). Using the software SOCPROG 2.8 (Whitehead, 2009), we (i) built a symmetric similarity matrix of pairwise associations (Whitehead, 2008) and (ii) calculated pairwise association indices by dividing the number of days that any two individuals were captured or tracked via telemetry at the same burrow by the number of days that both individuals were trapped or tracked via telemetry on the same day (Ebensperger et al., 2004). Total group sizes consisted of 3.95 ± 1.81 adults with 2.89 ± 1.57 females and 1.28 ± 0.57 males, $N = 19$ different social groups. Details of social group quantification are in Section A2.1 in the Appendix.

2.4. Ethics in animal use

All trapping, handling, and behavioural trials were conducted in accordance with the North Dakota State University Institutional Animal Care and Use Committee under protocol No. A16068 and the University of Tennessee at Chattanooga Institutional Animal Care and Use Committee under protocol No. 0507LH-02. Research was conducted under the Chilean permit issued by the Servicio Agricola y Ganadero (5028/2017).

2.5. Genetic analyses

We used the tissue samples of each degu (adults and pups) obtained at first capture to determine number of offspring (see Section A2.2 in the

Appendix for detailed methodology). We genotyped our samples using 10 microsatellite loci to determine kinship following the methods as described by (Ebensperger et al., 2019; Correa et al., 2021). We then checked for Hardy–Weinberg equilibrium using the CERVUS 3.0 software (Marshall et al., 1998). We detected deviations from the equilibrium in 3 out of 10 loci (Table A3 in the Appendix). To estimate paternity and maternity, we examined individual offspring, potential mothers, and potential fathers as trios in the population using CERVUS 3.0 (Table A4 in the Appendix). We used estimates of genetic maternity and genetic paternity to quantify reproductive success as the number of offspring weaned (i.e., litter size) by each female and male in the population, following Ebensperger et al. (2019). Males produced more pups (9.2 ± 5.9 (1–22)) than females (4.5 ± 2.1) 1–10) pups).

2.6. Statistical analyses

2.6.1. Repeatability

We quantified four measures of inter-individual behavioural variation: latency to emerge into the open field test (gamma distribution), proportion of time spent moving in the open field test (Gaussian distribution), total distance travelled in the open field test (gamma distribution), and the occurrence or absence of turning and charging at eraser end of pencil that was touching hindquarters (binomial distribution).

We examined four models to quantify repeatability of each examined behavioural measure, all of which included the following fixed effects: sex (converted to continuous variable, male = 1, female = 2) and for habituation over time by including trial number. We centred both sex and trial number on the mean to aid model convergence and interpretation of the results (see Table A5 in the Appendix for comparison results of models with sex as continuous or categorical variable). We included individual degu ID and social group ID as random intercepts. We only included adult males and females as we were interested in adult' behaviour in the group and their reproductive success. We fitted mixed models within a Bayesian approach using the 'brms' package (Bürkner, 2017, 2018, 2021) from the Stan environment (http://mc-stan.org/) to calculate repeatability. We chose a Bayesian approach as it reflects uncertainty by providing a posterior distribution for each estimated parameter. We used the 'get_prior' function to set our prior for each model but used identical parameter settings across all models (warmup = 500, iterations = 3000, thinning = 2, chains = 2). We

verified model convergence by means of inspecting model fit, the effective sample size, and the Rhat parameter. We square root transformed the latency to emerge from the hide and the total distance moved to meet assumptions of normality and used a Gaussian distribution for these two behaviours and for the proportion of time spent moving. For models with Gaussian distribution, we calculated repeatability as the individual variance divided by the total variance, which includes individual, group, and residual variance from the posterior samples. The degu response to the poke test followed a binomial distribution, where degus either did or did not attack the pencil. Following Nakagawa & Schielzeth (2010), we calculated the residual variance for the binomial distribution as $\pi^2/3$. Furthermore, we calculated the coefficient of variation for between individual and group variance as the square root of the variance in question divided by the mean of the behavioural measure. We then measured the marginal and conditional R^2 using the 'performance' package (Lüdecke et al., 2021). The marginal R^2 considers only the variance of the fixed effects, while the conditional R^2 takes both the fixed and random effects into account. We considered behaviours to be repeatable whenever credibility intervals were symmetrical and when the lower 95%CI was higher than 0.1 as the credibility intervals are constrained between 0 and 1. We followed the code of Hertel et al. (2020).

2.6.2. Assortment

We calculated assortment (r) on a scale of -1 to 1, where -1 represented negative assortment (individuals in a group are dissimilar), 1 represents positive assortment (individuals in a group are similar), and 0 represents no assortment (Newman, 2002). To determine if assortment was occurring for the repeatable behaviours, we built matrices of social networks using the 'asnipe' package and used the 'assortnet' package to determine assortment by repeatable behavioural traits (Farine, 2014). We only included social groups with two or more group members tested during the behavioural assays. We determined the significance of r by creating 50 000 network permutations, calculating a value for r for each permutation, and then comparing the r derived from the population to the simulated values and determining how many simulated values were as or more extreme than the original r value (Farine, 2014).

