ENVIRONMENTAL IMPACTS ON BEHAVIOR AND PERSONALITY IN THE CAVIOMORPH RODENT, *OCTODON DEGUS*

A Thesis
Submitted to the Graduate Faculty
of the
North Dakota State University
of Agriculture and Applied Science

By

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In Partial Fulfillment of the Requirements
for the Degree of
MASTER OF SCIENCE

Major Department:
Biological Sciences

April 2019

Fargo, North Dakota

North Dakota State University
Graduate School

Title

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

MASTER OF SCIENCE

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ABSTRACT

Environmental factors can have large impacts in shaping the way that animals behave. Biotic elements, such as predators and conspecifics that individuals interact with, are two environmental factors that animals may encounter on a regular basis. Here, we present the results of two studies examining the relationship of these biotic factors to behavior and personality in the degu (*Octodon degus*), a social rodent species endemic to central Chile. We found that long-term experimental isolation from predators has not impacted behavior, as indicated by an open field test in this species. We also found that social groups in this species do not adhere to either conformity or social niche specialization expectations with regard to personality, as determined in open field tests. These results raise further questions as to the mechanisms that govern behavior, as well as how personality evolved and is maintained in natural populations.

ACKNOWLEDGEMENTS

I would like to thank Dr. Erin Gillam, Dr. Ned Dochtermann, Dr. John McEvoy, Dr. Loren Hayes, Dr. Luis Ebensperger, Dr. Rodrigo Vásquez, Dr. Raphaël Royauté, Dr. Douglas Kelt, Dr. Peter Meserve, Dr. Carolyn Bauer, Sara Grillo, Kevin Cortes, Monica Anderson-Berdal, and Courtney Garrison for their valuable contributions during the development and implementation of this work. I would also like to thank Juan Monardez, Anne Sabol, Madeline Cychowski, Rachel Davis, Diana Polania, Javier Bustos Madrid, and Dylan Fountaine for their countless hours of assistance in the field. A special thanks to all those that I am lucky enough to call family and friends, as this work would not have been possible had it not been for your support. Finally, I thank the North Dakota State University Department of Biological Sciences as well as the North Dakota State University College of Science and Mathematics for their support during completion of this work.

DEDICATION

This work is dedicated to all of the degus that took part in these studies for allowing me the opportunity to view the world through their eyes.

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BFJNP	Bosque Fray Jorge National Park
BLUP	Best Linear Unbiased Predictor

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CHAPTER 1: IMPACTS OF LONG-TERM EXPERIMENTAL EXCLUSION FROM PREDATION IN THE RODENT, *OCTODON DEGUS*

1.1. Abstract

Predation acts as a powerful selective force, shaping both morphological and behavioral characteristics of prey species. Antipredator behaviors can manifest in several forms, such as signaling both to predators as well as conspecifics, fleeing after contact with a predator, or by altering behavior to avoid encounters with predators. However, it has been documented that some prey species that become isolated from predators may lose these antipredator behaviors. While the loss of these behaviors has been documented, to date no experiments have been carried out in naturally occurring populations to determine the time frame over which this loss may occur. Here, we assess behavior in an open field test for *Octodon degus* captured at a site where predators have been excluded for more than 25 years and compare their behavior to animals in an area where predators still have access. We did not find significant differences in the behavior of animals between sites, suggesting that either not enough time has passed since the implementation of predator exclusions for any discernible differences to evolve, or that exclusion from predators has no impact on behavior. Further refinements in methodology in future studies may help elucidate whether alterations in other behaviors are occurring in this population.

1.2. Introduction

As one of the primary sources of mortality in many naturally occurring populations, predation acts as an important selective force on the antipredatory morphology and behaviors of prey species. Thus, antipredatory morphological traits can arise in prey species, such as crypsis, protective armor, or chemical defenses (Apfelbach et al., 2005; Lima and Dill, 1990). Along with selection on these morphological characteristics, predation also exerts selective pressure on behavior of the prey species, leading to the development of predator avoidance behaviors (Apfelbach et al., 2005).

One option that prey species have to avoid predation is to respond behaviorally after a predator has been detected by signaling to conspecifics regarding the presence of a predator (Slobodchikoff et al., 1991), signaling to the predator (i.e. flagging behavior in white-tailed deer; Caro, 1995), or by fleeing the area altogether, a common tactic observed in many species (Lagos et al., 2009). Another option that prey species can use to avoid predation is to alter their behavior to minimize the likelihood of having an encounter with a predator at all. This is manifested in cases such as schooling behavior observed in many fish species (Seghers, 1974) and avoidance of areas where predators are likely to occur (Apfelbach et al., 2005).

Unlike selection on morphological characteristics, which takes place over a long period of time, behavior is highly plastic and can be adjusted to fit the perceived risk of predation (Lima and Bednekoff, 1999). This can take the form of changes in behaviors, such as habitat use, foraging, and activity over a short period of time, to decrease the chances of having an encounter with a predator when risk of predation is high (as cited in Lima and Dill, 1990). Conversely, when prey species experience a decrease in predation risk, antipredator adaptations can be lost. Loss of both antipredator morphological and behavioral traits has been observed in a variety of taxa that exist in environments with relaxed predation risk (Lahti et al., 2009), as is the case on many islands (Blumstein & Daniel, 2005). While the loss of such traits has been observed, the time frame over which they are lost has yet to be experimentally examined.

The present study assesses the antipredator behavior of common degu (*Octodon degus*) populations that have experienced either high or low levels of predation risk as part of a long-term manipulation experiment. We predicted that animals experiencing low predation risk would display riskier behaviors in comparison to animals experiencing high predation risk. Such a finding would imply the loss of antipredator behaviors.

1.3. Methods

1.3.1. Study Site

The current study was carried out in Bosque Fray Jorge National Park (BFJNP), Chile (71°39’47.54” W, 30°39’30.53” S). BFJNP is the site of a large-scale, long-term manipulation experiment set up to examine the influence of predation risk on small mammal and plant communities (Meserve et al., 2016). Predators in BFJNP consist mainly of several carnivorous bird species (Kelt et al., 2016) and the culpeo fox (*Lycalopex culpaeus*) (Gutiérrez et al., 2010; Meserve et al., 2016). The abundance of these predator species is relatively high in comparison to the surrounding area due to BFJNP being the largest intact scrub habitat in north-central Chile (as cited in Gutiérrez et al., 2010; Meserve et al., 2016).

Beginning in 1989, 16 grids were constructed (75 x 75 m = 0.56 ha) consisting of 4 treatments. For the purposes of this study, 2 of these treatments were utilized: 1) predator exclusion plots (n=4) and control plots (n=4) (for grid layout, see Yunger et al., 2007). The predator exclusion plots were constructed using chain-link fencing with ground-level holes to allow access for small mammals but block access to terrestrial predators. These plots were also covered by netting suspended above to block access to aerial predators. The control plots were accessible to both small mammals and predators (Meserve et al., 2016). Controls were initially constructed with low fencing containing holes, but, due to deterioration of the fencing, the perimeter of these grids is now demarked by the remaining wooden poles.

Having a system in which predators have been experimentally excluded for over 25 years was ideal for studying the behavioral impacts associated with relaxed predation risk. While long-term research at this site involves trapping all small mammals indiscriminately, the present study focused on the degu, a medium-sized rodent in this system.

1.3.2. Study Species

The degu is a semi-fossorial, diurnal rodent endemic to central Chile (Woods and Boraker, 1975). Degus are abundant and comprise a majority of the small mammal biomass in BFJNP (Meserve et al., 2016). The home-range of degus is roughly $38m^2$ (Hayes et al., 2007; Quirici et al., 2010; Quirici et al., 2011), and dispersing juveniles often occupy burrows spatially close to the burrow from which they disperse (Quirici et al., 2011). In our study site, degus in exclusion grids have been shown to survive significantly longer in comparison to the control grids (Meserve et al., 1993). Previous field studies have shown differences in microhabitat use (Lagos et al., 1995b) and foraging behavior of degus in the predator exclusion grids compared to degus within the control grids (Yunger et al., 2002). However, a subsequent study did not detect differences in foraging behavior between treatments, attributing this discrepancy to slight differences in methodology or potentially to temporal variations in population sizes (Kelt et al., 2004). The current study utilizes a standard behavioral test to evaluate the behavior of degus from the control and experimental plots.

