DOES PERSONALITY AFFECT COMPETITION, SOCIAL ORGANIZATION, AND FITNESS? A STUDY USING A SMALL SOCIAL MAMMAL, *OCTODON DEGUS*

By

Sara Grillo

Loren D. Hayes
Associate Professor
(Committee Chair)

Hope Klug
UC Foundation Associate Professor;
Interim Department Head
(Committee Member)

Timothy Gaudin
UC Foundation Professor;
Senior Associate Department Head
(Committee Member)

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Sara Grillo

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ABSTRACT

Animal personality represents consistent variation among individual behaviors that are repeatable across time and contexts. Recent research in behavioral ecology has revealed that animal personality influences ecological and evolutionary processes, and a growing number of studies demonstrate that personality can play a large role in the interactions among group-living animals. I studied the common degu (*Octodon degus*), a social and group-living rodent, to evaluate whether three personality traits (aggression, boldness, and activity level) play a role in shaping competitive interactions and composition of social groups, and whether these interactions influence the fitness of individuals in groups. Aggression was the only repeatable trait in the population, and I did not find personality traits to influence competitive outcome or group composition. Personality also did not affect fitness of individuals in groups. I discuss ecological and social contexts that might have influenced this population of degus and provide direction for future personality studies.

DEDICATION

I would like to dedicate this to Fray Jorge and the degus, for teaching more than the scientific method could discern.

ACKNOWLEDGEMENTS

I would first like to acknowledge my parents, whose unfaltering support allowed me the freedom to pursue my love for nature and her inhabitants. To my friends and family, near and far, for laughs, deep talks, and comfort when I needed it most. And to C; thank you for sharing in this experience with me and motivating me through the tough spots. I am very thankful for my collaborators Nick Johnson and Drs. Luis Ebensperger and Rodrigo Vásquez, for the lab space and assistance. To all the field technicians, this project would not have been possible without you. I would also like to thank my committee members, Drs. Hope Klug and Timothy Gaudin, for their time and expertise. Additionally, I would like to thank the National Science Foundation for funding my research and the University of Tennessee at Chattanooga for funding both my research and education. Lastly, I want to thank my dedicated adviser, Dr. Loren Hayes, for this amazing opportunity, for his guidance, help, and advice, and for always challenging me to become a better scientist. Oh, and for the gin-gins.

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LIST OF TERMS

Animal personality- repeatable differences in behavior among individuals that carry across time and context

Assortment- the pattern of associations and distribution of individuals in relation to conspecifics

Behavioral syndrome- suites of correlated personality traits that exist across time and context

Behavioral type- tendency in behavioral expression of a personality trait, i.e., if the personality trait is aggression, a behavioral type may be more or less aggressive

Fitness- the contribution of an individual to the gene pool of successive generations

Personality trait- repeatable measures of a certain behavior, i.e. aggression, boldness, activity level

Proactive- more exploratory, more bold, more aggressive, and less neophobic individuals

Reactive- less exploratory, less bold, less aggressive, and more neophobic individuals

Repeatability- the quantification of the consistency of traits across multiple measures, accounting for intra-individual variation

Social organization- group size and composition. This thesis is focused on the aspect of composition.

LIST OF ABBREVIATIONS

BLUP, best linear unbiased predictor

GLM, generalized linear model

GLMM, generalized linear mixed model

HPA, hypothalamic pituitary adrenal

LMM, linear mixed model

OFB, open field box

PCOW, per capita offspring weaned

CHAPTER 1

INTRODUCTION

Animal Personality

Animal behavior is, at its simplest, the response of animals to stimulus. It refers to anything animals do, from acts of foraging and mating to more complex mental capabilities such as learning. A major aim of behavioral ecology is to understand the current utility and fitness consequences of behavior. This is important for understanding the role of behavior in biological processes and environments. When asking these questions researchers have focused on inter- and intra-specific variation, where emphasis is placed on mean trait values and the differences between species or populations (Hayes and Jenkins 1997, Dingemanse et al. 2010). However, individuals can vary within and among themselves in species and populations (i.e., inter-individual variation) (Dingemanse et al. 2010). Although individual traits are measured when studying inter- and intra-specific variation, this approach ignores the individuality represented by inter-individual variation (Boake 1989, Hayes and Jenkins 1997, Sih and Bell 2008).

The study of personality, a field in the study of behavior, accounts for individuality by examining differences within and between individuals (Boake 1989, Bell et al. 2009, Dingemanse and Dochtermann 2013). Over the past 30 years, researchers studying animal personality have shown how individual variation in behavior can inform theory on ecological concepts like dispersal, naturalization of invasive species, and foraging, as well as evolutionary implications such as adaptive ability and maintenance of behavioral variation (Dall et al. 2004, Reale et al. 2007, Cote et al. 2010, Kurvers et al. 2010a, Bergvall et al. 2011, Wolf and Weissing 2012, Aplin et al. 2014, Patrick and Weimerskirch 2014, Blight et al. 2017, Michelangeli et al. 2017). Animal personalities are widespread in the animal kingdom and describe repeatable differences in behavior among individuals that carry across time and context (Gosling 2001, Sih et al. 2004a, Sih et al. 2004c, Reale et al. 2007, Sih and Bell 2008). These differences can be heritable and can be examined at multiple scales, among species, communities, and populations (Dingemanse et al. 2002, Drent et al. 2003). Personality traits are measured to determine an individual's behavioral type, or tendency in behavioral expression of a personality trait (Sih et al. 2004c)(Figure 1.1). Commonly measured personality traits are aggression, boldness, activity level, exploration, and sociability (Reale et al. 2007). Behavioral types exist on a spectrum for each trait. For example, if measuring aggression, behavioral types may vary from more aggressive to less aggressive. Researchers capture individuality in personality studies that differ from studies of phenotypic plasticity.

Behavioral plasticity is the ability of an individual to express more than one form a behavioral trait in response to internal or external stimuli (West-Eberhard 1989, Betini and Norris 2012). Behavioral plasticity differs from personality in that it examines the change in a behavioral trait over time and context, as opposed to the consistency in expression of that trait (Stamps and Biro 2016). Personality can stem from limited behavioral plasticity, as individuals are not infinitely plastic and so cannot express the full range of a given personality trait in every situation. However, personality and behavioral plasticity can interact, as seen when individuals vary in the type and magnitude of behavioral response to environmental stimuli (Bell 2005, Dingemanse et al. 2007, Dingemanse et al. 2010, Dochtermann and Dingemanse 2013). Whereas a population or species may be constrained in the range of behavioral responses they express, an individual can adjust their behavior in different situations, where different behavioral types adjust their behaviors better than others (known as reaction norms, see Dingemanse et al. (2010) (Sih et al. 2004b).In fact, the degree of plasticity itself can be considered a personality trait (Dingemanse et al. 2010). In other words, behavioral plasticity and animal personality are not mutually exclusive. To evaluate the consistency of behavioral traits over time, researchers calculate their repeatability.

Repeatability

Some individual traits change with time or across situations, whereas others do not. Repeatability_captures the consistency of these traits across multiple measures by accounting for intra-individual variation (Hayes and Jenkins 1997, Nakagawa and Schielzeth 2010). The variation among individuals in a population has been examined using quantitative genetics since the 1950s but only recently became the focus of behavioral studies, due to efforts by researchers to bridge the gap between statistical models, quantitative genetics, and ecology (Falconer and Mackay 1996, Bolker et al. 2009, Nakagawa and Schielzeth 2010, Dingemanse and Dochtermann 2013). Capturing the consistency of behavioral traits is particularly important, since they tend to be more labile than other traits (e.g., morphology). Repeatability also serves as a standardized estimate of consistency in measurements and can serve to compare trait variation across studies (Dingemanse and Dochtermann 2013).

Features of Repeatability

Historically, researchers have used the product-moment correlation, confirmatory factor analysis, and intra-class correlation to calculate repeatability (Hayes and Jenkins 1997). Some of these methods have limitations. For example, the product-moment correlation can only calculate consistency for two measurements at a time, which is a problem when an individual has more than two repeated measurements (Hayes and Jenkins 1997). The confirmatory factory analysis is somewhat complex and calculates repeatability using hypothesized models based on theory and pre-existing empirical research (Preedy and Watson 2012). This analysis is not commonly used as it does not directly estimate variance between- and within-individuals (Hayes and Jenkins 1997, Dingemanse and Dochtermann 2013).

The current consensus is that the best approach involves calculating the intra-class correlation, a method adopted from the field of quantitative genetics that accounts for between and within-individual variance (Falconer and Mackay 1996, Hayes and Jenkins 1997, Nakagawa and Schielzeth 2010):

$$R = \frac{\sigma_{\alpha}^{2}}{\sigma_{\alpha}^{2} + \sigma_{\varepsilon}^{2}}$$

where R is repeatability, σ_{α}^{2} is the between individual variance, and σ_{ε}^{2} is the within individual variance (Nakagawa and Schielzeth 2010). Phenotypic variation is the sum of the denominator, and is represented by $\sigma_{\alpha}^{2} + \sigma_{\varepsilon}^{2}$, the between- and within-individual variance components (Falconer and Mackay 1996, Dingemanse and Dochtermann 2013). In the context of personality research, repeatability measures the proportion of individual variation in behavior attributable to differences between individuals (Falconer and Mackay 1996, Nakagawa and Schielzeth 2010). Imagine, for example, that one is interested in the repeatability of burrow emergence time in a population of lizards. Given a population where all individuals consistently emerged after 20 minutes, the variation between individuals in that population (σ_{α}^{2}) would be low and the variation within individuals (σ_{ε}^{2}) would also be low. However, in a population where some individuals consistently emerged after 1 minute and others consistently emerged after 10, 15, and 20 minutes, the variation between individuals would be high and the variation within individuals would remain low, since each lizard is consistent in their emergence time.