2.6.3. Effect of individual behavioural variation on reproductive success

We used repeatable behaviours (poke response, see Results) in a multivariate framework (Houslay & Wilson, 2017; Hertel et al., 2020; Mitchell et

al., 2020) to assess the among-individual variance and covariance for degu individual behavioural variation and litter size. Specifically, we implemented a multivariate mixed modelling approach with the 'MCMCglmm' package (Hadfield, 2010) and followed the tutorial by Houslay & Wilson (2017). Prior to this approach, we used the Bayesian multivariate mixed modeling approach, but this model did not converge, and we decided to use the MCMCglmm package as another check. As this was the last method we used, we included these methods and results. We included the raw poke variable, which meant we had multiple measures per degu ID for the poke test but only one measure of litter size. We converted litter size to a relative fitness measure, which we scaled by dividing the number of offspring produced by the mean litter size across all adult degus. This relative fitness measure followed a gamma distribution, so we used the 'faux' package (DeBruine, 2023) to fit this variable to a normal distribution. We used a categorical distribution for the poke response and a Gaussian distribution for our transformed relative fitness measure. We included both response variables, we controlled for sex (centred) and trial (centred) and included degu ID as random effect. We fitted an unstructured 'us' R-matrix (within-individual variation) and an unstructured 'us' G-matrix (among-individual covariances) for degu ID. As we only have one relative fitness measure per individual, we set a fixed within-individual variance level to 0.0001 as variances must be positive. Furthermore, we specified that trial is only estimated for the poke response. We ran the model for 750 000 iterations, with a burn-in of 50 000, and a thinning interval of 175. Successive samples from the posterior distribution had high autocorrelation for the poke response, indicating nonindependence between successive samples (see Section A4 in the Appendix). Also, the trace plot of the poke response showed a trend in the time series, indicating that the model did not converge (Figure A2 in the Appendix). Therefore, we decided to use a Spearman correlation analysis to quantify the association between the poke response (proportion, 1 measure per individual) and the relative fitness. We converted the poke response from a binomial to a continuous measure by dividing the number of times that degus responded to being prodded by the total number of trials, which resulted in a measure bounded between 0 (individual never responded) and 1 (individual responded in all trials).

2.6.4. Data availability

Our code and data are available on the GitHub repository, https://github.com/annemarievdmarel/degu-individual-behavioural-variation/tree/main (van der Marel, 2023).

Table 1.
Descriptive statistics of the open field test obtained for 67 adult degus, including 46 females and 21 males.

Behaviour	Sex	Mean	SD	Min	Max
Latency to emerge from hide (s)	Female	104.34	105.02	0.00	415.62
	Male	106.87	98.03	0.00	395.10
Proportion of time spent moving	Female	0.50	0.13	0.10	0.80
	Male	0.54	0.15	0.10	0.88
Distance moved (cm)	Female	2178.37	1359.31	9.04	6683.68
	Male	2680.20	1290.52	13.40	6790.68

3. Results

After controlling for the fixed effects of sex and trial number, we found no repeatable traits based on the open field test (Table 1) at both the individual- and the group-levels examined (Table 2, Table A7 in the Appendix). Neither the latency to emerge from the hide, the proportion of time spent moving, nor the total distance moved were repeatable in adult degus. We found that the poke response was repeatable individually but not so at the group-level (Table 2). Differences in the coefficient of variation for between individual or group variation were statistically significant for individual latency to emerge from the hide during the open field test (Table 2). We found no group repeatability per behaviour (Table 2) and degus did not show significant group assortment by the poke response ($r = 0.04$, SE $= 0.07$, $p = 0.23$, Figure A3 in the Appendix), suggesting that individuals do not associate preferentially with individuals based on this behavioural trait.

We found that only sex had a statistical effect on the total distance moved, where males moved a greater distance (mean $\pm$ SE $= 2680.20 \pm 156.50$ cm, $N = 21$ males) than females (2178.37 ± 101.88 cm, $N = 46$ females; Table 2, Figure 1a). Degus showed habituation to the open field test arena and showed a decrease in the proportion of time spent moving and total distance moved with increasing number of trials, yet this effect was most pronounced in total distance moved (trial effect: Table 2, Figure 1b and c).