1.3.3. Trapping and Behavioral Trials

Trapping occurred from October – November 2016. We surveyed grids for visual cues indicating the presence of degu burrows (burrow entrances, fresh feces, tracks, runways, etc.). Tomahawk live traps (Tomahawk Live Trap Company, Hazelhurst, WI) were placed near active burrows and baited with plain, rolled oats. In predator exclusion grids, we placed traps at burrows in the interior of each grid, thus ensuring that captured degus were likely to have home ranges within the grid. Due to low degu densities in two of the control grids, we created surrogate controls by placing traps at burrows within 30m of two of the permanent control grids. Due to the spacing of the control grids, the home ranges of degus in these grids should not have overlapped with the predator exclusion grids. Traps were opened at sunrise, remained open for a maximum of 4 hours, and were checked periodically during this time to ensure that captured degus did not overheat (see Lagos et al., 1995a) and were not harassed by predators. Captured degus were taken to a location away from the grids where behavioral trials were performed.

Degu behavior was measured using an open field test, a test commonly used in a laboratory setting to measure multiple behaviors in a variety of taxa (Perals et al., 2017; Réale et al., 2007) including degus (Braun et al., 2003; Popović et al., 2009). Each degu was placed into a small, enclosed metallic hide within a larger open field box (89 x 89 x 142 cm) (Fig. 1.1). The hide was placed in a corner of the open field box and rotated among the four corners between trials to eliminate effects of hide placement. After a 3-minute acclimation period, a door was opened on the hide allowing the degu access to the open field box. Degus were recorded on video for 7 minutes, at which time the recording was stopped, and the degu was removed from the open field box.

All trapping, handling, and behavioral trials were conducted in accordance with the North Dakota State University Institutional Animal Care and Use Committee under protocol #A16068 and the University of Tennessee at Chattanooga Institutional Animal Care and Use Committee under protocol #0507LH-02. Research was conducted under Chilean permits issued by the Servicio Agricola y Ganadero (1259/2016).

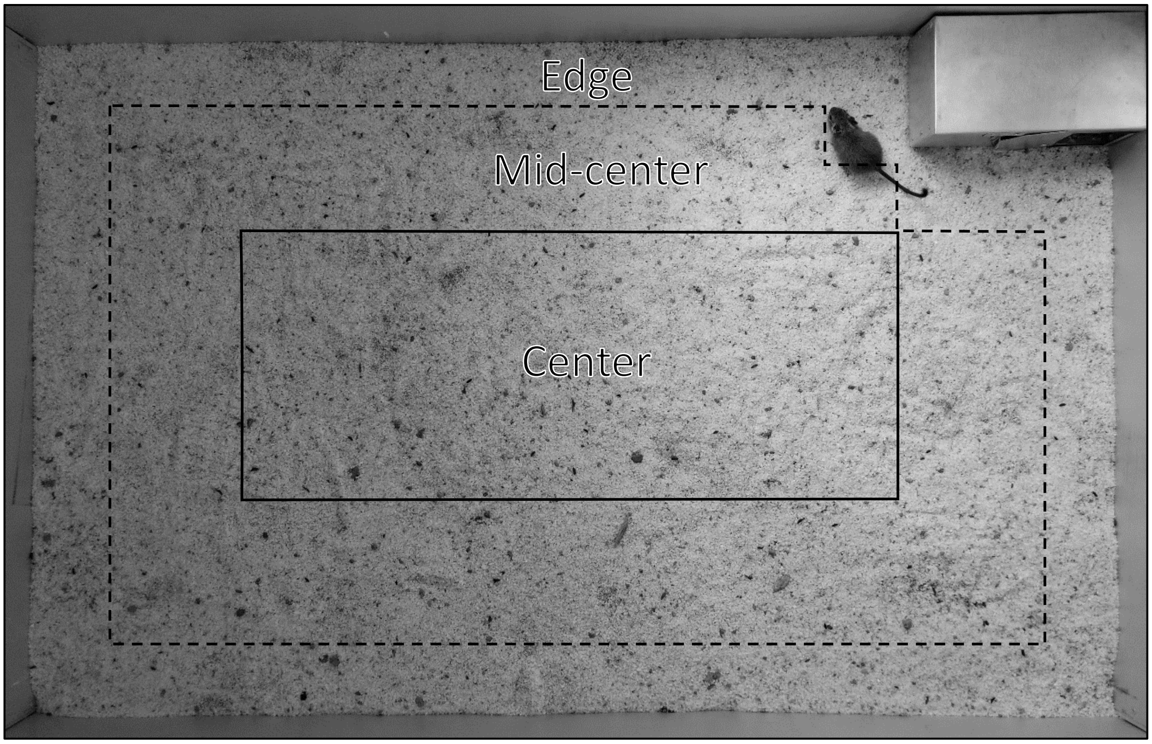

Figure 1.1. Image of the inside of the open field box with the metallic hide placed in the top right corner and a degu in the edge cumulative zone. The dashed line demarcates the transition from the edge to the mid-center cumulative zones. The solid line demarcates the transition from the mid-center to the center cumulative zones.

1.3.4. Video Analysis

Due to variation in the placement of the camera each day, videos were edited in Lightworks (EditShare LLC) to standardize the position of the open field box on the screen. This was done to make the videos uniform for analysis by Ethovision XT9 (Noldus Information Technology), a behavioral tracking software package. Edited videos were then converted to the mpeg2 format using Any Video Converter (Anvsoft Inc.) for compatibility with a behavioral tracking software. Within Ethovision XT, the open field box was divided into 150 zones which were then assigned to 1 of 3 cumulative zones based on their position: 1) center, the area in the center of the box; 2) mid-center, the area between the center and edge; and 3) edge, the area directly next to the walls of the box and the metallic hide (Fig. 1.1). Behaviors measured by

Ethovision XT included: time to emergence of full body (s), total time spent moving (s), and duration of time spent in each of the three cumulative zones (s). Each video was checked individually to ensure that the software was tracking correctly. One behavior, whether the degu fully emerged or not, was not explicitly recorded by Ethovision XT and was recorded manually from the videos.

1.3.5. Statistical Analysis

We used a generalized linear mixed effects model with a binomial error distribution and logit link function was used in the analysis of whether the degu fully emerged from the metallic hide or not. Linear mixed effects models were used to determine the role that risk of predation plays in latency to emergence from the hide, total proportion of time spent moving, and proportion of time spent in the edge cumulative zone. For all models, treatment, sex, and age of the animal were used as fixed effects and grid number was used as a random effect. Due to small sample sizes within each of the fixed effects categories, we did not test interactions of these variables. Models were fitted in R 3.4.4 (R Development Core Team 2018) with the lmer and glmer functions in the lme4 package. Results from the generalized linear mixed effects model and the linear mixed effects models were extracted using the Anova function in the car package, and the anova function using a Kenward-Roger degrees of freedom approximation in the lmerTest package (Kuznetsova et al., 2017) respectively. Summary statistics for each behavior can be found in Table A1.

1.4. Results

In total, we tested 71 individual degus. In the control grids, 36 degus (7 adult males, 8 adult females, 13 juvenile males, and 8 juvenile females) were included in analysis. In the predator exclusion grids, 35 individuals (6 adult males, 12 adult females, 12 juvenile males, and

5 juvenile females) were included in analysis (Table 1.1). We included all 71 individuals in the generalized linear mixed effects model testing for effects on full body emergence from the hide. Of the 71 individuals, 36 did not emerge from the hide (Fig. 1.2). Only the 35 individuals that fully emerged from the hide were included in the linear mixed effects models evaluating effects on latency to emerge, proportion of time spent moving, and proportion of time spent in the edge zone. Of these, 18 (2 adult males, 3 adult females, 8 juvenile males, and 5 juvenile females) were from control grids, and 17 (3 adult males, 7 adult females, 4 juvenile males, and 3 juvenile females) were from predator exclusion grids.