In the animal personality context, consistency in personality suggests that traits do not change with time or across situations. In other words, when a trait is not repeatable, the measured behavior is not consistently expressed and should not be considered for further analysis. Research shows that average repeatability lies around R= 0.35, so an individual is expected to express a given behavioral trait 35% of the time that trait is measured (Bell et al. 2009). It is important to note that multiple measurements are required for each individual, and that these measures should be taken in the same spatial, temporal, and environmental context to reduce sampling error (Boake 1989, Bell et al. 2009, Dingemanse and Dochtermann 2013). Increasing the number of measurements reduces phenotypic variance, particularly for traits with low repeatability, so one gains accuracy (not repeatability-Bell et al. 2009) by taking more measurements (Falconer and Mackay 1996, Dingemanse and Dochtermann 2013). However, this increase in accuracy is negatively exponential and stops after a certain number of measurements (Falconer and Mackay 1996, Dingemanse and Dochtermann 2013).

Repeatability of behavioral traits is significant to the study and evolution of animal personalities. Key components of personality research examine the cause of behaviors, selection on phenotypic variation, and the inheritance of selected traits. To understand how behavior is selected and inherited, one must recognize how variable that behavior is i.e. one must know the repeatability of the behavior. Only behaviors that are repeatable can respond to selection, since mathematical calculations show that repeatability sets an upper limit to heritability, where only highly repeatable traits can be subject to high heritability (Boake 1989, Falconer and Mackay 1996, Dingemanse and Dochtermann 2013).

Implications of Personality

Repeatable behavioral traits can correlate across individuals, such that one behavior is predictive of another. These behavioral syndromes, or suites of correlated traits, are analogous to personality in that they exist across time and context (Sih et al. 2004a, Sih et al. 2004c, Sih et al. 2012) (Figure 1.1). While traits can exist independently of one another and still account for personality, behavioral syndromes require correlation (Sih et al. 2004a, Sih et al. 2004c). Behavioral syndromes exist across multiple contexts, such that one personality trait is expressed similarly in each context e.g., where individuals are consistently aggressive not only in competitive interactions, but also in parental, mating, foraging, and predator risk situations (Riechert and Hedrick 1993). Similarly, personality traits may correlate across multiple categories, such that one behavioral type correlates with another e.g., more aggressive individuals are also more exploratory and bolder. However, behavioral syndromes may vary across time and life history, such that the pattern of correlation may change or disappear (Lee and Bereijikian 2008, Bengston and Jandt 2014).

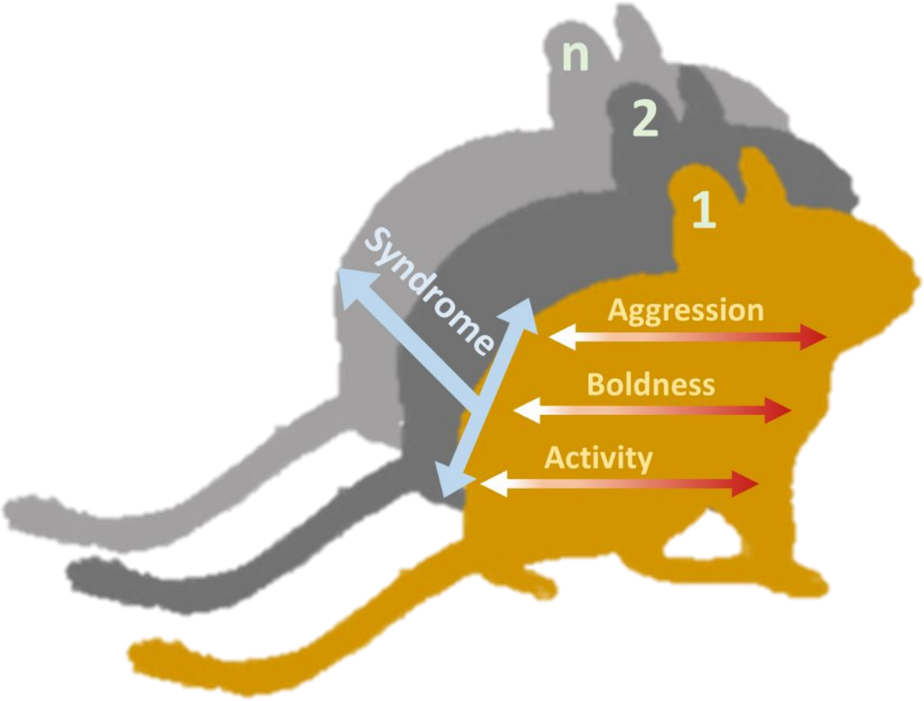

Figure 1.1 Conceptual model of personality traits, behavioral types, and behavioral syndromes. Personality traits such as aggression, boldness, and activity level exist within individuals and on a spectrum from one extreme to another (i.e. less to more aggressive, represented by red arrows). The way an individual expresses each personality trait makes up its behavioral type. When these traits correlate across individuals between time and/or context, they form a behavioral syndrome, as represented by the blue arrows

The concept of behavioral correlations suggests that individual traits do not evolve independently of one another. Instead, these suits of correlated behaviors may evolve as a package (Sih et al. 2004a, Sih et al. 2004c). The onset of behavioral syndromes as a paradigm in animal behavior shifted the field to study personality traits in conjunction with one another, instead of focusing on individual traits. In fact, when personality traits are studied in isolation, behaviors may seem suboptimal (Sih et al. 2004a, Sih et al. 2004c). For example, a syndrome of activity level across contexts could have trade-offs. It may be beneficial for an individual to be highly active during dispersal, but if this activity spills over when placed in an area with more predators, the individual may be exposed to higher predation risk than an individual with lower activity levels (Sih et al. 2012, Wolf and Weissing 2012). Without the considering the benefits across all contexts, a behavioral type may appear purely detrimental. As such, it is important to examine animal personality traits in conjunction with one another to understand potentially suboptimal behaviors.

Some behavioral syndromes are prevalent in nature and are present across many taxa. There is evidence of a proactive-reactive axis that includes correlations among exploration, boldness, aggression, and neophobia (fear of new situations or objects) (Koolhaas et al. 1999, Sih et al. 2004a, Sih et al. 2004c). Proactive individuals score higher on this spectrum and are more exploratory, more bold, more aggressive, and less neophobic. On the other hand, reactive individuals explore their habitat less, and respond less aggressively, boldly, and are more afraid of novel situations. In many cases, these suites of behavioral types are associated with life history strategies, such that an individual’s personality has direct and indirect fitness consequences (Biro and Stamps 2008, Smith and Blumstein 2008, Réale et al. 2010b). For example, more active, bold, and exploratory guppies (*Poecilia reticulata*) had increased longevity when exposed to predators (Smith and Blumstein 2010), and boldness in squid (*Euprymna tasmanica*) relates to brood hatching success (Sinn et al. 2006). Similarly, red squirrel (*Tamiasciurus* *hudsonicus*) activity and aggression levels correlate with growth rate and survival of offspring, and less exploratory/aggressive trout (*Salmo trutta*) grew faster than their more exploratory/aggressive conspecifics (Boon et al. 2007, Adriaenssens and Johnsson 2011).

Thesis Aims

We have improved our understanding of the link between personality traits and fitness consequences, and descriptive studies outlining the behavioral traits and syndromes of animal species are now common. However, to shed light on the mechanisms behind this link it is important to examine the function of personality in multiple facets of ecology (Reale et al. 2007, Réale et al. 2010a, Dall et al. 2012). For example, we know that red squirrel activity and aggressive levels correlate with growth rate and survival of offspring (Boon et al. 2007)—but how does this occur? Perhaps high activity levels improve foraging ability and so increase lactation quality, or more aggressive squirrels are better at protecting their nests by fending off predators. Studies on the relationships among personality, function, and fitness are scarce.

The aim of this thesis is to study the relationship among personality, function, and fitness in a social animal by i) exploring the relationship among individual personality, competition, and social organization and ii) quantifying fitness consequences of personality in ecological contexts. Both competition and social organization (in this thesis referring to whether individuals sort into groups based on personality traits) affect the dynamics of social groups, which can influence group-level success in social animals (Farine et al. 2015). To achieve these aims, I conducted my study in several phases (Figure 1.2). In phase one I examined individual personality by measuring the repeatability of personality traits and examining correlations among them to determine if they formed a behavioral syndrome. During phase two I evaluated the ecological function of personality, examining its influence on (a) outcome of dyadic competition trials and (b) social organization. Finally, in phase three I assessed the fitness consequences of personality by studying the relationship between sorting by personality traits and per capita offspring weaned in a group (Chapter 2). I used the degu (*Octodon degus*) as a model organism because these are highly social animals, and previous studies have found assortment by repeatable personality traits in wild populations (Ebensperger 1998, Chock et al. 2017). To conclude, I discuss the conservation implications of animal personality (Chapter 3).