Of 62 degus with poke test results, three individuals had no offspring and these three were included in the analysis. We found no correlation between the repeatable behaviour (poke response) and litter size ($r_s = -0.06$, Figure 2). We did find that reproductive success differed between males and

Table 2.
Bayesian posterior means and the 95% credible intervals for the fixed effects, and variance, repeatability estimates and coefficient of variation (CV) at the individual and group-level random effects using Bayesian mixed modelling for open field and poke test behaviours in adult degus.

Test	Behaviour	Effect	Estimate (95% CI)
Fixed effects			
Open field	Latency to emerge from hide	Sex	−0.42 (−2.24 to 1.31)
		Trial	−0.20 (−0.67 to 0.26)
	Proportion of time spent moving	Sex	−0.04 (−0.08 to 0.01)
		Trial	*−0.04 (−0.05 to −0.02)*
	Total distance moved	*Sex*	*−4.86 (−9.34 to −0.24)*
		Trial	*−2.81 (−4.29 to −1.41)*
Poke	Poke response	Sex	0.08 (−0.93 to 1.11)
		Trial	0 (−0.04 to 0.04)
Random effects			
Open field	Latency to emerge from hide	Individual repeatability	0.17 (0.02–0.31)
		Individual CV	0.23 (0.11–0.35)
		Group repeatability	0.03 (0.00–0.09)
		Group CV	0.08 (0.00–0.18)
	Proportion of time spent moving	Individual repeatability	0.08 (0.00–0.19)
		Individual CV	0.07 (0.00–0.12)
		Group repeatability	0.03 (0.00–0.09)
		Group CV	0.03 (0.00–0.08)
	Total distance moved	Individual repeatability	0.05 (0.00–0.15)
		Individual CV	0.07 (0.00–0.13)
		Group repeatability	0.06 (0.00–0.15)
		Group CV	0.07 (0.00–0.13)
Poke	Poke response	*Individual repeatability*	*0.42 (0.30–0.55)*
		Individual CV	na
		Group repeatability	0.03 (0.00–0.10)
		Group CV	na
R^2			
Open field	Latency to emerge from hide	Conditional	0.19 (0.06–0.30)
		Marginal	0.01 (0.00–0.04)
	Proportion of time spent moving	Conditional	0.21 (0.11–0.32)
		Marginal	0.13 (0.06–0.20)
	Total distance moved	Conditional	0.18 (0.08–0.26)
		Marginal	0.09 (0.03–0.15)
Poke	Poke response	Conditional	0.31 (0.27–0.35)
		Marginal	0.01 (0.00–0.03)

The marginal and conditional R^2 are included. Factors in italics represent the variable that has an influential effect on the behavioural trait.

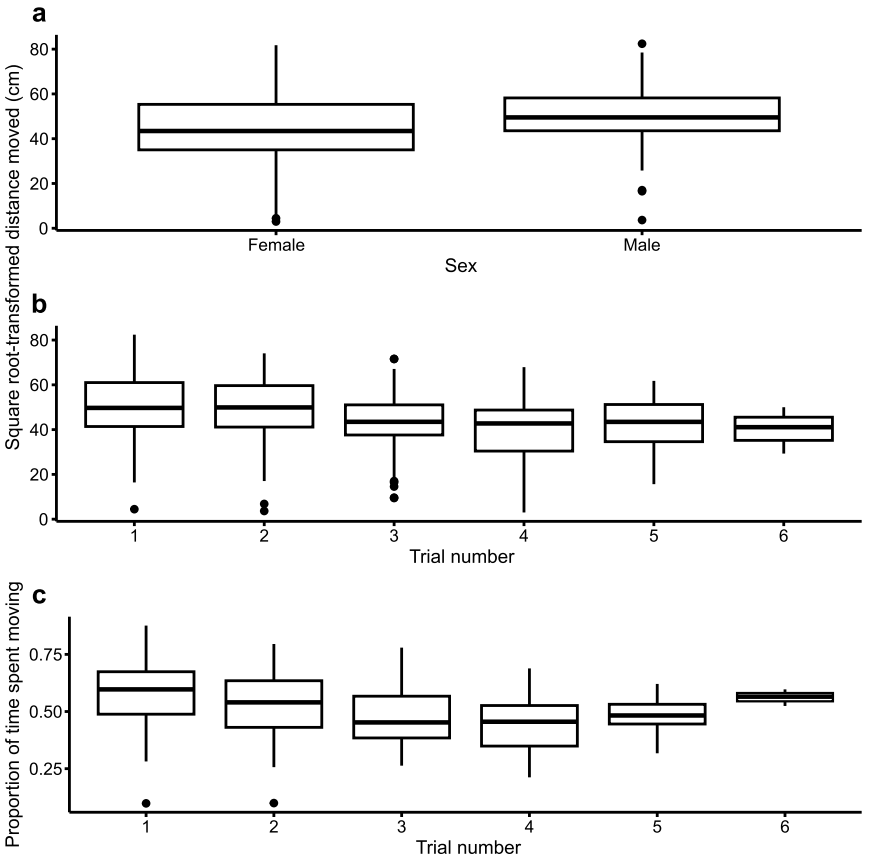

Figure 1. The effect of (a) sex on square-root transformed total distance moved and of trial number on (b) square-root transformed total distance moved and (c) the proportion of time spent moving in adult degus.

females, where males had a higher reproductive success than females (Table A6 in the Appendix).