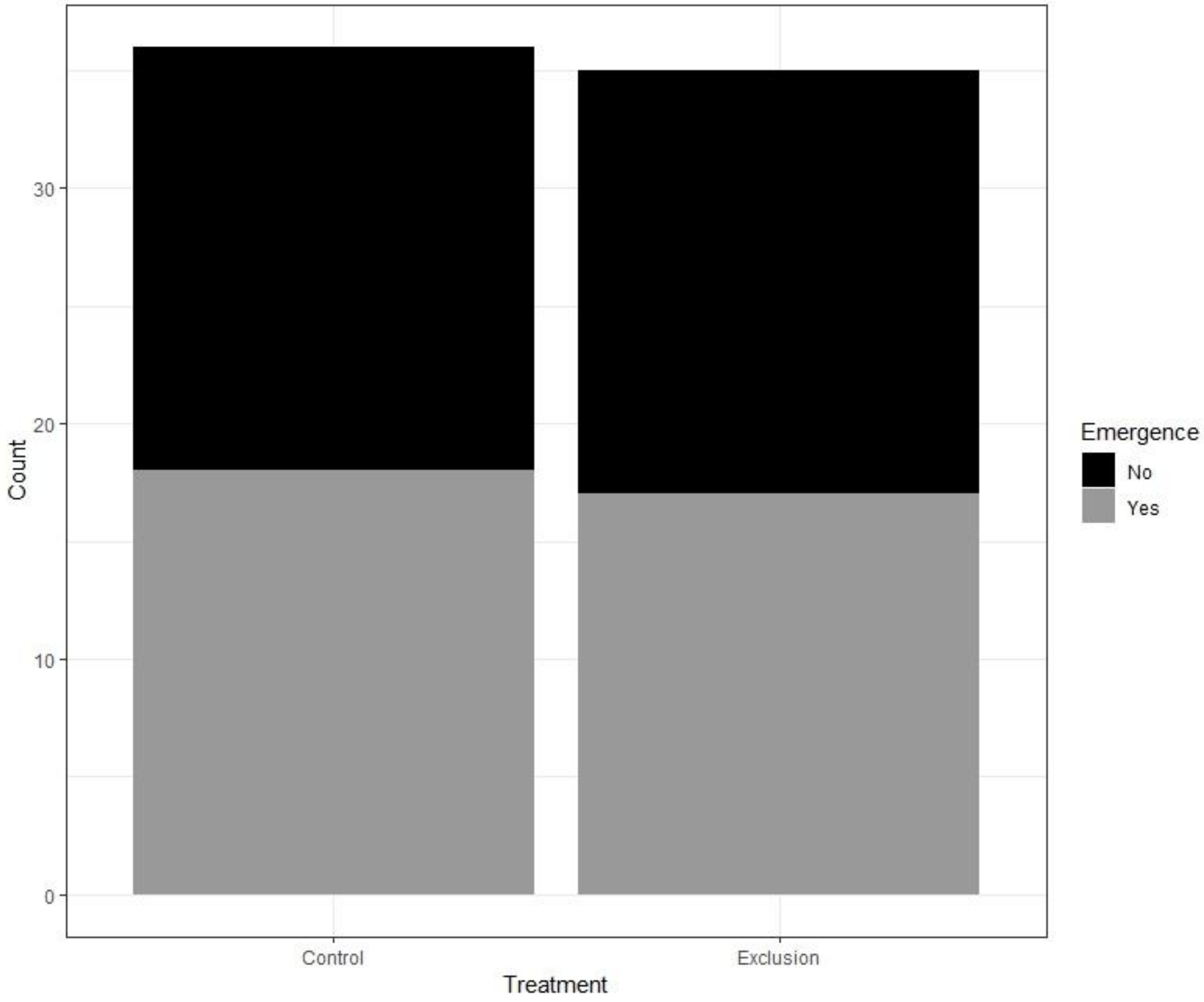

Figure 1.2. Number of individuals by treatment that emerged and did not emerge from the metallic hide.

Table 1.1. Sex and age class demographics by control and predator exclusion grids. Grid numbers with decimals indicate surrogate control grids. Numbers not in parentheses indicate animals included in generalized linear mixed effects model for full body emergence. Numbers in parentheses indicate animals included in linear mixed effects models for latency to emerge, proportion of time spent moving, and proportion of time spent in the edge zone.

	Adult Male	*Adult Female*	*Juvenile Male*	*Juvenile Female*	**Total**
Control					
3	2 (1)	2 (2)	4 (3)	3 (1)	11 (7)
6.1	0 (0)	2 (1)	3 (2)	1 (0)	6 (3)
11	2 (1)	2 (0)	4 (2)	2 (2)	10 (5)
11.1	3 (0)	2 (0)	2 (1)	2 (2)	9 (3)
Control Total	*7 (2)*	*8 (3)*	*13 (8)*	*8 (5)*	*36 (18)*
Exclusion					
1	1 (1)	3 (2)	5 (2)	2 (1)	11 (6)
2	2 (0)	4 (2)	4 (1)	1 (1)	11 (4)
10	1 (1)	3 (1)	2 (1)	0 (0)	6 (3)
14	2 (1)	2 (2)	1 (0)	2 (1)	7 (4)
Exclusion Total	*6 (3)*	*12 (7)*	*12 (4)*	*5 (3)*	*35 (17)*
Total Both Treatments	**13 (5)**	**20 (10)**	**25 (12)**	**13 (8)**	**71 (35)**

There was no effect of treatment ($\chi2=0.0062$, df=1, p=0.9373), sex ($\chi2=1.0408$, df=1, p=0.3076), or age class ($\chi2=0.7102$, df=1, p=0.3994) on whether a degu fully emerged from the metallic hide or not (Table 2). There was no effect of treatment ($F_{1,6}=1.3153$, p=0.2935), sex ($F_{1,27}=1.1785$, p=0.2873), or age class ($F_{1,27}=0.1854$, p=0.6702) on latency to emergence from the metallic hide. There was also no effect of treatment ($F_{1,6}=0.0893$, p=0.7748), sex ($F_{1,27}=2.4459$, p=0.1294), or age class ($F_{1,27}=1.9663$, p=0.1721) on proportion of time spent moving in the open field. Finally, there was no effect of treatment ($F_{1,5}=3.1933$, p=0.1304), sex ($F_{1,29}=2.6292$, p=0.1158), or age class ($F_{1,30}=0.3764$, p=0.5442) on proportion of time spent in the edge zone (Table 3).

Table 1.2. Results of the generalized linear mixed effects model testing for effects on full emergence of degus from the metallic hide.

		χ2	***d.f.***	***Pr(>χ2)***
Full Emergence	*Treatment*	0.0062	1	0.9373
	Sex	1.0408	1	0.3076
	Age	0.7102	1	0.3994

Table 1.3. Results of the linear mixed effects models testing for effects on latency to emerge, proportion of time spent moving, and proportion of time spent in the edge cumulative zone.

		Mean of Squares	***Numerator d.f.***	***Denominator d.f.***	***F value***	***Pr(>F)***
Latency to Emerge	*Treatment*	27.5568	1	6.2371	1.3153	0.2935
	Sex	24.6906	1	27.0201	1.1785	0.2873
	Age	3.8834	1	27.0638	0.1854	0.6702
Proportion Time Moving	*Treatment*	0.001220	1	6.2274	0.0893	0.7748
	Sex	0.033418	1	27.1726	2.4459	0.1294
	Age	0.026865	1	27.2442	1.9663	0.1721
Proportion Time in Edge	*Treatment*	0.071247	1	5.3276	3.1933	0.1304
	Sex	0.058662	1	28.8085	2.6292	0.1158
	Age	0.008398	1	29.6096	0.3764	0.5442

1.5. Discussion

For all four behaviors measured here (emergence, time to emergence, proportion of time spent moving, and proportion of time spent in the edge zone), we found that level of exposure to predation within the grids played no role in determining the response of degus to the open field test. Similarly, sex and age class were not predictive of behavioral response for all four behaviors. Our results are in accordance with the findings of Kelt et al. (2004), who found no differences in giving-up densities between small mammal communities in control grids and those in predator exclusion grids.