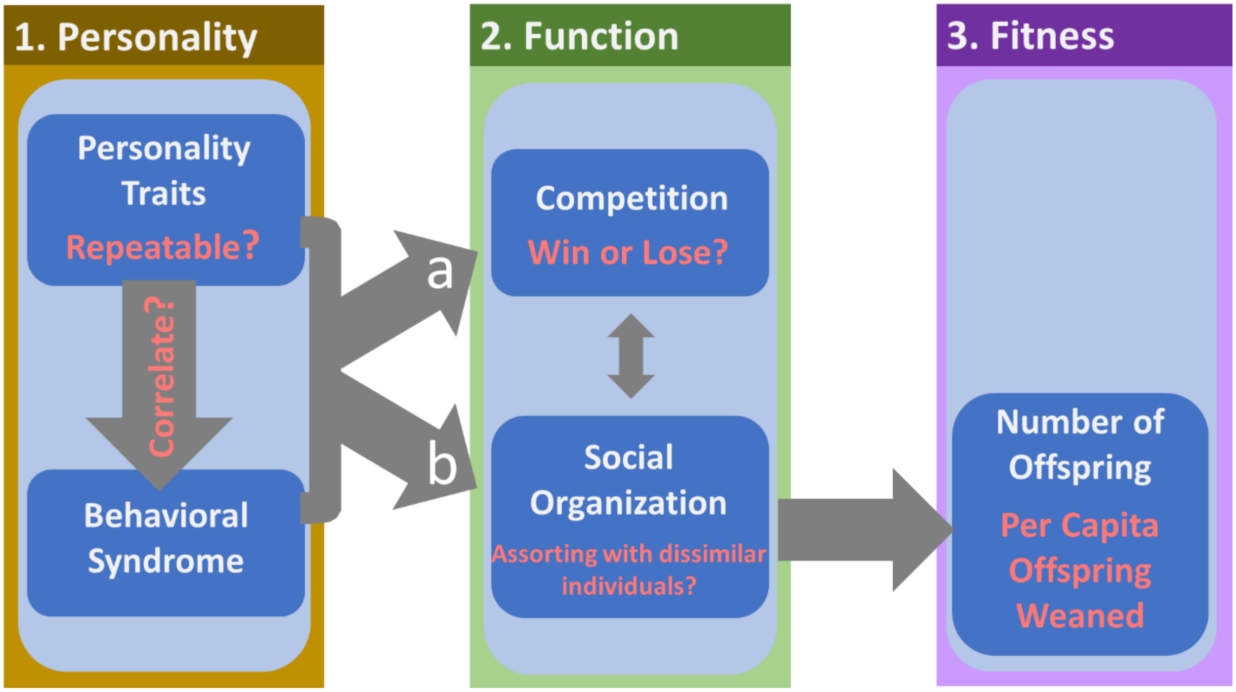

Figure 1.2 Conceptual model of the relationship among personality (phase one), its ecological function (phase two), and fitness (phase three). Personality traits can correlate to form behavioral syndromes, and both can affect (a) the outcome of competition and influence (b) the assortment of social groups. Social group assortment by personality can then affect fitness, one measure of which is number of offspring produced per female in each group (per capita offspring weaned)

CHAPTER 2

DOES PERSONALITY AFFECT COMPETITION, SOCIAL ORGANIZATION, AND FITNESS? A STUDY USING A SMALL SOCIAL MAMMAL, *OCTODON DEGUS*

Introduction

Animal personalities are widely documented in the animal kingdom and describe repeatable differences in behavior among individuals that carry across time and context (Gosling 2001, Sih et al. 2004a, Sih et al. 2004c, Reale et al. 2007, Sih and Bell 2008). Whereas studies on individual consistency and variation in behavior have shed light on the ecological and evolutionary implications of individual personalities (Dall et al. 2004, Reale et al. 2007, Cote et al. 2010, Kurvers et al. 2010a, Bergvall et al. 2011, Wolf and Weissing 2012, Aplin et al. 2014, Patrick and Weimerskirch 2014, Blight et al. 2016a, Michelangeli et al. 2017) the role of individual personality in group-living animals is an emerging topic in behavioral ecology (Magnhagen and Staffan 2005, Sih and Watters 2005, Webster and Ward 2011). Evidence suggests that the personality composition of a group can influence its collective performance (Pruitt et al. 2013, Wolf and Krause 2014, Cronin 2015). For instance, groups of water striders (*Aquarius remiges*) with hyper-aggressive males experience lower mating activity than those without hyper-aggressive males (Sih and Watters 2005). Additionally, bolder individuals in groups of Barnacle geese (*Branta leucopsis*) influence movement patterns and increase foraging success of the group, and models predict that personality composition of a group affects collective decision-making in sheep (*Ovis aries*) (Kurvers et al. 2009, Kurvers et al. 2010b, Michelena et al. 2010, Kurvers et al. 2011). The collective behavior of groups is often determined by associations among individuals in the group, which influence the composition of group-living animals (Ranta et al. 1993, Aplin et al. 2013, Farine 2014, Farine et al. 2015). For example, great tits (*Parus major*) with similar exploratory and neophobic behavioral types nest closer to and have increased preference for each other, forming groups of birds with similar personalities (Johnson et al. 2017). In general, theoretical and empirical studies demonstrate that associating with conspecifics based on similar traits improves group performance and increases the benefits of group living, which include reduced predation risk, access to resources, and thermoregulation (Hamilton 1971, Alexander 1974, Landeau and Terborgh 1986, Roberts 1996, Wilson and Dugatkin 1997, Ebensperger 2001, Krause and Ruxton 2002, Santos et al. 2006, Croft et al. 2009, Macdonald and Johnson 2015, Pogany et al. 2018). Furthermore, studies on mating pairs of similar personalities show that associating with like individuals increases probability of reproduction and fertilization, and results in higher reproductive success (Sinn et al. 2006, Gabriel and Black 2012, Rangassamy et al. 2015).

However, many animals associate with individuals of different phenotypes (Wilson 1998, Keiser et al. 2016), and these associations with dissimilar individuals benefit collective behavior. For example, the social spider (*Anelosimus studiosus*) exhibits increased prey capture in groups of individuals with varied personality traits (Keiser and Pruitt 2014) and guppy (*Poecilia reticulata*) shoals experience increased foraging success with differences in personality of constituents (Dyer et al. 2009). Disassortative associations may also increase fitness benefits, e.g., in gypsy ant (*Aphaenogaster senilis*) colonies where production, examined as colony growth, larvae survival, and queen and worker production, correlated positively with differences in individual personality traits (Blight et al. 2016b). Similarly, individuals in groups of the social spider (*Anelosimus studiosus*) exhibit increased prey capture and increased egg-case masses (a proxy for fitness) with dissimilar composition of personality traits (Pruitt and Riechert 2011). Additionally, great tit (*Parus major*) fledglings of negatively assorted mating pairs were in better condition than those of pairs at similar ends of the behavioral spectrum (Both et al. 2005), and cockatiel (*Nymphicus hollandicus*) pairs with dissimilar personality traits hatched more eggs than pairs with similar personality traits (Fox and Millam 2014).

The benefits gained from associating with dissimilar individuals may stem from the advantages each individual acquires, i.e. one personality may be better at foraging while the other is better at territory defense. An exemplary model of this concept is demonstrated as division of labor in social insects where individuals perform different tasks to support the colony, stemming from genetic and behavioral variation (Jeanson and Weidenmüller 2014). Further, consistent behavioral variation exists within each task group and improves collective performance, such as in worker honey bees (*Apis mellifera*), where differences in foraging approach improve resource accumulation of a colony compared to colonies with homogeneous foraging approaches (Jones et al. 2004, Burns and Dyer 2008, Muller and Chittka 2008, Walton et al. 2016). One advantage of associating with dissimilar individuals may occur as different behavioral types utilize different habitats and reduce indirect competition for resources (Farine 2014). In social species, minimizing the effects of competition could facilitate affiliative social interactions and reduce competition among group members, thereby improving their success within the group (Alexander 1974, Freeland 1976, Côté and Poulinb 1995, Zemel and Lubin 1995, Grand and Dill 1999, Krause and Ruxton 2002).

A major cost for group-living animals is competition for limited resources (Alexander 1974, Zemel and Lubin 1995, Grand and Dill 1999, Krause and Ruxton 2002). Personality can influence competitive ability of individuals, and could provide an advantage in resource acquisition, territory defense, and other contest situations (Webster and Ward 2011, Briffa et al. 2015). Theoretical and empirical studies suggest that most contests are asymmetric, where opponents are not equally matched, and that intrinsic characteristics such as size and weapons can influence an individual's competitive ability (Maynard Smith and Parker 1976, Schoener 1983, Persson 1985, Leimar et al. 1991, Faber and Baylis 1993, Nakayama and Fuiman 2010). In terms of personality, more proactive individuals tend to have increased competitive ability. In dyadic competitive trials between two fish species (*Gasterosteus aculeatus* and *Pungitius pungitius*), bolder individuals acquired more food regardless of species, suggesting personality plays a large role in contest outcome (Webster et al. 2009). Similarly, proactive personalities improve competitive ability in great tits (*Parus major*), zebra finches (*Taeniopygia guttata*), rainbowfish (*Melanotaenia duboulayi*), and sheepshead swordtails (*Xiphophorus birchmanni*)) (Verbeek et al. 1996, Cole and Quinn 2011, Colléter and Brown 2011, David et al. 2011, Wilson et al. 2013).

Theory states that the cost of competition may be reduced if individuals adjust their behavior in response to that of their competitor's to avoid escalating a fight and minimize energy expenditure (Maynard Smith 1982, Dall et al. 2012). In the classic hawk-dove scenario, the evolutionarily stable strategy is for a population to adopt variable behaviors, with a proportion of individuals acting as hawks (always escalating fights) and the others acting as doves (always submitting in fights), given that hawks win resources and doves prevent excess energy expenditure (Maynard Smith 1982, Dall et al. 2004). Some hypothesize this type of interaction may even maintain variation in personality traits if these adjustments in behavior remain consistent over time and individuals develop alternative strategies (Dall et al. 2004). Individuals in group-living species may adjust their behavior to minimize the cost of competition, or they may associate with dissimilar individuals to achieve the same result (Webster and Ward 2011, Farine et al. 2015). In groups with established competitive dynamics, whether from preferential assortment or from behavioral adjustment, those with more dissimilar personalities may save energy by minimizing the cost of competition, and so be able to allocate energy to reproductive output. Therefore, fitness benefits in groups may increase if the composition of groups represents negative assortment of personalities. Evaluating how personality influences competitive interactions and group composition brings us one step closer to understanding the role of personality in group-living animals, and how these interactions may influence success of individuals in groups.

Study Organism and Objectives

The aim of my study is to examine the consequences of personality on competitive ability and social group assortment, and the fitness consequences related to social assortment. To this end, I need to answer the following questions:

1. Are behaviors repeatable and do they form behavioral syndromes?
2. Do personality traits/syndromes provide competitive advantage?
3. Do animals assort based on personality traits/syndromes?
4. Are there fitness consequences to assortment based on personality trait/syndromes?