4. Discussion

Adult degus showed consistent individual behavioural differences for the poke response but not in the traits measured from the open field test. In contrast to our predictions, we did not find evidence of consistent assortment across social groups based on the tested repeatable behavioural trait.

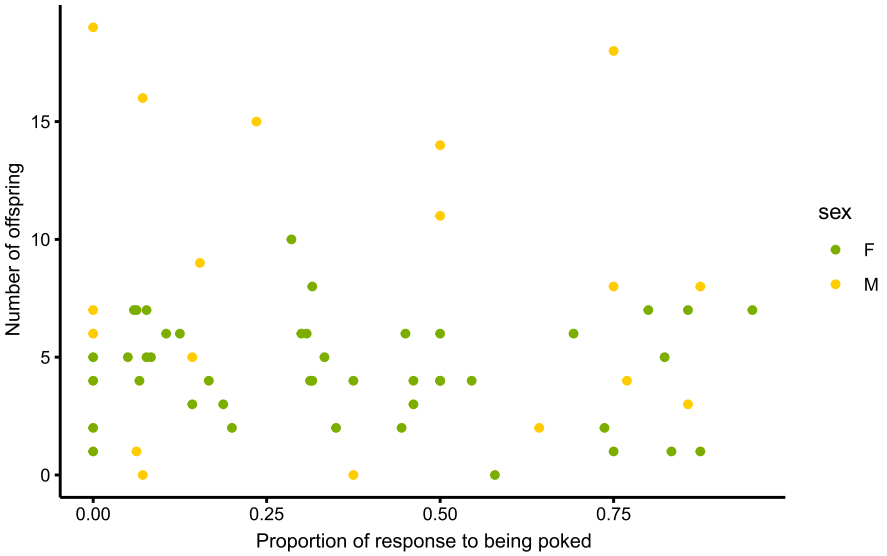

Figure 2. The absence of a correlation between individual behavioral variation and reproductive success. We measured the poke response as the proportion of times adult degus responded to being poked (0 = never responded and 1 = always responded).

While behavioural repeatability occurs for certain behavioural contexts, it is not an important factor in driving the composition of social groups in this population. Furthermore, we did not find that behavioural variability in the poke response was associated with differences in litter size (i.e., reproductive success).

4.1. Repeatability of individual behavioural differences

We observed that individuals differed consistently in their response to being prodded, which paralleled the results in Chock et al. (2017) in a degu population of central Chile. In contrast to Chock et al. (2017), we did not find that exploration was repeatable. This difference likely arose from differences in experimental designs, ecological conditions at the respective study sites, and the number of observed individuals and groups between studies. We studied exploration using an open field test where the degus were tested in an asocial context, whereas Chock et al. (2017) studied exploration in a social setting. As degus are a social species, the stress of being alone in an open field test may have influenced our results. But on the other hand, we obtained

a larger sample size and therefore had greater statistical power. In El Salitre (our study), we included data from 73 adults (51 females, 22 males) from 32 active burrows, while Chock et al. (2017) included data from 24 adult degus (9 females, 15 males) from 39 active burrows. Multiple populations of the same species can behave differently, e.g., house sparrows *Passer domesticus* (Bókony et al., 2012), great tits *Parus major* and blue tits *Cyanistes caeruleus* (Gaona-Gordillo et al., 2023), delicate skinks *Lampropholis delicata* (Brand et al., 2021), and red squirrels *Sciurus vulgaris* (Wauters et al., 2019), and, therefore, caution is warranted when generalizing the results of one study population across a species. Conversely, intra-specific comparisons allow one to study adaptation to the environment (Archard & Braithwaite, 2010). Especially, in changing environments comparing behaviour among populations may provide insight into evolutionary processes in adaptation to the environment (Brodin et al., 2013).

Behaviours may be less repeatable and more plastic when they are sensitive to environmental effects, such as traits subject to selection under predation risk or density (Bell et al., 2009; Réale et al., 2010; Laskowski et al., 2022). For example, predator presence can affect boldness and activity levels differently in prey species (Brown et al., 2005; Harris et al., 2010; Brown et al., 2014). Degus are preyed upon by numerous terrestrial and aerial predators (Jaksić et al., 1981) and are subject to changes in behaviour due to predation risk (Lagos et al., 1995; Vásquez et al., 2002). The constant risk of predation might drive selection towards an optimal behavioural response, where individuals respond in similar ways (Dingemanse et al., 2007). Thus, sensitivity to environmental effects may reduce the level of among-individual variation and thereby reduce repeatability (Boake, 1989; Nakagawa & Schielzeth, 2010).