The most likely explanation for our findings is that degus have not been isolated from predators long enough to observe changes in behavior. Blumstein et al. (2000) found that tammar wallabies (*Macropus eugenii*) still react to visual predator cues despite having been isolated for roughly 9,500 years from predators. It has been suggested that behaviors associated with an underlying physiological response may be less sensitive to changes in selection pressures (Coss, 1999, as cited in Blumstein et al., 2000). How degus respond to predation risk may be better explained by physiological mechanisms which are less susceptible to change, especially over short periods of time.

There are a variety of other possible explanations for the lack of behavioral differences. As stated by Kelt et al. (2004), one possibility is that the degus in the predator exclusion grids do not perceive reduced predation risk. One potential explanation for a lack of perceived protection is that, since predators still exist in the vicinity of the degus in the exclusion grids, these degus are still reacting to visual, olfactory, or acoustic predator cues. As the degus in the predator exclusion grids are able to pass freely to the outside of the grid and since fencing does not visually block the predators, the degus are still able to come into contact with a variety of predator cues.

Another possibility is that high gene flow may have limited divergence among the plots. As the degus are able to move freely in and out of the predator exclusion plots, there exists the potential for gene flow, which could dilute any effects of selection on behavior in this system. Gene flow has been shown to constrain antipredator adaptations in the past (Storfer & Sih, 2009), and it is likely that the degus in the exclusion grids frequently breed with degus from outside of the exclusion grids. The amount of gene flow among grids should be examined in future studies to determine if this is one mechanism that could be acting as a constraint in this system.

Another potential explanation is that the open field test used in our study is not an accurate measure of behaviors that may be experiencing relaxed selection from predation in the predator exclusion grids. It is possible that response to a novel environment is not dependent on past experiences with predators. For example, it has been observed in baboons that response to a novel object was not correlated with antipredator behavior (Carter et al., 2012). Similarly, no difference in behavior would be expected between degus in control grids and those in predator exclusion grids if antipredator behavior is not comparable to response to a novel environment in this species. Further, it may be possible that the methodology for the open field test in our study was flawed. Three of the four behaviors measured in this study were reliant on the degu emerging from the metallic hide, which resulted in relatively low sample sizes for these behaviors, thus decreasing the power to detect differences in these behaviors.

Here, we found no differences in behavior between animals in natural predation conditions and animals in relaxed predation conditions. The lack of difference may be attributable to either underlying physiological mechanisms associated with behavior or to the animals not perceiving that there is reduced risk of predation within the exclusion grids, as they may come into frequent contact with several kinds of predator cues. Future work examining other types of behaviors in the two study populations will be valuable for teasing apart these different hypotheses.

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CHAPTER 2: PERSONALITY AND SOCIAL ASSORTMENT IN THE RODENT, *OCTODON DEGUS*

2.1. Abstract

Understanding the evolution and maintenance of animal personality, defined as consistent individual differences in behavior, has become a topic of interest in the field of behavioral ecology in the last 15 years. Much attention has been given to examining the conditions under which high behavioral repeatability, which coincides with low plasticity, has evolved. One body of thought posits that limited plasticity is a product of physiological or genetic constraints, while another suggests limited plasticity in behavior may be adaptive in nature, resulting in greater fitness under some circumstances. One factor that may act as a selective force on behavior repeatability is the pattern of social interactions between conspecifics. It may be advantageous for animals to form social groups with individuals with similar personalities, referred to as the conformity hypothesis; alternatively, competition for resources may result in selection favoring the formation of social groups composed of individuals with dissimilar personalities, known as the social niche specialization hypothesis. Here, we present a test of the comformity versus the social niche specialization hypothesis in a wild population of *Octodon degus.* We identified several social groups, tested animals in an open field test to quantify personality traits, and determined assortment based on personality across social groups in the population. We found evidence of personality for multiple traits in an open field test, but no assortment based on these traits was present in our population. The findings do not lend support to either the conformity or social niche specialization hypothesis in this species. Our results highlight the importance of evaluating personality in a broader context to better understand the evolution and maintenance of repeatable behavior.

2.2. Introduction

Animal personality, or individual differences in behavior that are consistent across time and contexts (Gosling, 2001), is well studied in the field of behavioral ecology. Much work has been carried out to quantify personality in populations across taxa (Bell et al., 2011; Réale et al., 2007), however little is currently known about the ultimate mechanisms that led to the development of personality. Recently, conceptual and empirical work has been carried out to understand the origin of animal personality and why consistent behavior would arise when behavioral flexibility may be favorable, such as when animals need to respond to an environment that is not always predictable (Réale et al., 2007; Réale et al., 2010).

Two hypotheses seek to explain the origin of personality: the constraint hypothesis and the adaptive hypothesis (Bell, 2012). The constraint hypothesis suggests that proximate mechanisms act in such a way as to limit the plasticity of behavior within individuals (Sih et al., 2004; Bell, 2012), while the adaptive hypothesis posits that the limited plasticity is itself a result of natural selection (Bell, 2005; Bell, 2012). Due to the inherent differences between these two hypotheses, tests of the constraint hypothesis put focus on genetic and physiological mechanisms underlying behavior, whereas the adaptive hypothesis tests the relationships between external forces (i.e. environment) and the behavior of an individual (Dingemanse et al., 2007). For instance, environmental factors, such as predation, have been shown to lead to personality differences between populations (Dingemanse et al., 2007), and predation has also been suggested as a selective pressure, driving the formation of traits related to personality within populations (Bell and Sih, 2007).

One key aspect of an individual’s environment is the conspecifics within a population that an individual regularly interacts with, or their social group. Group living can arise when the benefits of close association with conspecifics, such as predator avoidance, acquisition and maintenance of access to resources, and increased mating opportunities, outweigh the costs (Krause & Ruxton, 2002, as cited in Silk, 2007). Although belonging to a social group can benefit members of the group, costs associated with living in social groups generally include increased competition among group members for limited resources. However, this competition can be mitigated by individuals behaving differently than others in their group, a concept known as the social niche specialization hypothesis (Bergmüller & Taborsky, 2010; Montiglio et al., 2013). For example, some individuals may consistently travel further within the home range of the group to forage, while others may not stray far, thus reducing competition with other group members for those resources. The reduction in competition afforded through social niche specialization has been hypothesized to act as a source of positive feedback that may explain the formation and maintenance of personality within populations of social animals (Bergmüller & Taborsky, 2010; Wolf and Weissing, 2010).

An alternative hypothesis to the social niche specialization hypothesis, the conformity hypothesis, asserts that social groups will be composed of individuals with similar personalities (McCune et al. 2018). Strong social bonds of individuals with similar personalities has been demonstrated in a variety of taxa including three-spined sticklebacks (*Gasterosteus aculeatus*) (Pike et al., 2008), great tits (*Parus major*) (Aplin et al., 2013), Mexican Jays (*Aphelocoma wollweberi*) (McCune et al, 2018), California Scrub-Jays (McCune et al., 2018), and chimpanzees (*Pan troglodytes*) (Massen & Koski, 2014). Selection may favor similar groups due to negative consequences associated with intra-group conflicts driven by interactions of individuals with dissimilar personalities (Oliveira et al., 2001, as cited in McCune et al., 2018), or due to increased benefits accrued from grouping of animals with similar personalities such as enhanced foraging ability (Keiser & Pruitt, 2014). Given the inherent differences between these two hypotheses, high inter-individual variance in personality would be expected under the social niche specialization hypothesis, while low inter-individual variance would be expected under the conformity hypothesis.

We aimed to answer questions about behavioral repeatability and personality composition of social groups by studying a natural population of the common degu (*Octodon degus*), a semi-fossorial rodent species endemic to central Chile (Woods and Boraker, 1975). Degus are diurnal and forage above ground, but utilize burrows for shelter and as nests (Fulk, 1976; Kenagy et al., 2002). While degu social groups are not kin based (Quirici et al., 2010; Davis et al. 2015), degus have been shown to practice plural breeding with communal care (definition from Silk 2007), with females of a group nursing (Ebensperger et al., 2002), retrieving (Ebensperger et al., 2006a), as well as huddling and grooming the offspring of their social group indiscriminately (Ebensperger et al., 2007). Degus in large social groups have been shown to receive benefits from group living in the form of reduced predation risk as well as reduced energetic costs when making burrows (Ebensperger & Bozinovic, 2000; Ebensperger & Wallem, 2002; Ebensperger et al., 2006b). Degu personality has been quantified in a previous study, with individuals showing repeatable reactions to being prodded as well as repeatable movement within a trap (Chock et al., 2017). The study carried out by Chock et al. (2017) also lends support for the social niche specialization hypothesis, as animals assorted in groups that contained dissimilar individuals in regard to their movement within the trap.