I aim to answer these questions by examining the commonly repeatable traits of aggression, boldness, and activity level in wild degus (*Octodon degus*), a group-living rodent endemic to Chile (Ebensperger et al. 2004, Hayes et al. 2009). Degus are diurnal and semi-fossorial, remaining in underground burrows overnight. Although kin composition among group members is similar to random comparisons within the population (Quirici et al. 2010, Davis et al. 2015), females in social groups breed communally and will groom and nurse offspring indiscriminately (Ebensperger et al. 2002, Ebensperger et al. 2010). Previous studies have found repeatability in boldness and activity level of rodents using open field boxes (OFB), and in aggression of degus by conducting prod tests (Gould et al. 2009, Chock et al. 2017). The present study measures boldness as the latency to emerge from shelter and the time spent around the edge versus center of the OFB andactivity level as total distance moved in the OFB, since these represent ecologically relevant behaviors (e.g., they could influence predator avoidance) and are commonly assayed in the OFB (Gould et al. 2009). Aggression was measured as the tendency to charge an object when prodded, given that this behavioral test has yielded repeatable measurements of aggression in previous studies (Hansen 1996). Studies have also found that degus assort based on personality traits but have not examined the fitness consequences of such assortment (Chock et al. 2017).

I aim to answer these questions by conducting the following:

1. **Measure personality traits and determine correlations among them**. Based on the existence of repeatable traits and proactive-reactive behavioral syndromes in many animal taxa, I predict that aggression, boldness, and activity level are repeatable and form a behavioral syndrome, where individuals that charge more will also emerge quicker from shelter, spend more time in the center of an OFB, and move a greater distance in the OFB.
2. **Examine competitive ability of individuals in a dyadic competition trial**. Given that proactive personalities and increased competitive ability correlate in numerous animal taxa, I predict that personality relates to competition outcome and that individuals with more proactive traits (more aggressive/bold/active) will win more competitive trials.
3. **Determine social groups and assortment by personality**. Since assorting with dissimilar individuals may minimize costs associated with competition, I predict that more aggressive/bold/active individuals form groups with less aggressive/bold/active individuals,
4. **Calculate per capita reproductive success of each group and correlate to assortment value**. Assuming that individuals form groups with dissimilar individuals to reduce costs associated with competition and can allocate energy towards reproduction, I predict that groups with more dissimilar individuals will have increased per capita offspring weaned (PCOW).

Methods

Live-trapping and behavioral measurements were conducted on a natural population of degus during the 2017 austral winter-spring (August-November) in El Salitre (-30.691767, -71.630659), a 1.79 ha area near Parque Nacional Fray Jorge, Chile (Figure 2.1). The timing of data collection corresponded to the period of 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 night (Fulk 1976). We live-trapped each burrow system six days per week from early August to mid November by placing 10 Tomahawk traps (Tomahawk model 201, Tomahawk Live Trap Company, Tomahawk, WI) around the burrow openings (Figure 2.2). To capture individuals prior to foraging movements, traps were opened and baited with rolled oats an hour prior to sunrise and prior to degu emergence. After 1.5-2 hours we closed traps and moved animals to a central location for processing (Ebensperger et al. 2014). New individuals were uniquely marked with ear tags (Monel 1005-1, National Band and Tag Co. Newport, KY) for identification. During subsequent captures we determined identity, body mass (to 0.1g), location of capture, and sex. We also noted female reproductive status (pregnant or lactating). All behavioral observations were conducted on site. Degus were released at the burrow system from which they were captured after processing and behavioral observations, approximately 4-7 hours after capture.

Bioethics: The care and use of animals followed all applicable international, national, and institutional guidelines, including those of American Society of Mammalogists (Sikes 2016). The study was approved by the UTC Institutional Animal Use and Care Committee (IACUC #: 0507LH-02) and conducted under Chilean permits issued by the Servicio Agricola y Ganadero (5028/2017).

Figure 2.1 Geographic location of El Salitre (red star, -30.691600, -71.630581). This site is characterized by a matorral habitat dominated by cactus and shrubland, with herbaceous understory and occasional bare, sandy areas

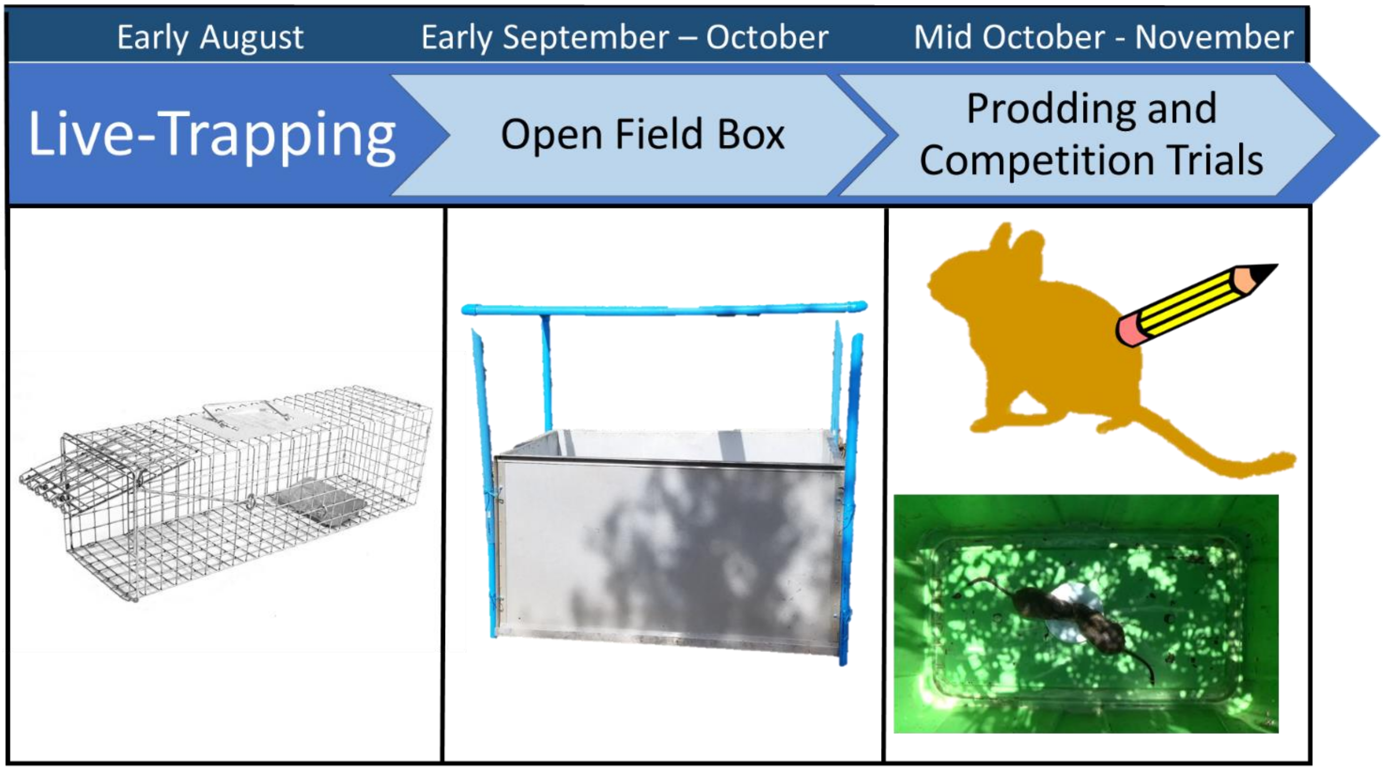

Figure 2.2 Timeline of live-trapping, behavioral trials, and competition trials. Live-trapping was conducted from early August through mid-November to determine social groups and capture animals for behavioral trials. Open field box trials were conducted from early September to early October to measure boldness and activity level. Prodding and competition trials were conducted from mid-October through mid-November to measure aggression and competitive ability, respectively

Personality

Subjects were tested in an open-field box to determine repeatability in latency to emerge from shelter, distance moved in the box, and amount of time spent in the edge versus center of the arena (Figure 2.3). Open field boxes are commonly used to assay personality traits in rodents (Gould et al. 2009), and have previously been used on degus (Meunier and Fischer 1985, Braun et al. 2003, Ashkenazy-Frolinger et al. 2015). Trials took place between September and early October and were repeated an average of four times per individual, once per day with two or more days between trials

(Figure 2.2). We placed subjects in a closed metal shelter within the arena (89 x 89 x 142cm) and allowed them to acclimate for 3 min. The shelter was then opened and the degus filmed for 7 min with observers out of view. One researcher (N.E.J.) manually timed latency to emerge from shelter and used the Noldus Ethovision XT9 program to analyze time spent around the edge, midcenter, and center of box, as well as total distance moved.

To measure repeatability of aggressive behavior, I used the eraser-side of a pencil to gently poke individual hindquarters through the wire-mesh Tomahawk traps (Poke test: Chock et al. (2017)). Adult animals were observed every day they were trapped from mid October to early November, approximately 15 min after relocation to the central location and prior to handling (Figure 2.2). Charging behavior was recorded dichotomously (0= no charge, 1= turn and charge pencil). I did not know the identity of subjects during these trials.

Figure 2.3 Left: open field box *in situ* with tetrapod (in blue) to hold video camera in place. Right: still image from video of behavioral trial. The box in the lower left corner of the OFB served as a hide for subjects, to which they acclimated for 3 minutes and, once opened, could return to for shelter

Competition Trials

I conducted dyadic competition trials with all female group members to assess competitive ability (Kilgour and Brigham 2013). All trials took place between mid October and mid November (Figure 2.2). Degu motivation and ability to acquire oats from a food dish were observed prior to dyadic trials. Individuals were then placed in dyads with all other degus from the same group, so that each female in a group competed against each other. Each competition trial lasted 2 min and was repeated 4-5 times per dyad, with one or more days between trials. Trials were conducted when all females in a group were captured the same day. The order in which dyads were tested was randomized, and if individuals competed consecutively they were given a 5 min rest between trials. Food was withheld for 5-6 hrs prior to trials to increase motivation (Kilgour and Brigham 2013). As individuals finished with trials they were fed *ad libidum* until all trials were complete, at which time they were released.

Individual motivation and ability to acquire oats were observed in the trial arena (59.7 x 46.1 x 40.7 cm) prior to competition dyads. Degus were placed in the corner and acclimated for 5 sec. Those that approached and consumed the food within 1 min of release continued to dyadic trials. Competition trials consisted of two degus placed in diagonally opposite corners equidistant from food. Trials were filmed with observers out of view. Videos were randomized, and the identity of subjects was unknown to me during analysis. Outcome was determined based on time dominating food and displacement of competitor upon approach to oats. Individuals either won, lost, tied (both individuals attempted to dominate food the source but one did not succeed over the other), or had unknown outcome (both individuals approached and consumed oats simultaneously without displacing the other) (de Vries 1995). The proportion of trials won by individuals was calculated from dyads with 4 or more repeated trials, after excluding dyads with tied and unknown outcomes (which resulted in the removal of 7 dyads).

