

PERSONALITY AND BEHAVIORAL SYNDROMES OF THE BIG BROWN BAT,
EPTESICUS FUSCUS

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Personality and Behavioral Syndromes of the Big Brown Bat,
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ABSTRACT

As the study of animal personality has significantly expanded in the last decade, a growing amount of research has focused on the impacts of sociality and group dynamics on behavioral repeatability. The research presented here focused on examining personality in a captive colony of a common bat species, the big brown bat (*Eptesicus fuscus*). Chapter 1 focused on calculating repeatability along common personality axes, as well as examining relationships between these axes (behavioral syndromes). High repeatabilities were observed for two behavioral axes (exploration and activity) and a significant correlation was found between these axes, confirming a common behavioral syndrome. Chapter 2 focused on examining if individuals exhibit reduced repeatability of behavior when regularly switching between social groups. We found little evidence for increased plasticity in regards to changing social group composition, indicating that animals have relatively fixed behavioral types, exhibiting limited plasticity despite the composition of their social group.

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DEDICATION

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1. DETERMINATION OF PERSONALITY AND BEHAVIORAL SYNDROMES IN THE BIG BROWN BAT, *EPTESICUS FUSCUS*

1.1. Introduction

Animal personality can be defined as consistent differences between individuals in their behavior across time and contexts (Dingemanse et al 2010). In the last two decades, a considerable research effort has been devoted towards assessing the repeatability of behavior, as well as examining within-individual correlations between behaviors, known as behavioral syndromes (Hollander et al 2008; Careau, V., & Garland, T. 2012; Dingemanse et al 2010). Looking across a wide diversity of taxa and personality axes, strong support for moderate to high repeatability in personality traits has been found, although substantial variation exists (Bell et al 2009). This general trend aligns with research estimating that animal approximately 52% of variation in animal personality traits is attributable to additive genetic variation (Dochtermann et al 2014).

The most commonly studied personality axes include boldness, exploration, activity, and aggression. Unfortunately, a lack of clear definitions has led to confusion about these terms (Dochtermann and Nelson 2014). For instance, boldness has been interpreted as being the propensity to take risks, especially in novel situations (Coleman & Wilson 1998; Toms et al 2010), whereas Reale et al. (2007) defined boldness as an individual's response to a risky situation alone, excluding reactions to novel situations and stimuli altogether. Furthermore, tests of boldness have varied in quantifying behavioral responses to novel objects, responses to a novel environment, and responses to predation risk (Toms et al 2010); none of which are comparable or use standardized testing methods. Part of this issue is driven by a tradeoff between

using a standardized design versus making modifications to a test or definition so that it is ecologically relevant to a given study system (Carter et al 2013).

Exploration is generally defined as a response to a novel environment. For example, Dochtermann and Nelson (2014) found high repeatability in exploration behavior when individuals were exposed to both novel maze and obstacle course arenas. Activity is defined as a measure of movement in a non-risky and a non-novel environment. For example, Smith and Doupnik (2005) found that the amount of time spent swimming was repeatable in captive American bullfrog tadpoles, *Rana catesbeiana*, housed in experimental tanks. Aggression can be defined as any agonistic behavior directed towards conspecifics (Bierbach et. al, 2015). For example, Wilson et al (2013) found that multiple measures of aggression, such as number of approaches and attacks, were repeatable in male-male contests of sheephead swordtail, *Xiphophorus birchmanni*.

Behavioral syndromes are non-zero between- individual correlations, such as aggression and exploration (Dingemanse et. al, 2012). Behavioral syndromes can also exist in relation to physiological processes or habitat variation (Careau et al 2015; Cury de Barros et al 2010). For example, roe deer use different habitats for foraging based on their individual boldness in risky situations (Bonnet et al 2015). The strength of behavioral syndromes can exhibit variation over time (Sinn et al 2010) in response to local environmental conditions (Bengston et al 2014).

While personality and behavioral syndromes have been investigated in a wide diversity of species, there are still some taxa in which these concepts are understudied; one such group is bats (Order Chiroptera). To our knowledge, only two studies have investigated personality or behavioral syndromes in bats (Kilgour and Brigham 2013; Menzies et al 2013). The objective of

this study was to test for the presence of personality and behavioral syndromes in a captive colony of big brown bats, *Eptesicus fuscus*.