Our specific objectives were to assess behavioral repeatability within a degu population and examine if social group composition supports the social niche specialization or conformity hypothesis. We measured several behaviors in a field setting that are different from those measured by Chock et al. (2017). We predicted that we would find evidence of repeatable behavior, and that social groups would consist of individuals with dissimilar personalities. If we determined these predictions to be true, this study would lend support to social niche specialization as an adaptive explanation for the evolution and maintenance of personality in degus.

2.3. Methods

2.3.1. Burrow Identification and Trapping

This study was carried out on a natural population of degus in a 1.79 ha area called El Salitre (71°37’50.09” W, 30°41’29.70” S), located outside the borders of, but near, Bosque Fray Jorge National Park, Chile. To determine which burrows were active, areas that showed signs of activity were selectively trapped, and captured degus were radio collared and tracked after sunset to determine which burrows were in use. Radio collars were removed upon subsequent capture. Following assessment of activity in the area, burrows were numbered and 10 Tomahawk live traps (Tomahawk Live Trap Company, Hazelhurst, WI) were placed near the entrances to active burrows. Trapping occurred six days per week between August-November of 2017, overlapping with the period in which gestation, parturition, and rearing of offspring occurs in adult female degus (Ebensperger et al., 2014). Traps were opened one hour prior to sunrise and closed one hour after sunrise to ensure that captures occurred at or near the home burrows of the degus. Captured degus were transferred from the burrow at which they were captured to a processing station. Upon first capture, animals were fitted with ear tags (Monel 1005-1, National Band and Tag Co. Newport, KY) 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 mass (g).

2.3.2. Social Group Quantification

Quantification of social groups closely followed the methods of an ongoing long-term study on degu sociality in another population (Ebensperger et al., 2011; Ebensperger et al., 2014). After parturition, females weighing less than 150g were fitted with 5g collars (BD-2C; Holohil System Limited, Carp, Ontario, Canada), and females weighing more than 150g were fitted with 7g collars (PD-2C; Holohil Systems Limited, Carp, Ontario, Canada). Radio telemetry was performed nightly between 1.5 hours after sunset and 1.5 hours before sunrise for a minimum of 21 consecutive days for each female. We used an FM-100 receiver (for transmitters tuned to 164.000-164.999 MHz frequency; advanced Telemetry Systems, Isanti, MN, U.S.A.) and a hand held 3-element Yagi antenna (AVM Instrument Co., or Advanced Telemetry Systems). Upon locating the animal, the burrow at which they were sleeping was recorded.

A symmetric similarity matrix of pairwise associations was created using both trapping and telemetry data (Whitehead, 2008). We calculated pairwise association indices by dividing the number of days that any 2 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). Social group composition was determined by conducting hierarchical cluster analysis of the association matrix in SOCPROG 2.8 software (Whitehead, 2009). Only groups with an average association greater than 0.2 (i.e. 20% overlap of burrow system location) in the SOCPROG cluster analysis were considered during group determination. Fit of the data was confirmed 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). While all radio collared females were included in this analysis, individuals that had not been radio collared had to have been trapped at the same burrow for a minimum of 4 days to be included.

2.3.3. Behavioral Trials

Behaviors of the individual degus were measured using an open field test. This type of test is commonly used to measure behavior across taxa (Perals et al., 2017; Réale et al., 2007) and has been utilized in the past with degus (Braun et al., 2003) Behavioral trials for adults took place from September-early October, while behavioral trials for juveniles took place from October-early November. Degus were placed in a small metallic hide which was then placed in the corner of a larger open field box (89 x 89 x 142cm). The corner in which the hide was placed was rotated before the beginning of each trial to eliminate effects of hide placement. Degus were acclimated to the hide for a 3-minute period, at which time a door on the hide was opened and the animal could move freely within the open field box. Each individual trial lasted 7 minutes and was recorded on video. We aimed to have individual degus participate in a minimum of 3 trials.

All trapping, handling, and behavioral trials were conducted in accordance with the North Dakota State University Institutional Animal Care and Use Committee under protocol #A16068 and the University of Tennessee at Chattanooga Institutional Animal Care and Use Committee under protocol #0507LH-02. Research was conducted under Chilean permits issued by the Servicio Agricola y Ganadero (5028/2017).

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 LLC). Exported files from this program were then changed to the mpeg2 video format with Any Video Converter (Anvsoft

Inc.) for compatibility with EthoVision XT 14 (Noldus Information Technology). In EthoVision XT, the open field box was divided into 150 zones which were then assigned to one of three cumulative zones based on their position: 1) center, the area in the center of the box; 2) mid-center, the area between the center and edge; and 3) edge, the area directly next to the walls of the box and the metallic hide. Behavioral data extracted included whether or not the animal emerged from the hide, latency to emergence (s), duration in the open field box (s), distance moved (cm), time spent moving (s), time spent in each of the cumulative zones (s), and velocity (cm/s). Each video was checked individually to ensure that the software tracked the animal correctly.

2.3.4. Statistical Analysis

2.3.4.1. Personality

Of the measured behaviors, four were used as response variables in models: latency to emerge, proportion of time spent moving, proportion of time spent in the edge zone, and velocity. One behavior, emergence from hide, was not included in analysis because emergence was nearly ubiquitous in the population, suggesting that this behavior was not suitable for determining differences between individuals in the population. Time spent moving and time spent in the edge zone were included as proportions to make them more independent from other behavioral measurements. We used the log of velocity to aid in model fitting. For all response variables, linear mixed effects models were fitted. All models contained fixed effects of sex, age, an interaction of sex by age, and video number. Date and ID were used as random effects in all models. Models were fitted in R 3.4.4 (R Development Core Team 2018) with the ‘lmer’ function in the lme4 package. Results for fixed effects were extracted from linear mixed effects model using the ‘anova’ function using a Kenward-Roger degrees of freedom approximation in the lmerTest package (Kuznetsova et al., 2017) (Table A2). To determine the intra-class correlation coefficient (repeatability) of ID, the ‘rpt’ function in the rptR package was used (Stoffel et al., 2017). Best linear unbiased predictors (BLUPs), values representative of an individual’s behavior relative to other individuals in the group, were extracted from models using the ‘ranef’ function in the lme4 package.

2.3.4.2. Social Assortment

To determine if assortment was occurring for any of the behaviors, matrices of social networks were created using the asnipe package and assortment by behavioral traits was calculated using the assortnet package based on the BLUPs for each behavior (Farine, 2014). Assortment (*r*) is calculated on a scale of -1 to 1, where -1 represents negative assortment (individuals in a group are dissimilar), 1 represents positive assortment (individuals in a group are similar), and 0 represents no assortment. Significance of *r* was determined by creating 45,000 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 (Chock et al., 2017). This calculation yielded a p-value, and calculated p-values were stable at 45,000 permutations. Due to observed variance differences between groups, this analysis was performed twice for all behaviors to ensure that the addition of pups was not impacting the *r* value for the population (Fig. 2.1). The analysis was performed once for all individuals in all social groups and again for only the adults in all social groups.