4.2. Assortment

We did not find support for either the social niche specialization or the conformity hypothesis. Degus are not more likely to group with similar or dissimilar degus with respect to the willingness to attack a human handled object than expected by chance. Similar to our results, some species do not assort by individual behavioural variation, such as common waxbills, *Estrilda astrild* (Gomes et al., 2022) or baboons, *Papio ursinus* (Carter et al., 2015). In baboons, assortment by individual behavioural variation was mainly found in grooming networks but not proximity networks (Carter et

al., 2015). We looked at assortment in cohesion networks, where we combined the locations where we trapped and radio-tracked the degus over the entire field season. The examination of more fine-scale networks, such as daily foraging networks or interaction networks, might reveal different results. For example, foraging success or predator avoidance during social foraging may depend on group composition (Jolles et al., 2020). We may infer that in the context of group-living, differences in exploration in a social context (Chock et al., 2017), and not in the willingness to attack, provide greater benefit to degus in these social groups. Alternatively, the possibility that degu females assort into groups with similarly masculinized females (Correa et al., 2021) may mask the effects of individual behavioural variation on assortment.

4.3. Individual behavioural variation and reproductive success

We found no evidence that differences in the poke response were associated with differences in reproductive success. Including only data from one field season may have resulted in that we did not find an association, or the poke response does not provide relevant behavioural context for reproductive success in degus and the trade-off is simply absent between these two traits (Dochtermann, 2023). Instead of differences in individual behavioural variation, other socioecological factors, such as the interactions between food abundance and degu density, the number of males per group and the degree of masculinization in females influences reproductive success (Ebensperger et al., 2014; Hayes et al., 2019; Correa et al., 2021).

We found a clear sex difference for relative fitness. This result is unsurprising as degus mate with multiple opposite-sex individuals, and where males, but not females, benefit (Ebensperger et al., 2019). In our study, the females conceived offspring with an average of two males and males conceived offspring with an average of five females and we found greater skew in male reproductive success. Yet, the poke response did not differ between sexes. Males and females have different costs and benefits of group-living, where group-living seems relatively more costly for the females (Ebensperger et al., 2016, 2019; Hayes et al., 2019). But neither repeatability of nor assortment by individual behavioural variation explains this finding.

4.4. Future work

We found evidence of behavioural repeatability in one trait in our study population, but we did not find evidence in support of the social niche special-

ization and conformity hypothesis or that the repeatable trait was associated with reproductive success. Future studies could evaluate the link between behavioural variation and masculinization, assortment by masculinization levels, and the mechanisms behind the sex differences in the costs of group-living in degus. Evaluating how individual behavioural variation influences group composition brings us one step closer to understanding the role of individual behavioural variation in group-living animals.

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Appendix

A1. Open field test schematic

Figure A1. (Left) Open field box in situ with tetrapod (in blue) to hold video camera in place. (Right) Still image from video of behavioural trial. The box in the lower left corner of the OFB served as a hide for subjects, to which they acclimated for 3 min and, once opened, could return to for shelter.

A2. Methodological details

A2.1. Social group quantification

Social group membership of adult degus resulted from a combination of night-time telemetry (before dawn), and early daytime live trapping at burrow systems. We conducted night telemetry on all adult females for a minimum of 21 nights (mean = 40.0, SE = 1.7 nights). Females weighing 110–150 g were fitted with 5 g radiocollars (BD-2C; Holohil Systems, Carp, ON, Canada) and those weighing more than 150 g were fitted with 7 g radiocollars (PD-2C; Holohil Systems) with unique frequencies. We used an FM-100 receiver (for transmitters tuned to 164.000–164.999 MHz frequency; advanced Telemetry Systems, Isanti, MN, USA) and a handheld 3-element Yagi antenna (AVM Instrument or Advanced Telemetry Systems). Upon locating the animal, we recorded the burrow at which they were hiding.

Live trapping at burrow systems consisted of placing 10 Tomahawk traps (Tomahawk model 201, Tomahawk Live Trap, Hazelhurst, WI, USA) around burrow openings at each burrow system six days per week. Traps were opened and baited with rolled oats 1 h prior to sunrise and closed one hour after sunrise to ensure that captures occurred at or near the home burrows of

Table A1.
Total number ($n = 391$) of genotyped adult and offspring degus (2017).

Year of study	Number of adult females	Number of adult males	Number of offspring	Total
2017	63	29	299	391

the degus. Captured degus were transferred from the burrow at which they were captured to a processing station. On the first and all subsequent captures, we recorded animal ID and burrow number.