Social Organization

Determination of social group membership required a combination of live-trapping at burrow systems (described above) and night-time or early morning telemetry tracking of adults to burrow systems. We conducted night telemetry on all adult females for a minimum of 21 nights (mean= 42.0, SE= 1.7). Females weighing 110-150 g were fitted with 5g radiocollars (BD-2C; Holohil System Limited, Carp, Ontario, Canada) and those weighing more than 150 g were fitted with 7g radiocollars (PD-2C; Holohil Systems Limited, Carp, Ontario, Canada), both types of collarswith unique frequencies. Degus were tracked once per night approximately 1.5 hours after sunset or 1.5 hours before sunrise using an FM-100 receiver (for transmitters tuned to 164.00-164.999 MHz frequency; advanced Telemetry Systems, Isanti, MN, U.S.A.) and a hand held three element Yagi antenna (AVM instrument Co., or Advanced Telemetry Systems).

For both trapping and telemetry data, I constructed symmetric similarity matrices using pairwise associations. Pairwise association indices were calculated by dividing the number of nights that pairs of individuals were captured at or tracked with telemetry to the same burrow system by the number of nights that both individuals were trapped or tracked on the same day (Ebensperger et al. 2004). To determine social group composition, I conducted hierarchical cluster analysis of the burrow trapping and night telemetry association matrix in the SOCPROG 2.8 software (Whitehead 2009). Only individuals trapped 4 or more days were included in the analysis. 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. I used the cophenetic correlation coefficient to evaluate the correlation between the level of clustering in the dendrogram output with the association indices, with values of 0.8 or greater effectively representing the data (Whitehead 2009). I chose maximum modularity criteria to cut off the dendrogram and define social groups (Newman 2004).

Fitness Consequences

I determined the number of offspring weaned by each social group by quantifying the number of offspring captured for the first time at burrow systems used by social groups. Per capita offspring weaned (PCOW) was determined by dividing the number of offspring captured at each burrow system by the number of adult females in the social group utilizing that burrow system. This method assumes equal litter sizes for all females in a group.

Statistical Analysis

Personality

I used generalized linear mixed models (GLMM) to determine the main predictors of variation in binary personality traits (tendency to charge or not, and emergence or not) in the population, and linear mixed models (LMM) for continuous and normally distributed personality traits (distance moved and proportion time spent on edge) (Dingemanse and Dochtermann 2013). The full model included personality trait as the response variable, sex and observation number as fixed effects, and date of observation and animal ID as random effects (as in Chock et al. (2017)). Response variables were fit according to their distribution (e.g. binary responses were fit with a binomial distribution and logit link function). Models were run in the R software (version 3.5.0) using the 'lme4' package (Bates et al. 2015, R Core Team 2018). I calculated the intra-class correlation coefficient to measure repeatability of each personality trait in the population using the 'rptR' package (Stoffel et al. 2017). Personality traits were not repeatable if the confidence intervals nearly overlapped with zero, even if the result was significant, as this suggests a behavior repeats close to zero percent of the time. Behavioral syndromes were not calculated since aggression (to charge or not) was the only repeatable trait. Therefore, subsequent analyses focused on aggression alone. I analyzed the females independently to calculate the effect of reproductive state and mass at time of trial on aggression. This GLMM included aggression as the response variable, fixed effects of reproductive state, mass at time of trial, and their interaction, and random effects of date of observation and ID. I centered the values for mass at time of trial to scale the interaction and adjusted the contrast coding to orthogonal polynomials to have a direct comparison between reproductive states (Dalal and Zickar 2012). I also tested for repeatability of aggression in the female-only model. I extracted BLUPs (best linear unbiased predictors) for each individual at the population level and the female-specific model. BLUPs represent the mean of random effects and serve as individual measures of repeatable personality traits relative to conspecifics (Robinson 1991, Chock et al. 2017).

Competition Trials

I ran a generalized linear model (GLM) to determine the effect of differences in aggression and animal mean body mass on competition outcome (as in McEvoy et al. (2013)). I indexed mean body mass as the mean body mass during lactation (henceforth addressed as mean body mass) and as a proxy for animal size. Animal size is known to have an effect on competitive ability and so it was included in this model (Maynard Smith and Parker 1976, Schoener 1983, Persson 1985, Leimar et al. 1991, Faber and Baylis 1993, Nakayama and Fuiman 2010). I used the BLUPs extracted from the female-only model because competition trials were conducted with females from each group. Since competition trials were conducted as dyads, individuals were not independent of one another, so I randomly selected one individual from each dyad and used the difference in BLUP and mean body mass to run the analysis (as in McEvoy et al. (2013)). Proportion wins were used as the response variable, with difference in BLUP and difference in mean body mass as predictor variables. Models were run using the ‘betareg’ package to account for the beta distribution of the response variable (Cribari-Neto and Zeileis 2010). I calculated the correlation between BLUP and mean body mass in females using a Spearman's rank correlation. Finally, I examined anecdotal data for effects of reproductive state on competitive outcome.

Social Organization

I tested if male and female adults assorted by aggression level using the 'assortnet' package in R (Newman 2002, Farine 2013), which calculates strength and significance of assortment by trait. Assortment (*r*) is measured from -1 to 1, with 0 representing no assortment, -1 representing negative assortment (grouping with unlike individuals), and 1 representing positive assortment (grouping with similar individuals). I only included groups in which all members had a BLUP for aggression. I calculated a p-value for *r* by running 50,000 permutations of the original network and comparing the original *r* to the number of values from permuted networks that were as or more extreme (Chock et al. 2017). The p-values calculated this way were stable at 50,000 permutations. I also evaluated assortment after excluding males, since only female group members were used in the competition trials.

Fitness Consequences

I used Spearman's rank correlation to examine the relationship between PCOW and the difference between the largest and smallest BLUP in the groups composed by male and female adult animals in the population, since the data was not normally distributed even after transformation. I also evaluated this relationship after excluding males.

Results

Personality

The overall model for personality traits measured in the OFB included 77 adult degus (54 females, 23 males), with a total of 300 observations over a period of 25 days (observations per degu: mean = 3.9, SE = 0.1, range = 1-6). The overall model for aggression included 63 degus (45 females, 18 males), with a total of 804 observations over a period of 21 days (observations per degu: mean = 12.8 SE = 0.7, range = 1-20). Only aggression (tendency to charge or not) was repeatable in the population (r = 0.35, SE = 0.06, CI = 0.21-0.45, $p < 0.001$) (Table 2.1). Boldness (emergence or not and proportion of time spent on edge versus center) had a significant p-value but had confidence intervals that nearly overlapped with zero, indicating that personality traits were not repeatable (Table 2.1). Since aggression was the only repeatable trait I was not able to evaluate the formation of a behavioral syndrome. The female-specific model for aggression included 45 degus with a total of 630 observations over a period of 21 days (observations per degu: mean = 14.0, SE = 0.8, range = 1-20). There was a statistically significant interaction between body mass at trial and reproductive state on aggression (z = 2.79, p = 0.005). Pregnant females were less likely to charge the pencil than non-lactating females when accounting for mean body mass at the time of trial, and there was no difference among non-lactating and lactating or pregnant and lactating females when accounting for mean body mass at time of trial.. Aggression in the female-specific model was repeatable (*r* = 0.36, SE = 0.07, CI = 0.21-0.48, $p < 0.001$).

Table 2.1 Repeatability for each personality trait measured calculated using the intra-class coefficient of variation (r). Only aggression is repeatable. Although boldness (emergence or not) and activity (distance moved) have significant p-values, the confidence intervals that nearly overlap with zero indicate that personality traits are not repeatable

Trait	**Repeatability (r)**	**SE**	**CI**	**p-value**
Aggression (poke)	0.35	0.06	0.21-0.45	<0.001
Boldness (emergence)	0.17	0.08	0.02-0.33	<0.001
Boldness (prop.time edge)	0.16	0.07	0.04-0.30	<0.01
Activity Level (distance moved)	0.04	0.05	0-0.16	0.21

Competition Trials

The model for competition trials included 29 degus (all females), with a total of 16 dyads and 72 trials over a period of 15 days (observations per dyad: mean = 4.5, SE = 0.1, range = 4-5). There was no effect of aggression (z = 0.11, p = 0.91) or mean body mass (z = 1.85, p = 0.06) on proportion of trials won, suggesting that neither gives female degus a competitive advantage (Table 2.2). Additionally, there is no correlation between aggression and mean body mass (n = 45, r = 0.04, p = 0.81).

Table 2.2 Predictor effects for the outcome of competitive trials, using individual aggression and mean body mass

Response Variable	Predictor Effect	Estimate	Std. Error	Z value	P value
Competition Outcome	Aggression	0.02	0.14	0.11	0.91
	Mean Body Mass	0.03	0.02	1.85	0.06

Social Organization

There were 79 degus assigned to 19 social groups in the population. The model for assortment by aggression in the population included 46 degus (15 males and 31 females), with a total of 12 groups in which all members had a BLUP for aggression. The models for assortment by aggression and by mean body mass included 31 degus (all females), with a total of 11 groups in which all members had a BLUP for aggression. Degus did not show significant group assortment by aggression or mean body mass in either the population as a whole (aggression: r = -0.21, SE = 0.08, p = 0.99) or in the female-specific model (aggression: r = -0.01 , SE = 0.11, p = 0.67 ; mean body mass: r = 0.00, SE = 0.13, p = 0.67), suggesting that individuals do not associate preferentially with individuals based on personality or mean body mass (Figure 2.4).