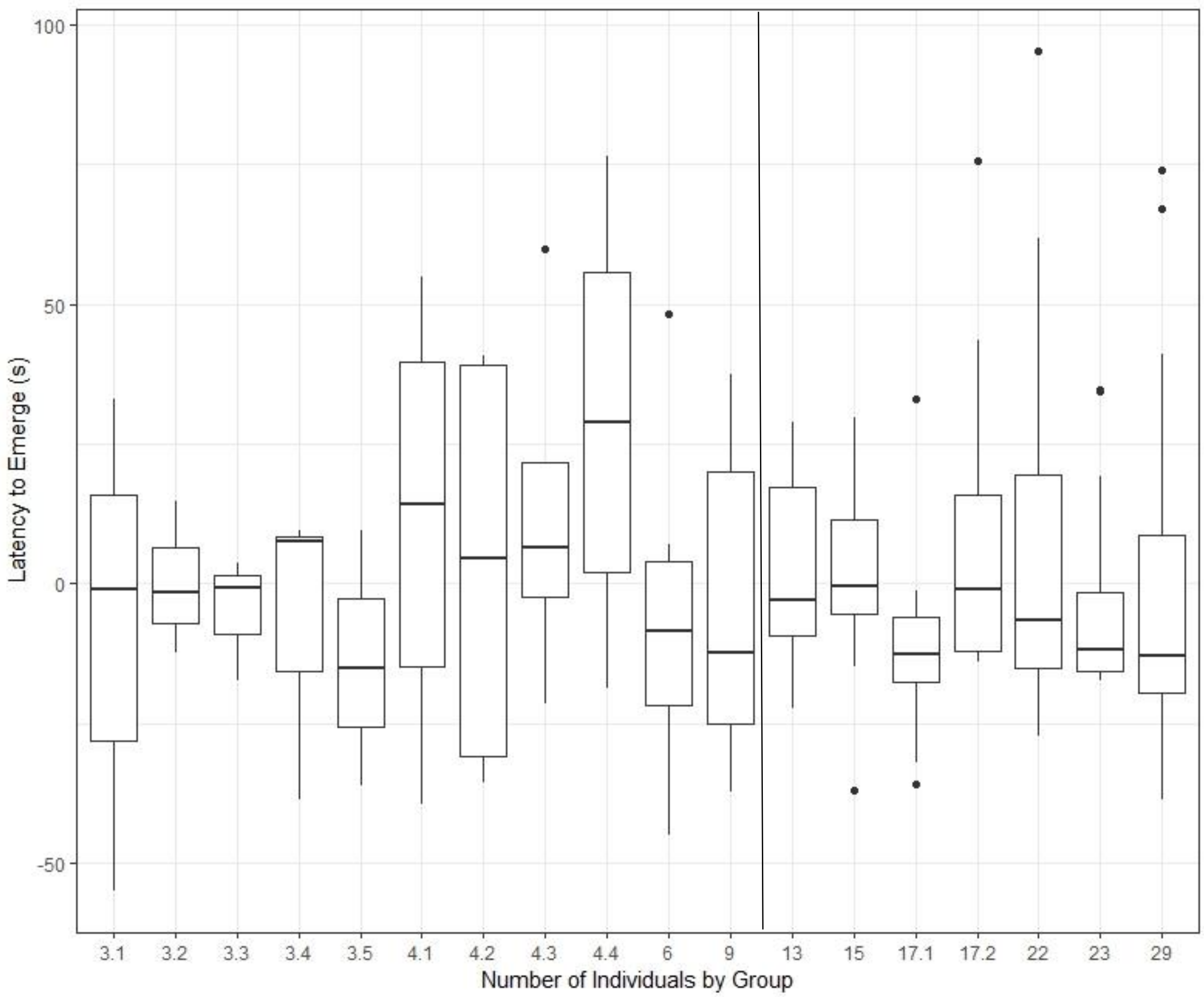

Figure 2.1. Boxplot of latency to emerge BLUPs by number of individuals per group. Numbers with decimal points represent order and are not representative of partial individuals. The solid black line between 9 and 13 individuals represents the separation between groups with only adults and one pup tested and groups in which multiple adults and pups were tested. See appendix for boxplots of other behaviors.

2.4. Results

2.4.1. Personality

Overall, our linear mixed effects models included 73 adults (51 females, 22 males) and 110 juveniles (59 females, 51 males), with a total of 550 observations over 51 days (observations per degu: mean=3.0, sd=1.03, range=1-6). We found evidence of personality for all 4 behaviors included in our analysis. Latency to emerge (r=0.175, p<0.001), proportion of time spent moving (r=0.124, p<0.001), proportion of time spent in the edge zone (r=0.166, p<0.001), and velocity (r=0.125, p<0.001) were all found to be repeatable in our population (Table 2.1). Repeatability values appear to be low in comparison to the reported average of 0.37 (Bell et al., 2009). However, past efforts to quantify repeatability generally did not include the influence of fixed effects, such that repeatability estimates are conservative due to the inclusion of fixed effects in the models in this study (Wilson, 2018).

Table 2.1. Results of repeatability test for ID using rpt function.

Behavior	*r*	*SE*	*CI (95%)*	*p*
Latency to Emerge	0.175	0.043	0.096-0.261	3.50E-06
Proportion Time in Edge	0.124	0.041	0.05-0.209	0.000297
Propotion Time Moving	0.166	0.045	0.083-0.257	3.62E-06
Velocity	0.125	0.039	0.051-0.205	0.000236

2.4.2. Social Assortment

In the analysis for social assortment, we used BLUPs extracted from the linear mixed effects models for all 183 individuals in the population. One individual was dropped from the analysis for social assortment because it was in a group alone. The remaining 182 individuals were spread out across 18 social groups consisting of adults and pups (range of individuals in groups: 3-29). Due to time constraints, pups were not tested for personality in 10 social groups, meaning that assortment in those groups was assessed only for adults. Only 1 pup was tested in 1 of the groups. Multiple pups and adults were tested in the remaining 7 social groups.

Across all individuals, we did not find evidence of social assortment for any of the measured behaviors. Groups did not consistently assort based on latency to emerge (r=-0.004, p=0.62), proportion of time spent in the edge zone (r=-0.012, p=0.49), proportion of time spent moving (r=0.03, p=0.07), or velocity (r=0.016, p=0.13) (Table 2.2). In the analysis of only adults, we again found no evidence for social assortment. Adults did not consistently assort into groups based on latency to emerge (*r*=-0.025, p=0.502), proportion of time spent in the edge zone (*r*=0.048, p=0.216), proportion of time spent moving (*r*=0.001, p=0.383), or velocity (*r*=0.028, p=0.278).

Table 2.2. Results from assortment analysis for all individuals in all social groups and adults in all social groups.

	Behavior	*r*	*SE*	*p*
All Individuals				
	Latency to Emerge	0.0282	0.01963	0.0834
	Proportion Time in Edge	-0.0042	0.01902	0.6226
	Proportion Time Moving	-0.0217	0.01934	0.3168
	Velocity	-0.0074	0.0196	0.5401
Adults Only				
	Latency to Emerge	-0.02467	0.06168	0.502
	Proportion Time in Edge	0.04774	0.06193	0.21607
	Proportion Time Moving	0.0014	0.06365	0.38258
	Velocity	0.02797	0.07252	0.27756

2.5. Discussion

We set out to test if degus show consistent individual differences in several behaviors and to determine whether individuals assort in social groups based on these behaviors. Consistent with our prediction regarding personality, we found evidence of individual repeatability for latency to emerge, proportion of time spent in the edge zone, proportion of time spent moving, and velocity in the population. However, in contrast to our predictions, we did not find evidence of consistent assortment across social groups based on these behaviors. Our results suggest that while behavioral repeatability occurs for these behaviors, it is not an important factor in determining the composition of social groups in this population.

To our knowledge, this is the first time that an open field test has been used to quantify personality for this species, and our detection of personality in the population suggests that this test may be an appropriate approach for questions regarding behavioral repeatability in future studies. However, future research should focus on assessing the ecological relevance of these behaviors. Past field studies have examined behaviors in degus, such as foraging behavior (Kelt et al., 2004), vigilance (Vásquez et al., 2002), and microhabitat usage (Lagos et al., 1995; Vásquez et al., 2002). While these studies focused on behavior at the population level, they did not account for individual differences in behavior. We suggest that work should be carried out to determine how behaviors in an open field test correlate to behaviors in a natural setting, with regard to individual differences, so that stronger inferences can be drawn from future lab and field studies.