We built a symmetric similarity matrix of pairwise associations using both trapping and telemetry data (Whitehead, 2008). We calculated pairwise association indices by dividing the number of days that any two individuals were captured or tracked via telemetry at the same burrow by the number of days that both individuals were trapped or tracked via telemetry on the same day (Ebensperger et al., 2004). We determined social group composition by conducting hierarchical cluster analysis of the association matrix in SOCPROG 2.8 software (Whitehead, 2009). We considered only groups with an average association greater than 0.2 (i.e., 20% overlap of burrow system location) in the SOCPROG cluster analysis. We confirmed fit of the data with the cophenetic correlation coefficient, a correlation between the actual association indices and the levels of clustering in the diagram (Ebensperger et al., 2014), with values greater than 0.8 effectively representing the data (Whitehead, 2008). Maximum modularity criteria were chosen to cut off the dendrogram and define social groups (Newman, 2004). We included all radio collared females or individuals that were trapped four or more days. Total group sizes consisted of 3.95 ± 1.81 adults with 2.89 ± 1.57 females and 1.28 ± 0.57 males, $n = 19$ different social groups.

A2.2. Genetic analyses

We extracted DNA from a small piece (1×5 mm) of one ear cartilage tissue per individual (see Table A1 for total number of genotyped degus), using the Reliaprep DNA animal tissue miniprep system kit (Promega) and the tail mouse protocol. We worked with 10 microsatellite loci (Table A2), including 9 from *O. degus* (Quan et al., 2009) and one from *Spalacopus cyanus* (Schroeder et al., 2000), following the methods described by Correa et al. (2021) and Ebensperger et al. (2019). These loci were amplified with labeled primers with a fluorescent dye (FAM, VIC, NED, or PET) for subsequent screening in an ABI3500 (Thermo Fisher). Locus-specific annealing

Table A2.
Sequence, annealing temperature (T_a), size, and number of alleles of 10 microsatellite loci used to genotype degu adults and offspring.

Locus	Repeat motif	Primer sequence (5′ → 3′)	T_a (°C)	PCR product size (bp)	Number of alleles	GenBank Accession No.
OCDE1	$(CTTT)_{7CTCT}(CTTT)_{10}$	F: VIC-CTAGGTGCCAGAGACCCTTG R: CAAAGACCCTGGGTTCAATC	60	152–184	9	FJ418930
OCDE2	$(CA)_{13}$	F: VIC-GTTCGAGCTGCCTAGTGAGG R: ACTGGACATGGTGGTGTGTG	64	200–214	7	FJ418931
OCDE5	$(GAAA)_{11GAGA}(GAAA)_7$	F: FAM-CAAAGACCCTGGGTTCAATC R: CATGATTGAGCTTGCCTCTG	58	196–228	9	FJ418934
OCDE7	$(GAAA)_{13}(GA)_4$*	F: FAM-CAAGCTTGTCAAAGCACAGG R: GGCAGAAAATTCTGGACAGG	64	191–229	17	FJ418936
OCDE9	$(GA)_{23}$	F: FAM-CATGTAGTTTTCCAGGCACT R: TTCCTCCACTTTCTGACAAT	58	169–197	13	FJ418938
OCDE10	$(TG)_{13}$	F: NED-AAGGCAGCAGTTGGGAGAACAA R: TGAGATTGTCCTTTGAGTCCACATGA	64	157–185	10	FJ418939
OCDE11	$(CA)_{5TATA}(CA)_4$ GAGACAAATA$(CA)_{20}$	F: PET-TAGGAAGGAAAGGAGCTGGA R: CAACAAGCTCGGGTGATTTA	58	164–180	8	FJ418940
OCDE12	$(GT)_{15}$	F: PET-GCAGAGCTAAGGACTAAAGGTTCCA R: CCAAGTTGCTAAGAGGTCCCTTG	62	174–224	19	FJ418941
OCDE14	$(GT)_{20}(TG)_2$	F: FAM-GCTCTGGGGGCAATCAATATTCT R: AAACCACTACTTCTGCACTGTTCCA	58	150–174	12	FJ418943
SCY3	$(CA)_{20}$	F: NED-AAGTTGAGGCTAGTTGTTTG R: GATCACAGGCACCACATAC	52	125-151	12	AF250221

*OCDE7 was originally described as $(GAAA)_{15}$, a four motif repeat (Quan et al., 2009). However, the forward and reversal sequencing of this marker in our Molecular Facility revealed this is two motif repeat marker.

Table A3.
Analysis of Hardy–Weinberg expectations for each locus from study year 2017.