1.2. Methods

1.2.1. Study Species and Animal Capture

Big brown bats are one of the most common species in North America and have previously been shown to do well in a captive environment (Photo A1). The natural social structure of this species during the summer breeding season is for males to be solitary or form small bachelor groups, while females form maternity colonies containing 10s to 100s of females and their offspring (Kilgour et al 2013; Webber et al 2016; Silvis et al 2014). In tree-roosting populations, individuals exhibit a fission-fusion social structure in which the colony is divided into multiple tree cavities on a given night (Willis and Brigham 2004). Across nights, individuals mix and new subgroups are formed, possibly to maintain long-term social bonds across a larger population (Kashima et al 2013; Kerth et al 2011; Willis & Brigham 2004; Kilgour & Brigham 2013; Lučan et al 2009).

Non-pregnant and non-lactating female big brown bats were collected from May to June 2016 at a variety of locations in East and Central North Dakota. Bats were captured using either hand nets (at known roosts) or mist nets. Sixteen females were transferred to the NDSU Conservation Research Facility at the Red River Zoo in Fargo, ND (Photo A2) and subsequently used in behavioral trials. Information on standard life history variables, such as mass, forearm length, and body condition, was gathered from each animal at the time of intake. Each individual was also given a unique pattern of colored forearm bands for identification. In the first two weeks of captivity, animals were housed individually in cloth bags. During this two-week period, bats were trained to eat mealworm larva (*Tenebrio molitor*), enriched with a bat-specific

growth medium (Barnard 2013), out of a feeding dish. Once trained, individuals were divided randomly into groups of four individuals (four groups total) and housed in large flight cages (2.5m x 2.5m x 2.5m). Within each flight cage, one bat house was provided for the animals to roost (Photo A3). Food and water were placed on platforms mounted within the cages, and refreshed on a nightly basis. Upon moving to the large flight cages, animals were given 2-5 days to acclimatize to their new environment and social group before trials began.

1.2.2. General Trial Setup

Behavioral trials measuring aggression, exploration, and activity were conducted repeatedly on each individual from June to September 2016. All trials were conducted between 20:30 and 00:00 on a given night. The four types of test arenas used were: 1) a triangular arena (for dyadic interactions), 2) a four-arm maze, 3) a hole board, and 4) an open field arena. During a given trial, a clear Plexiglas lid was placed over the arena in use to allow clear visibility of the trials and prevent escape. Video and audio data for all trials were gathered using a Sony Camcorder with NightShot capability; a lamp equipped with an IR lightbulb aided in illuminating the arena during trials to ensure high quality recordings were captured. For all trials, the camera was positioned 0.5 m above the arena and oriented downwards to permit video capture of the entire arena space. Each bat was run through each of the maze, holeboard, and activity arenas on four separate occasions, and was exposed to 12 dyadic competitions in the aggression arena, only ever competing against bats outside their own subgroup.

1.2.2.1. Aggression Trials

Aggressive behavior was assessed by randomly pairing individuals with a conspecific from outside their subgroup and allowing the dyad to compete over a single food item. Data was collected over a three-week period, with no trials conducted during the second week. During

their specific trial days, selected individual bats were tested in 3-4 unique dyads per night, with a minimum of 5 minutes of rest between trials. In a given night, an individual was limited to a maximum of four trials per night to avoid potential behavioral changes due to satiation.

Animals were not tested on consecutive nights.

The test arena was an equilateral triangle (0.45m x 0.15m) (Photo A4). To promote competition, bats were not fed prior to the start of trials; hence, animals had not eaten for 12-24 hours and were likely hungry. At the start of the trial, a mealworm was placed in one corner of the arena, and the selected dyad was positioned at equal distances from the mealworm in opposite corners; animals were then released simultaneously and the Plexiglas lid replaced. Trials continued until the mealworm was consumed; if the prey was not consumed within 3 min, the trial was terminated. Upon completion of a single trial, the arena was wiped down with a mild cleaning solution to remove the scent of the previously tested dyad. After all trials were complete for the night, animals were given supplemental feeding, then returned to their flight cage, where food and water were also available. Aggression scores of an individual were calculated based on total number of competitions won, duration of the competitions, and frequency of different aggressive behaviors (biting, charging, production of social calls).

1.2.2.2. Activity Trials

To measure individual activity level, a standard open field test was used. When being tested, an individual was placed into a plastic arena (0.5m x 0.35m x 0.15m) that was divided into separate zones using colored tape (Photo A5). Initially, the individual was blocked from entering the arena to prevent a premature start to the trial. The trial began when the entrance was unblocked, the bat had full visibility of the arena, and the arena was covered with a transparent lid. Trials lasted 3 minutes. Activity level was determined by the location of the individual

within the arena throughout the duration of the behavioral trial, the cumulative time spent in each zone, total time spent moving, the number of unique zones visited, total distance traveled (cm) and the total number of zones visited, including revisits (Dochtermann & Nelson, 2014).