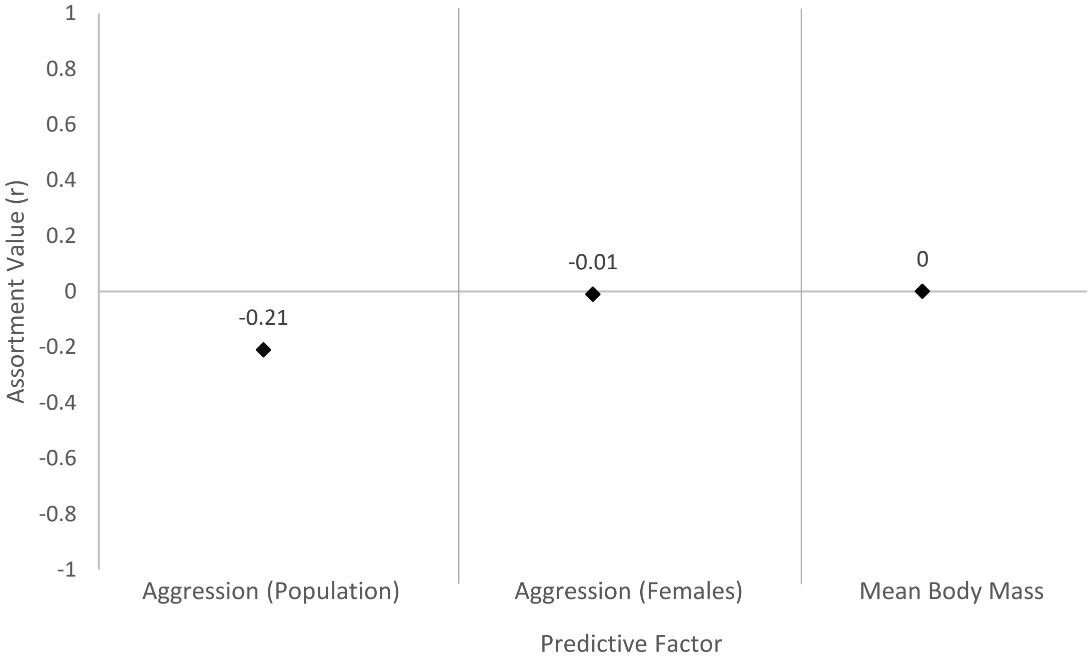

Figure 2.4 Assortment by aggression in the population, aggression in females, and mean body mass of females. Assortment (r) is measured from -1 to 1, with 0 representing no assortment, -1 representing negative assortment (grouping with unlike individuals), and 1 representing positive assortment (grouping with similar individuals). None of these values are significant and suggest that individuals do not associate preferentially with conspecifics based on personality or mean body mass

Fitness Consequences

There was not a statistically significant correlation between PCOW and difference in highest and lowest BLUP in groups in either the population as a whole (n = 12, rho = 0.11, p = 0.73) or in the female-specific model (n = 11, rho = 0.48, p = 0.14).

Discussion

Summary of Main Results

I set out to test whether aggression, boldness, and activity level were repeatable (representing personality traits) in a wild population of degus, and if personality traits correlated with each other to form a behavioral syndrome. Additionally, I examined whether personality traits and behavioral syndromes provided a competitive advantage in contest situations, and whether personality traits and behavioral syndromes predicted patterns of assortment in social groups. Lastly, I evaluated whether assorting based on personality traits and behavioral syndromes resulted in increased fitness benefits for social groups. I found evidence for an aggressive personality trait, but contrary to my predictions boldness and activity level were not repeatable, so that I could not demonstrate the presence of a behavioral syndrome. As aggression was the only repeatable personality trait, it was the only trait used in further analyses. Aggression did not provide a competitive advantage and degu social groups were not assorted by personality. Further, personality composition of social groups did not yield a fitness benefit (Table 2.3).

Table 2.3 Summary of research questions and predictions with respective results

Question	Prediction	Results
Are behaviors repeatable and do they form behavioral syndromes?	Aggression, boldness, and activity level are repeatable Traits form syndrome	Only aggression (poke) repeatable Cannot form syndrome without multiple personality traits (need multiple traits to form a correlation)
Do personality traits/syndromes provide competitive advantage?	Aggression relates to competition outcome More aggressive individuals are better at competing	Personality has no effect on competitive advantage No, personality has no effect on competitive advantage
Do animals assort based on personality traits/syndromes?	More aggressive individuals form groups with less aggressive individuals	Animals do not assort at all
Are there fitness consequences to assortment based on personality trait/syndromes?	Groups with more dissimilar individuals will have increased per capita offspring weaned (PCOW).	There is no correlation between PCOW and the difference between most and least aggressive individuals in a group

Personality

I observed that individuals differed consistently in their response to being prodded, a measure of aggression, but not in their time spent around the edge vs. center of the OFB, their tendency to emerge from shelter, or in their total distance moved in the OFB (measures of boldness, boldness, and activity level, respectively). These results partially met my prediction that behavior is repeatable, but did not support my prediction that proactive traits form a behavioral syndrome, given that only repeatable behaviors may form a syndrome. It is important to note that boldness was not considered a personality trait given that the confidence intervals closely overlapped with zero. Although it is conservative to say that behaviors with confidence intervals that closely overlap with zero are not repeatable, this decision is relatively subjective, and there are no published discussions concerning which threshold determines if a behavior is repeatable (i.e., what are acceptable versus nonacceptable confidence intervals when repeatability is significant). The field of animal personality would benefit from a more structured and consistent approach to determining repeatability.

Theory predicts that behavior may be more consistent and repeatable when linked to the morphological or physiological state of an animal, since these intrinsic characteristics are stable and the cost of changing them is large (Dall et al. 2004, Biro and Stamps 2008, Wolf and McNamara 2012, Dochtermann and Dingemanse 2013). Previous studies on female *Octodon degus* have found that aggression is linked to testosterone levels (Bauer et al. 2018), which suggests that this personality trait correlates with physiological characteristics and might explain why I found aggression to be repeatable. On the other hand, behaviors may be more plastic and less consistent when they are sensitive to environmental effects, such as traits subject to selection under predation risk (Bell et al. 2009, Réale et al. 2010a). Previous studies have found differences in boldness and activity levels of prey caused by predator presence (Lawler 1989, Brown et al. 2005, Magnhagen and Borcherding 2008, Harris et al. 2010). Degus are preyed upon by numerous terrestrial and aerial predators (Jaksié et al. 1981) and are subject to changes in behavior due to predation risk, expressing differences in space use in differing levels of risk (Lagos et al. 1995). The constant risk of predation might drive selection towards an optimal behavioral response, where individuals respond in similar ways (Dingemanse et al. 2007). This may reduce the level of among-individual variation and thereby reduce repeatability (Boake 1989, Nakagawa and Schielzeth 2010).

Competition Trials

I observed that individual aggression level was not predictive of competitive ability, contrary to my prediction that more proactive traits (i.e. more aggressive) provide a competitive advantage. In previous studies of competitive dyads of Midas cichlids (*Cichlasoma citrinelum*), the more aggressive individuals won more contests when the fish were acclimated to each other for a short amount of time (1-2hrs) (Barlow et al. 1986). However, individual size was a stronger predictor of contest outcome and larger fish won more fights when acclimation time increased to 24 hours. This suggests that aggression may play a large role in initial competitive interactions, such as first encounters, but the role of aggression wanes as familiarity with conspecifics increases. Based on telemetry data, the degus in this study had been living in social groups for approximately two months prior to competitive trials, allowing enough time for animals to acclimate to members of their groups, which may explain why aggression levels did not predict contest outcome within groups. Furthermore, whereas this study did not demonstrate a significant effect of mean body mass on competition, I observed that of 16 dyads, 13 were consistently won by the individual with a higher mean body mass, a potential trend that suggests mean body mass may influence competitive outcome given a larger sample size. These observations corroborate the findings above of Barlow (1986), but future studies might benefit from evaluating whether *Octodon degus* display a trend in competitive outcomes similar to Mydas cichlids by conducting experiments in which dyads have no prior knowledge of each other. In this way, researchers may better elucidate the role of personality in competitive interactions.

Alternatively, this study characterized competitive ability in the context of food acquisition, given that many studies rely on food to stimulate behavioral response. However, my field site experienced unusually high food abundance the year of my study and in the preceding two years, and competition for food resources could have been low. This may have resulted in lower perceived value of food and weakened pressure to win contests for access to food, thereby reducing the effect of aggression on competitive outcome. In fact, ants (*Formica xerophila*) display higher levels of aggression when the resource value is high compared to when it is low (Tanner and Adler 2009). Additionally, aggression levels in rainbow trout (*Oncorhynchus mykiss*) are tied to relative food abundance, with aggression levels decreasing when food becomes highly abundant (Toobaie and Grant 2013). Instead, perhaps aggression improved competitive ability in other contest situations in which competition was higher and success yielded increased fitness, such as access to mates or to social groups.

Social Organization

Degus did not assort based on aggression level, contrary to my prediction that social groups would be composed of dissimilar individuals. Since my prediction was based on the premise that negative assortment occurs to minimize the cost of competition, the finding that aggression did not influence competitive outcome reinforces my observation that degus do not group preferentially by this personality trait. Perhaps my measure of aggression (response to prodding) was not reflective of the ecological role I assumed (improved competitive ability), and tests that validate the measure of aggression with field observations of competition would serve as better predictors of competitive ability (Reale et al. 2007). I also evaluated whether individual mean body mass predicted social assortment, as some animals assort in groups based on comparable traits (Hoare et al. 2005, Farine 2014) and grouping by mean body mass may explain the lack of assortment by aggression in this species. However, I found that degus do not assort by mean body mass (Figure 2.4). These results indicate that either degus do not assort preferentially when forming groups, or there are other characteristics by which they associate. Chock et al. (2017) found that degus assort negatively based on exploratory behavior, with more exploratory individuals grouping with less exploratory individuals. Given that degus sort based on exploratory behavior, we may infer that in the context of group-living, differences in exploration, and not aggression, provide greater benefit to individuals in these social groups. More exploratory individuals exhibit increased space use (Boon et al. 2008, Boyer et al. 2010), so groups with dissimilar exploratory individuals may benefit, since animals utilize different habitats to forage, decreasing indirect competition, as opposed to the direct competition as measured in this study (Bergmüller and Taborsky 2010). However, the relationship between space use and personality traits is most commonly studied in the context of dispersal, and empirical examples of personality-dependent space use other than dispersal are rare (Sih et al. 2012, Wolf and Weissing 2012, Spiegel et al. 2015). Future studies would benefit from evaluating the role of exploration and other personality traits in habitat utilization, and could inform theory on the relevance of personality in ecology and in group formation.