Locus	2017				
	NA	H_{Obs}	H_{exp}	p-value	HW
OCDE1	10	0.835	0.839	0.080	NS
OCDE2	13	0.853	0.834	0.167	NS
OCDE5	10	0.835	0.838	0.126	NS
OCDE7	7	0.692	0.709	0.041	NS
OCDE9	10	0.848	0.791	0.005	*
OCDE10	11	0.781	0.778	0.010	NS
OCDE11	9	0.815	0.793	0.008	NS
OCDE12	17	0.905	0.881	0.001	**
OCDE14	14	0.905	0.888	0.045	NS
SCY3	9	0.848	0.841	0.002	*

Data include the number of alleles (NA), observed heterozygosity (H_{obs}), expected heterozygosity (H_{exp}), Hardy–Weinberg p-value after Bonferroni corrections (p-value), and significant deviations from Hardy–Weinberg expectations highlights (HW). NS, not significant; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. The number of genotypes used during these analyses are given in Table A1.

Table A4.
Number of genotyped offspring assigned to a candidate mother and father, assigned to a candidate mother only, assigned to a candidate father only, and unassigned (2017).

Year of study	Number of offspring assigned to a candidate mother and father	Number of offspring assigned to a candidate mother only	Number of offspring assigned to a candidate father only	Number of offspring unassigned	Total
2017	239	0	0	60	299

temperatures are provided in Table A2. All loci amplified successfully and were polymorphic, and genotypes of all individuals were complete with no missing data. We tested the Hardy–Weinberg observed and expected heterozygosity with CERVUS 3.0 software (Marshall et al., 1998). Deviations from Hardy–Weinberg expectation were detected in 3 out of 10 loci (Table A3) and were not the consequence of null allele presence. All markers were checked for null alleles with MicroChecker software (van Oosterhout et al., 2004). This finding was expected because our study population was open,

non-panmitic, and characterized by a relatively high level of genetic relatedness (Quirici et al., 2011).

We used the CERVUS 3.0 software (Marshall et al., 1998) to estimate maternity and paternity. To do so, we examined the offspring, potential mothers, and potential fathers as trios in the population. Confidence calculation on CERVUS 3.0 was made using the logarithm to the base 10 of the odds score option. All 10 selected loci had a combined exclusion probability of 99.9% when neither parent was previously known (Table A4).

A3. Model results with sex as factor

Table A5.
To validate our choice of using sex as continuous variable instead of as a factor, we ran our repeatability models in 'brms' with sex categorized as female and male and compared model fit using LooIC and convergence.

Response	Sex	LooIC	Warnings
Latency to emerge from hide	Numeric	1490.40	None
	Factorial	1489.17	None
Proportion of time spent moving	Numeric	−300.28	None
	Factorial	−300.91	None
Total distance moved	Numeric	2023.88	None
	Factorial	2024.32	None
Poke response	Numeric	848.56	None
	Factorial	848.85	Divergent transition after warmup

A4. Multivariate framework results

Our MCMCglmm model looking at individual behavioural variation and reproductive success (litter size) did not converge as we had high autocorrelation and a trend in the time series using the model as specified below.

```
Mprior <- list(R=list(V=diag(c(1,0.0001),2,2), nu=1.002, fix=2),
G=list(G1=list(V=diag(2), nu=2,alpha.mu=rep(0,2), alpha.V=diag(25^2,2,2))))

MCMCglmm(cbind(scale(poke, scale=F), normfitness) ~
trait-1 + # a distinct intercept for each trait
at.level(trait,1):scale(trial, scale=FALSE) + # fixed effects are estimated only for
poke trait
```

```
trait:sex_scale, #estimates for the effect of these variables on each of our behaviours
random =~ us(trait):id, #fit an 'unstructured' (us) covariance matrix
for the grouping variable ID
rcov =~ us(trait):units, # residual variance, 'withinindividual variation'
family=c("categorical","gaussian"),
prior=Mprior,
nitt=750000, burnin=50000, thin=175,
verbose=TRUE,
data=as.data.frame(df))
```