We did not find support for either the conformity or the social niche specialization hypothesis. Although we did not find evidence for either hypothesis, more work would need to be carried out to completely rule out these hypotheses and to tease apart adaptive explanations for the evolution of personality. Chock et al. (2017) found negative assortment of animals based on exploratory behavior. As previously suggested, ecologically relevant correlates of behavior as measured in their study would need to be assessed in order to determine whether social niche partitioning is actually occurring in this species. Furthermore, we suggest that future work focus on designing a robust test of both the constraint and adaptive hypotheses by incorporating behavior both within and outside of the burrow (partitioning of parental care, foraging, usage of microhabitats, etc.), potential genetic and physiological mechanisms for the maintenance of behavior, and fitness consequences associated with different personality traits.

Currently, work is being carried out that is directly related to the present study in that individual and group fitness consequences associated with repeatability of different behaviors and associated patterns of group composition are being assessed. Once relatedness data is analyzed from collected tissue samples, the maternity and paternity of each pup can be determined. This data will allow us to determine the heritability of personality in degus and evaluate whether certain group personality compositions or individual personalities are associated with greater direct fitness.

Here, we performed a test of the social niche specialization and conformity hypotheses as adaptive explanations for the evolution and maintenance of personality in degus. Although we did find evidence of behavioral repeatability in several traits in our study population, we did not find evidence in support of either hypothesis. Future work focused on understanding behavioral repeatability of degus within the context of a broader framework will be valuable for drawing more direct conclusions about possible explanations for the evolution and maintenance of personality in this species.

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APPENDIX. SUPPLEMENTAL TABLES AND FIGURES

Table A1. Summary statistics for behaviors for each age class and sex both in predator exclusion and control grids.

	Latency to Emerge	**Proportion Time Moving**	**Proportion Time Edge**	**n=**
Control Adult Male	121.085 (6.306)	0.647 (0.054)	0.738 (0.024)	2
Exclusion Adult Male	20.920 (17.354)	0.638 (0.081)	0.698 (0.016)	3
Control Adult Female	18.729 (7.213)	0.502 (0.036)	0.565 (0.108)	3
Exclusion Adult Female	99.659 (42.426)	0.542 (0.072)	0.551 (0.059)	7
Control Juvenile Male	184.727 (35.594)	0.515 (0.046)	0.795 (0.054)	8
Exclusion Juvenile Male	62.544 (42.745)	0.532 (0.059)	0.563 (0.088)	4
Control Juvenile Female	111.503 (57.913)	0.503 (0.055)	0.686 (0.053)	5
Exclusion Juvenile Female	79.789 (59.370)	0.517 (0.050)	0.642 (0.107)	3

Table A2. Fixed effects from linear mixed effects models for latency to emerge, proportion of time spent moving, proportion of time spent in the edge zone, and velocity. Significant p-values are in bold.

Latency to Emerge	*Sum Sq*	*Mean Sq*	*NumDF*	*DenDF*	*F value*	*Pr(>F)*
sex	338.2	338.2	1	171	0.0552	0.8146
age.class	310988	310988	1	82.78	50.74	**3.55E-10**
video.number	8076	8076	1	113.4	1.318	0.2534
sex:age.class	2579	2579	1	171.8	0.4209	0.5174
Proportion Time Moving						
sex	0.02332	0.02332	1	174.3	1.816	0.1795
age.class	0.1637	0.1637	1	72.56	12.75	**0.000637**
video.number	0.666	0.666	1	184.9	51.88	**1.45E-11**
sex:age.class	0.04929	0.04929	1	173.8	3.839	**0.05166**
Proportion Time in Edge						
sex	0.02089	0.02089	1	173.3	2.092	0.1499
age.class	0.2165	0.2165	1	79.13	21.68	**1.28E-05**
video.number	0.004084	0.004084	1	146.9	0.409	0.5235
sex:age.class	0.000899	0.000899	1	173.3	0.09	0.7646
Velocity						
sex	0.8549	0.8549	1	176.8	5.382	**0.02149**
age.class	0.08037	0.08037	1	72.81	0.506	0.4792
video.number	4.068	4.068	1	260.9	25.61	7.90E-07
sex:age.class	0.8451	0.8451	1	175.5	5.321	**0.02224**

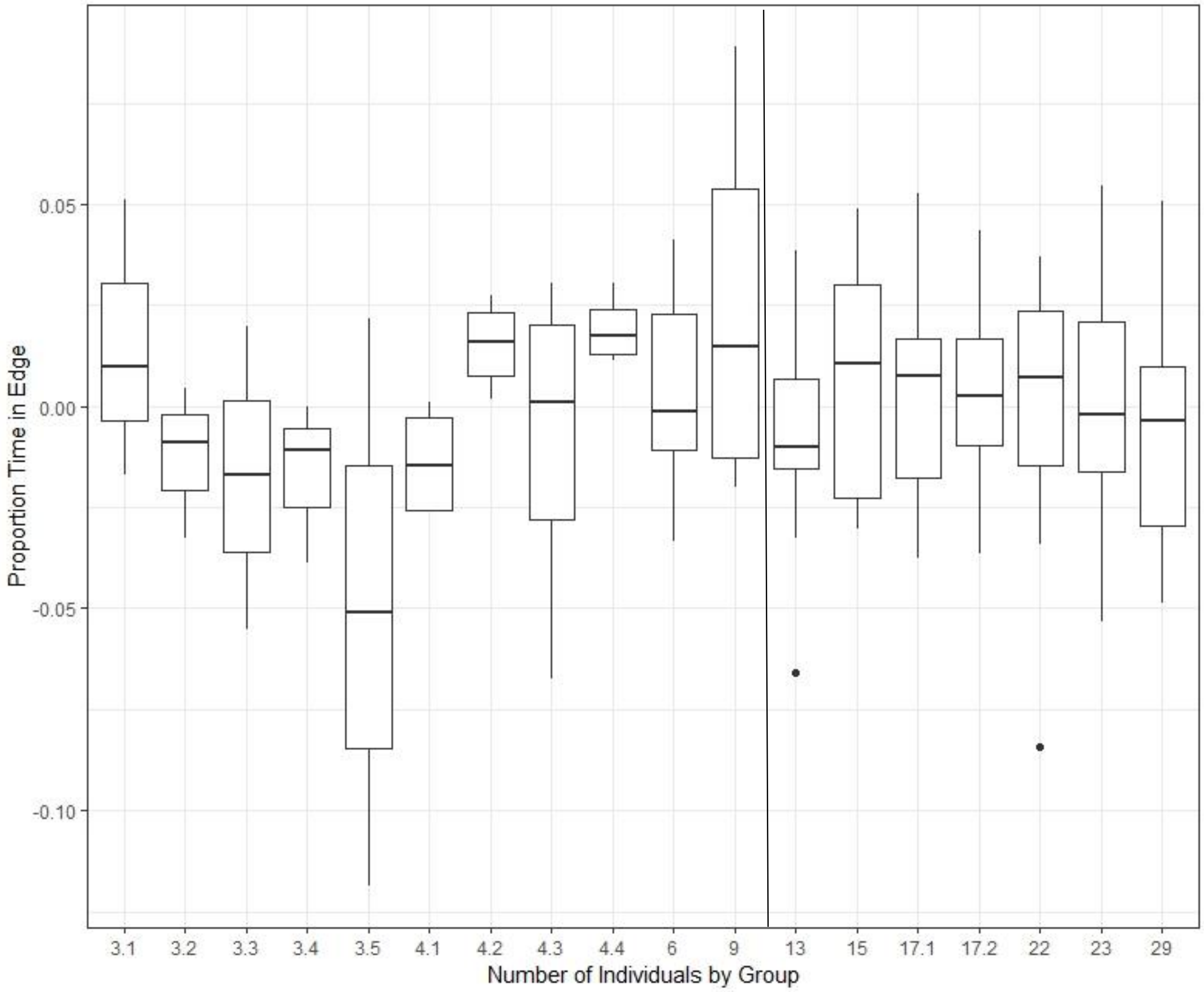

Figure A1. Boxplot of proportion of time spent in the edge zone BLUPs by number of individuals per group. Numbers with decimal points represent order and are not representative of partial individuals. The solid black line between 9 and 13 individuals represents the separation between groups with only adults and one pup tested and groups in which multiple adults and pups were tested.