Fitness Consequences

The difference between most and least aggressive members in a group did not predict PCOW in degus, suggesting that individuals in social groups do not incur a fitness benefit from the personality composition of group members. In this study, I calculated individual fitness (PCOW) based on total offspring weaned per group divided by the number of females per group. This measurement does not quantify true individual fitness and instead utilizes group-level measurements. Group-level measurements of fitness have been used prevalently in studies of social insects, where reproduction occurs at the colony level. Here, the colony is commonly considered a unit, with selection acting on the colony as well as individuals within it (Hölldobler and Wilson 2008, Pinter-Wollman 2012, Jandt et al. 2014). However, group-level measures of fitness may not be adequate in degus because social groups are relatively unstable (Ebensperger et al. 2009, Ebensperger et al. 2016) and individual reproductive success can vary considerably among females in the same group (Wey et al. 2013, Hayes et al. 2019). Instead, individual measures of fitness in relation to group-level interactions may serve as a better indicator of personality effects on reproductive success within groups. Further, benefits of group living are complex and modulated by numerous components, not limited to group size, ecological factors, and sex ratios. Recent studies found that reproductive success of degus was influenced by the interaction between group size and both food abundance and degu density, and that the number of males per group affects PCOW and standardized variance in direct fitness (Ebensperger et al. 2014, Hayes et al. 2019). Including measures of personality would benefit future studies, as it may elucidate the mechanisms behind such findings, and clarify how the interactions among group members in varying ecological conditions, variable group sizes, and with different sex ratios may be influenced by the behavioral type of individuals in the group.

CHAPTER 3

CONSERVATION IMPLICATIONS

Animal personality represents consistent variation in the behavior of individuals that is repeatable across time and context, and is widely documented in the animal kingdom (Gosling 2001, Sih et al. 2004a, Sih et al. 2004c, Reale et al. 2007, Sih and Bell 2008). Research in behavioral ecology has revealed that personality influences ecological and evolutionary consequences for individuals, populations, and species (Sih et al. 2012, Wolf and Weissing 2012). A growing number of studies demonstrate that personality is heritable and affects the life history, dispersal, parasite transmission, productivity, predation rate, and fitness of numerous taxa (Dingemanse et al. 2002, Drent et al. 2003, Reale et al. 2007, Wolf et al. 2007, Biro and Stamps 2008, Smith and Blumstein 2008, Cote et al. 2010, Mutzel et al. 2013, Santos et al. 2015, Keiser et al. 2016, Michelangeli et al. 2017). Given the large role of personality in ecological systems and processes, integrating personality research into plans to protect and maintain species could improve the success and cost-effectiveness of programs as diverse as reintroductions of endangered species to management of farmed populations (Blumstein and Fernández-Juricic 2004, Réale et al. 2010a). The emerging field of conservation behavior aims to assist in the conservation of wildlife by applying concepts of animal behavior and personality, and highlights how personality affects numerous aspects of wildlife conservation and management (Blumstein and Fernández-Juricic 2004, Blumstein and Fernández-Juricic 2010, Smith and Blumstein 2013, Merrick and Koprowski 2017).

Table 3.1 Implications of personality on management and conservation strategies

Applied Management and Conservation Strategy	Personality Trait	Implication	Taxonomic Group	Reference
Trappability and Detection Probability	Boldness, Activity level, Exploration	Proactive individuals are more likely to be captured than reactive individuals, affecting population size estimates and capture for captive breeding/translocation programs. Alternative sampling methods can avert these issues.	Fish, reptile, bird, mammal	(Anthony and Blumstein 2000, Biro and Dingemanse 2009, Garamszegi et al. 2009, Carter et al. 2012, Biro 2013)
Translocation and Reintroduction Success	Boldness, Exploration, Docility	Behavioral type affects post-release survival. Focusing efforts on sensitive behavioral types may improve success of translocation/reintroduction programs.	Mammal	(Bremner-Harrison et al. 2004, Sinn et al. 2014, Baker et al. 2016, Haage et al. 2017, West et al. 2019)
Habitat Protection and Landscape Connectivity	Aggression, Boldness, Movement, Activity level	Personality traits influence space use and migration, and individuals move through their habitat in consistently different ways. Models that incorporate these factors may better predict spatial use of species.	Fish, reptile, bird, mammal	(Fraser et al. 2001, Boon et al. 2008, Chapman et al. 2011, Vegvari et al. 2011, Spiegel et al. 2015, Holtmann et al. 2017, Hertel et al. 2019)
Invasive Species	Exploration, Boldness,	Invasive species tend to have more proactive individuals at the invasion front, which could inform efforts to manage and control invasive species as they enter new areas.	Crustacean, fish, bird	(Fitzgerald and Martin 2005, Fogarty et al. 2011, Chapple et al. 2012)
Human Disturbance	Boldness, Fearfulness	Proactive individuals tend to be less sensitive to human disturbance. The effects of disturbance on survival of species may affect variability of personality traits, which may influence adaptive ability.	Bird	(Carrete and Tella 2010, Arroyo et al. 2017, Merrick and Koprowski 2017)

Personality influences trappability and detection probability of many animal taxa, a major component of estimating the size of wildlife populations for conservation and management (Anthony and Blumstein 2000). Studies have found sampling bias toward more proactive (i.e., more bold, exploratory, and aggressive) individuals (Biro and Dingemanse 2009, Garamszegi et al. 2009, Carter et al. 2012, Biro 2013) which may underrepresent the number of reactive (i.e., less bold, exploratory, and aggressive) individuals and the total size of populations in question. To avert such problems, researchers suggest increasing the use of alternative sampling methods, such as camera traps and eDNA, to estimate this parameter (Biro and Dingemanse 2009, Merrick and Koprowski 2017). A bias towards proactive individuals may also affect capture for captive populations and translocation programs.

Translocation and reintroduction success are dependent on personality traits of individuals, and multiple studies demonstrate how behavioral type can affect post-release survival. In a translocation program for burrowing bettongs (*Bettongia lesueur*), proactive individuals were more likely to survive after release than reactive individuals (West et al. 2019), and bold Tasmanian devils (*Sarcophilus harrisii*) had better survival rates than less bold individuals post release (Sinn et al. 2014). Similarly, bold captive-bred swift foxes (*Vulpes velox*) were more likely to die after release than less bold individuals (Bremner-Harrison et al. 2004). In European mink (*Mustela lutreola*), bold individuals had increased survival after reintroduction, but exploration was both negatively and positively related to survival, depending on location (Haage et al. 2017). One suggestion to improve survival success has been to account for the interaction between personality and HPA (hypothalamic pituitary adrenal) axis stress response of individuals when selecting those for translocation and reintroduction, which may facilitate identification of individuals that need more care during these events (Baker et al. 2016). Some suggest monitoring physical response of particularly sensitive behavioral types to prevent unneeded stress or casualties during movement (Merrick and Koprowski 2017). Pre-release training can also improve the survival of reintroduced individuals, and programs may benefit from focused training efforts for behavioral types with a lower chance of survival. Similarly, differences in learning rates can be consistent in populations, and training efforts could focus on individuals with longer learning times (White et al. 2017).

Personality can also affect other aspects of conservation and management efforts. For example, when selecting habitats to protect or deciding on areas in which to add migration corridors, conservation biologists might consider that individuals move through habitats in consistently different ways, and migratory propensity is affected by personality traits (Fraser et al. 2001, Boon et al. 2008, Chapman et al. 2011, Spiegel et al. 2015, Holtmann et al. 2017). For instance, aggressive bobtailed lizards (*Tiliqua rugosa*) move further from the center of their home range than less aggressive lizards, and are less likely to use areas with a lot of cover and certain vegetation types (Spiegel et al. 2015). Bolder cyprinid fish (*Rutilus rutilus*) are more likely to migrate than less bold individuals (Chapman et al. 2011). Additionally, common cranes (*Grus grus*) hatched in undisturbed habitats consistently select undisturbed migratory stop-over sites within and across years of migration, despite ecological differences across sites, and black bears (*Ursus americanus*) demonstrate repeatability in movement, activity level, and space use (Vegvari et al. 2011, Hertel et al. 2019). While some of these personality traits do not fall under clear categories (i.e. aggressive, bold), within-individual repeatability classifies these behaviors as aspects of personality. Accounting for repeatable differences in individual personalities and movement patterns could improve the predictive power of models used for selecting habitat to protect and landscapes to connect (Spiegel et al. 2015, Lesmerises and St-Laurent 2017, Liukkonen et al. 2018).

Variation in personality influences how populations and species react to their environment, including human disturbance. Differences in individual response to human disturbance have implications for invasive species management and consequences for maintenance of personality variation in populations. For instance, invasive species tend to have more proactive individuals at the invasion front, which could inform efforts to capture or control invasive species as they enter new areas, and could improve the efficacy of models classifying traits associated with invasiveness (Fitzgerald and Martin 2005, Merrick and Koprowski 2017). Human disturbance might also select for individuals that have a higher tolerance for human presence and diminish variability in behavioral types. For example, repeatable flight initiation distance (the distance at which individuals flee when approached by a potential threat) in individuals may affect the persistence of variation in this personality trait, as those with longer flight initiation distances may be less tolerant of human presence and fare worse as habitat patch size decreases (Carrete and Tella 2010). Likewise, bolder female Montagu's harriers (*Circus pygargus*) have higher nesting success rates under high human disturbance compared to less bold individuals (Arroyo et al. 2017). Given than personality is heritable, this may influence the evolutionary trajectory of personality types in such populations. On the other hand, harvested populations experience differential capture of more proactive individuals, with bolder animals having a higher chance of capture, increasing the ratio of less bold individuals (Merrick and Koprowski 2017). Diversity in behavioral types aids in adaptive ability of populations and species (Sih et al. 2004c, Reale et al. 2007, Wolf et al. 2007, Baker et al. 2016), and maintaining variation in personalities is important in conservation and management efforts, especially in the face of environmental change, growing human populations, and habitat alteration and destruction. As such, conservation biologist should consider the effects these problems have on managed populations, and incorporate strategies to help maintain diversity of personality traits.