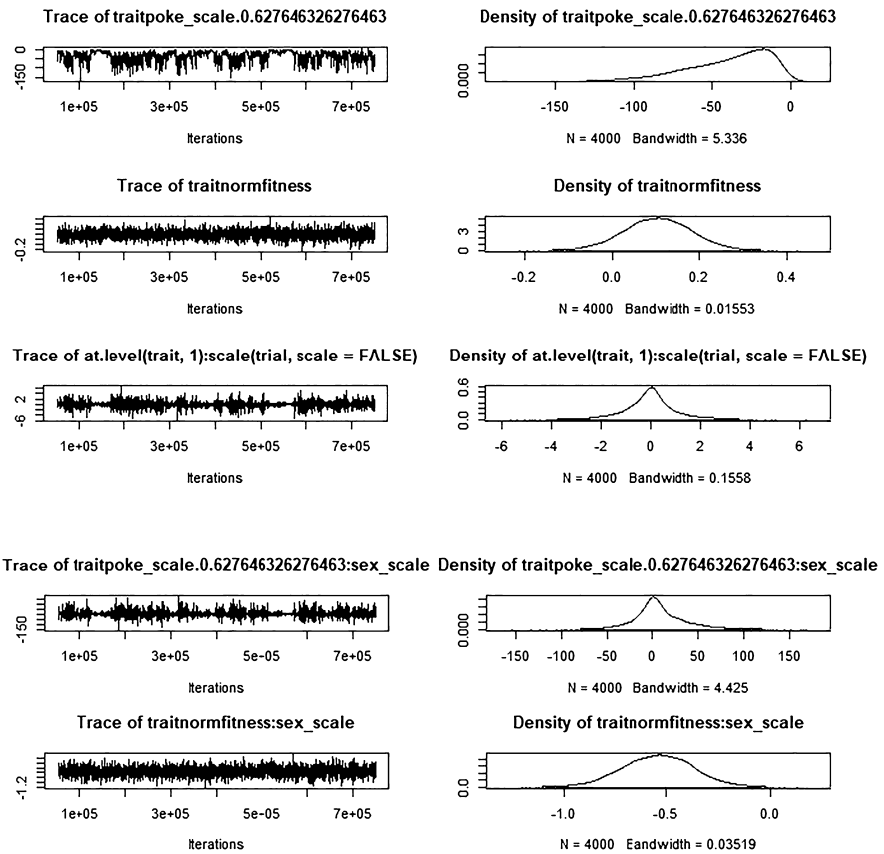

Figure A2. Trace plots (left-hand panels) and density plots (right-hand panels) of the dependent and independent variables of our multivariate mixed model. Plots are created using the MCMCglmm package.

Table A6.
Posterior mean and credible intervals of the independent and dependent variables of our multivariate framework.

Trait	Posterior mean	Lower 95% CI	Upper 95% CI	Eff. sample	pMCMC
Poke response	−39.67	−92.27	−3.15	119	*0.001*
Relative fitness	0.10	−0.05	0.25	4000	0.173
Trial	−0.09	−2.67	2.81	3911	0.90
Sex: poke	8.21	−56.82	75.76	2161	0.78
Sex: fitness	−0.55	−0.87	−0.18	4000	*0.002*

A5. Variance components of the individual behavioural variation traits

Table A7.
Variance components to calculate repeatability of individual behavioural variation in adult degus from a population in northern Chile.

Test	Behaviour	Variance component	Estimate (95% CI)
Open field	Latency to emerge from hide	Among-individual variance	4.573 (0.556–8.887)
		Among-group variance	0.705 (0.000–2.551)
		Residual variance	21.825 (17.364–26.881)
	Proportion of time spent moving	Among-individual variance	0.002 (0.000–0.004)
		Among-group variance	0.001 (0.000–0.002)
		Residual variance	0.016 (0.013–0.019)
	Total distance moved	Among-individual variance	12.262 (0.000–36.185)
		Among-group variance	14.078 (0.000–38.365)
		Residual variance	200.774 (165.82–241.83)
Poke	Poke response	Among-individual variance	2.565 (1.298–3.996)
		Among-group variance	0.14 (0.00–0.57)
		Residual variance	3.29

A6. Assortment

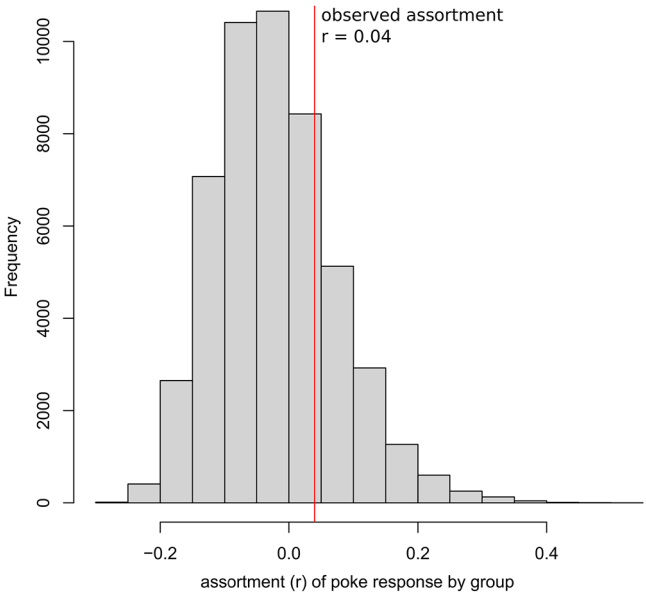

Figure A3. Frequency of simulated assortment of the poke response by group and the observed assortment (red solid line).