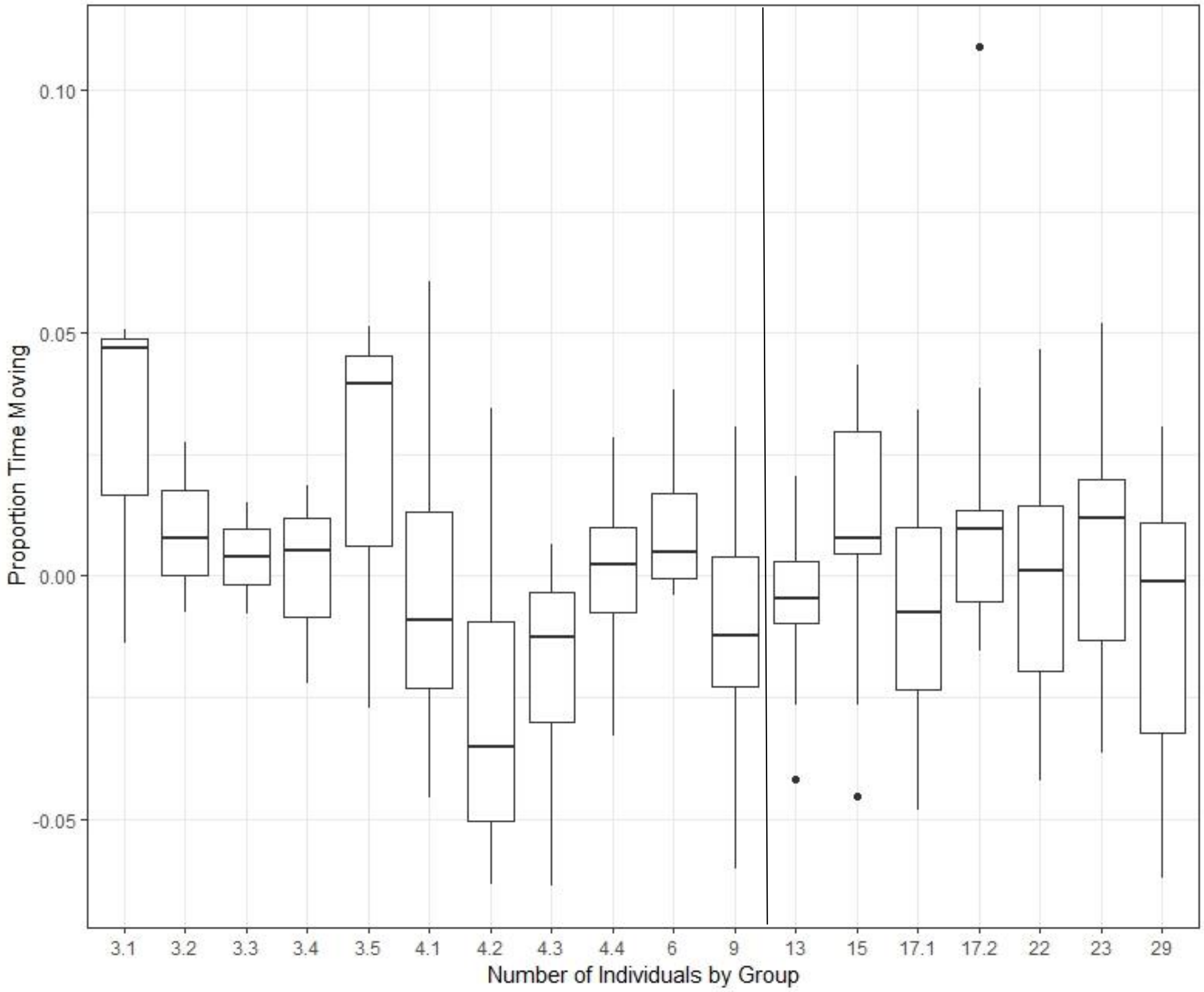

Figure A2. Boxplot of proportion of time spent moving BLUPs by number of individuals per group. Numbers with decimal points represent order and are not representative of partial individuals. The solid black line between 9 and 13 individuals represents the separation between groups with only adults and one pup tested and groups in which multiple adults and pups were tested.

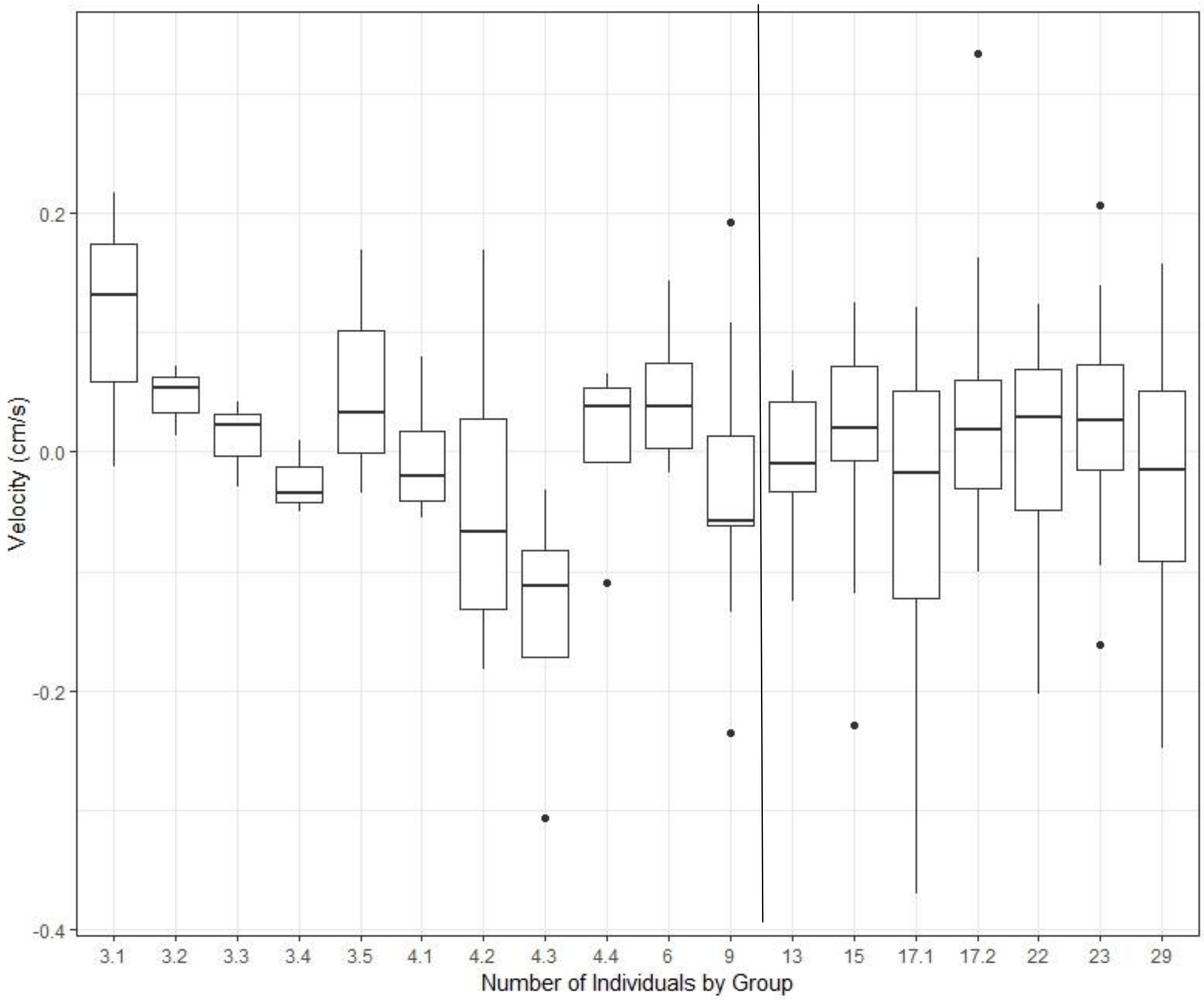

Figure A3. Boxplot of velocity BLUPs by number of individuals per group. Numbers with decimal points represent order and are not representative of partial individuals. The solid black line between 9 and 13 individuals represents the separation between groups with only adults and one pup tested and groups in which multiple adults and pups were tested.