Whereas the objective of the present study did not focus directly on conservation, the results inform theory on competitive interactions, assortative group formation, and the fitness consequences of grouping by personality traits. These processes are pertinent to conservation and management efforts of both group- and solitary-living animals. Competition is prevalent in nature and may become even more so as animals are forced to inhabit new niches or as densities increase due to habitat destruction and fragmentation. Understanding how personality may influence competition within and among species, and how variability in behavioral types could modulate its cost, is important for facilitating management efforts. Further, if species demonstrate preferential assortment based on individual personality traits, and such associations result in increased fitness benefits, management efforts of group-living animals may improve success by adjusting the composition of animal groups in captivity and prior to release or translocation (Paulino et al. 2018). Indeed, matching giant panda (*Ailuropoda melanoleuca*) pairs based on personality traits increases reproductive success (Martin-Wintle et al. 2017).

Animal personalities play a large role in ecology and evolution, and accounting for personality in conservation plans has already proven useful in understanding the outcome of management efforts (Merrick and Koprowski 2017). However, animal personality is still underrepresented in wildlife management and conservation strategies, and literature highlighting the role of personality in processes relevant to conservation and management is scarce (Blumstein and Fernández-Juricic 2004, Blumstein and Fernández-Juricic 2010). The challenge now lies in bridging personality studies with conservation and management strategies to make research questions more applicable for conservation scientists, and to improve efforts to support and protect species of interest (Blumstein and Fernández-Juricic 2004, Merrick and Koprowski 2017).

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APPENDIX A

STATISTICAL PROGRAMMING CODE (R)

R Code Sample

Personality-

```
if (!require("pacman")) install.packages("pacman")
pacman::p_load(permute, MASS, plyr, ggplot2, rptR, lme4, effects, assortnet, asnipe)

## Poke Test
setwd("C:/Users/kch466/Documents/.")

pokedata<-read.csv("./PokeTestOnlyAll.csv")

## GLMM: with poke as response, sex and observation number as fixed effects, and date and ID as
random effects

poke.glmsex<-glmer(poke~ sex + obs+ (1|date) +(1|id),
                family=binomial(link=logit), data=pokedata)
poke.glmsex
summary(poke.glmsex)


## Linearity and Residuals (glmm assumptions)

ggplot(data.frame(sex=pokedata$sex,pearson=residuals(poke.glmsex,type="pearson")),
      aes(x=sex,y=pearson)) +
  geom_point() +
  theme_bw()

ggplot(data.frame(obs=pokedata$obs,pearson=residuals(poke.glmsex,type="pearson")),
      aes(x=obs,y=pearson)) +
  geom_point() +
  theme_bw()

qqnorm(residuals(poke.glmsex))

## Comparing Models for Best AIC (lower)

 #model2: removes ID
 model2<-glmer(poke~ sex + obs+ (1|date), +  family=binomial(link=logit), data=pokedata)
 model2

#model3: removes date
 model3<-glmer(poke~ sex + obs+ (1|id), +  family=binomial(link=logit), data=pokedata)
 model3

## Repeatability
```

```
poke.rpt<-rpt(poke~ sex + obs  +(1|date)+ (1|id),
        data=pokedata, grname=c("date", "id", "Fixed", "Residual"),
        datatype="Binary", link="logit", ratio=T, adjusted=F, nboot=1000)
poke.rpt


##BLUPs

blups<-ranef(poke.glmsex)

blups
```

Competition

```
if (!require("pacman")) install.packages("pacman")

pacman::p_load(permute, MASS, plyr, ggplot2, rptR, lme4, effects, assortnet, asnipe)

setwd("C:/Users/s2gri/Dropbox/Sara Grillo/Thesis/Data/R/Poke/Poke Data")

comp<-read.csv("./comp.blup.bmlac.csv")


## Distribution of Data

if (!require("fitdistrplus"))install.packages("fitdistrplus")
descdist(comp$pwin, boot=500)


## GLM: with proportion win as response variable, difference in BLUP and mean body mass as predictors

if (!require("betareg"))install.packages("betareg")

betatpwin<-betareg(transpwin ~ blupdif + bmdif, data = comp)

betatpwin

summary(betatpwin)


## Pearson: with BLUPs and mean body mass as correlates

bluplac<-read.csv("./BLUPbmlac.csv")
shapiro.test(bluplac$blup)
shapiro.test(bluplac$interval)
intervalsqrt<-sqrt(bluplac$interval)
shapiro.test(intervalsqrt)
```

```
cor.test(bluplac$bmlac,intervalsqrt, method= "pearson", use="complete.obs")
```

Social Organization

```
individuals <- read.csv ("femidgroup.csv")

names (individuals) <- c("ID","GROUP")
individuals$DATE <- as.Date (individuals$DATE, "%m/%d/20%y")
individuals <- individuals[order(individuals$GROUP,individuals$ID),]
gbi <- get_group_by_individual(individuals, data_format="individuals")
network <- get_network (gbi, data_format="GBI", association_index="HWI")
network.ordered <- sort.list (network)
write.csv (network, "degu.network1.csv")

#Data for Poke Test

vert.values.poke<-(read.csv("femidblup.csv"))

##Assortment Test

poke.r <- assortment.continuous (graph=network, vertex_values=vert.values.poke[,"femblup"],
weighted=FALSE, SE=TRUE)

bmlac.r <- assortment.continuous (graph=network, vertex_values=vert.values.poke[,"bmlac"], SE=TRUE)

poke.r
bmlac.r

#Network Permutations -

##by poke

test.np <- network_permutation (
  gbi, data_format="GBI", permutations=50000, association_index="HWI", association_matrix=network)


poke.np <- vector (mode="numeric", length=50000)
for (i in 1:50000) {  #length(dim(test.np)[1]))
  poke.np [[i]] <-
    assortment.continuous (graph=test.np[i,,], vertex_values=vert.values.poke[,"femblup"])$r}


#p value

p.poke.r <- length (poke.np[poke.np >= poke.r$r])/50000

p.poke.r
p.poke.r*2
```

Fitness Consequences

```
mfpcow<-read.csv("./mfpcow.csv")
```

```
cor.test(mfpcow$cov,mfpcow$PCOW, method= "spearman", use="complete.obs")
```

APPENDIX B

OUTPUTS FROM STATISTICAL PROGRAMMING CODE (R)

Personality

GLMMs (binary data) and LMMs (continuous data), with personality trait as response variable, sex and observation number as fixed effects, and date of observation and animal ID as random effects

Table 1- Population level GLMMs

Trait	Fixed Effect	Estimate	Std. Error	Z value	P value
Aggression (poke)	Sex	-0.078611	0.515814	-0.152	0.8789
	Observation #	0.007186	0.031516	0.228	0.8197
Bold (emergence)	Sex	-0.09118	0.53596	-0.170	0.8649
	Observation #	0.32830	0.19257	1.705	0.0882

Table 2- Population level LMMs

Trait	Fixed Effect	Estimate	Std. Error	DF	T value	P value
Activity (distance moved)	Sex	5.0907	2.1229	80.1317	2.398	0.01881*
	Observation #	-2.5466	0.7639	40.5191	-3.334	0.00184**
Bold (prop.time edge)	Sex	0.015564	0.022016	74.84677	0.657	0.513
	Observation #	-0.002232	0.006162	30.394958	-0.362	0.720

Table 3- Female specific GLMM

Trait	**Fixed Effect**	**Estimate**	**Std. Error**	**Z value**	**P value**
Aggression (poke)	Preg v Lac	0.130069	0.542980	0.240	0.81068
	Neither v Repro	-0.803357	0.351854	-2.283	0.02242*
	Mass	-0.006967	0.006672	-1.044	0.29636
	PregVLac*Mass	-0.007497	0.013267	-0.565	0.57201
	NeitherVRepro*Mass	0.036148	0.012952	2.791	0.00526**

Table 4- Female specific pair-wise interactions between reproductive state, accounting for mean body mass

Pair-wise Intrxn	**Value**	**DF**	**Chisq**	**p-value**
No-Preg	-0.039897	1	7.6857	0.01670 *
No-Yes	-0.032400	1	4.8506	0.05527.
Pregnant-Yes	0.007497	1	0.3193	0.57201

Table 5- Repeatability of aggression in female-specific model

Trait	**Repeatability**	**SE**	**CI**	**p-value**
Aggression (poke)	0.362	0.07	0.206-0.477	<0.001

Competition

Table 6. Descriptive table of mean body mass difference for competitive dyads. Proportion wins and mean body mass difference are calculated based on the subject listed first in the dyads.

Dyad	Proportion Win	Mean Body Mass Difference
131-135	0	7.6
121-125	0	-19.6
140-121	0.75	19.4
143-121	1	17.7
143-140	0.75	-1.7
109-108	1	40.9
129-161	1	27.4
132-111	0	-43.2
163-162	0	-26.7
167-171	0.8	10.7
168-172	1	0.8
170-179	0	-5.2
180-170	0.75	0.8
181-173	0	-6.6
119-150	0.25	30.5
188-127	0	17.1
127-189	1	-23.6
189-188	0.8	6.5

Table 7. Percent wins by reproductive state in competition trials. Dyads with matched reproductive states were excluded.

Lactating	Neither	Pregnant
0.22	0.44	0.33

VITA

Sara Grillo was born in Caracas, Venezuela, to Ana and David Grillo. She has two older brothers, Andres Trujillo and Juan Carlos Trujillo. She moved to upstate New York in 2002, where she attended Onondaga Central Schools. In 2015, she completed a Bachelor of Science in Environmental Science and Ecology at the State University of New York at the College at Brockport. Sara spent summers conducting undergraduate research and working on the Great Lakes Marsh Monitoring Program. After graduation, she attended the University of Tennessee at Chattanooga, where she conducted her thesis research under Dr. Loren Hayes.