1.2.2.3. Exploration Trials

Exploration was assessed using two different testing arenas; a radial arm maze and a hole board test. The arena for the hole-board test was a Plexiglas box (0.6m x 0.4m x 0.15m) equipped with a plywood base in which six, evenly spaced holes were cut into the plywood (Photo A6). These holes were 5cm deep, which meant that bats could only see the contents of the hole by dipping their head into the opening. Two holes within the arena were randomly selected and 1” mealworms were placed inside. Prior to the beginning of the trial, the bat was held outside of the arena. The trial began when the bat was released into the arena through a small opening and the arena was covered with a transparent lid. Trials lasted 3 minutes, regardless of the bat’s behavior. Bats that did not enter the arena within the first 15 seconds were gently nudged with a hand. Calculated exploratory scores included the proportion of time spent active, time spent inactive, total number of head dips, retrieval of mealworms, and average head dips per minute (Menzies et. al, 2013).

Using a four-arm maze (Photo A7), individual levels of exploration could be determined in terms of response to barriers and directionality in a novel environment. Initially, the test individual was placed in the center of the maze, but was cut off from the arms by barriers. Four mealworms were placed in a dish at the end of one of the four maze arms. After a one-minute acclimation period in the maze center, the barriers were removed and the center lid of the arena was replaced, marking the start of the trial. Trials lasted 5 minutes and were considered finished once the bat had reached and retrieved all mealworms or the full time had elapsed. Location of

the mealworms was randomized between arms on subsequent trials to eliminate any potential learned behavior. Exploration was scored by the latency of initial movement, number of arms visited (unique and repeated), time spent in each arm, time and frequency spent in the center, and the length of the trial.

1.2.3. Behavioral and Statistical Analysis

Data from the four trial types were assessed for within-individual consistency and for the existence of two common behavioral syndromes (aggression-exploration and exploration-activity). All videos were coded in Noldus Observer, excluding the open field trial, using a behavioral analysis template. This program allows the observer to break down each trial by coding pre-determined variables. Variables classified as behavioral events include active (secs), inactive (secs), charging, and flight attempt, while variables classified as behavioral states included dip, entering maze arm, bite, social call and win. Averages, total durations of movement or trial length, and totals of all coded variables were calculated. Results from the coded videos were then uploaded to JMP 13 and R version 3.3.1, and used in a principal component analysis (PCA). PCA reduced the number of measured behavioral traits into composite, synthetic variables or principal component (PC) scores, which are independent of each other. Additionally, a Bartlett test was used to confirm equal variances. The scores for each trial were then used to test for levels of repeatability, by the ratio of among-individual variation over the sum of among- and within- individual variance of the individual. Additionally, scores were run through a generalized linear mixed-effects model (GLMM) with a normal error distribution to determine the presence and strength of correlations (i.e. behavioral syndromes) and produce adjusted repeatabilities. GLMMs incorporate both fixed and random effects, allowing the impacts of predictor variables on the mean of response variables to be assessed, as

well as variation within and among levels of a predictor variable (Dingemanse and Dochtermann 2013). For the GLMM analysis, date and replicate were fixed variables while bat ID, subgroup, (and opponent for aggression) were assigned as random effects.

1.3. Results

1.3.1. Personality

Several experimental variables loaded strongly onto the PC scores. The number of retained PC scores varied from 1-3 factors, depending upon the trial type (Table 1.1). Based on the factor loadings from the retained PC scores, we designated a single explanatory variable for each trial type (i.e. “Total Distance Moved” for open field trial), which was then the basis of additional analyses. For aggression trials, “# Social Calls” was selected as the explanatory variable due to strong loading on PC1 (0.56); although “# Charges” loaded more strongly on the first PC score (0.63), this behavior was only consistently exhibited by a few individuals, hence it was not an appropriate variable for all study animals. For the open field trial (activity), “Total Distance Moved” loaded most strongly on the first PC score (0.71), and was selected as the activity variable for further analysis. For the hole board trial (exploration), both “# Head Dips” and “Time Spent Active” had the same loading on the only retained PC factor (0.71). Given that “# Head Dips” directly indicates exploratory behavior, while “Time Spent Active” could be more reflective of general activity level, “# Head Dips” was selected as the explanatory variable for this trial type. For the radial arm maze (exploration), “Mean Duration (Center)” was retained as the explanatory variable due to the highest loading on PC 1 (0.55) and the fact that animals had to cross the center to switch arms.

Table 1.1. Principle component loadings for each trial type. Loadings greater than 0.4 are bolded to indicate significance in explaining each PC factor.

	PC1	PC2	PC3
Activity			
Total Distance Moved	0.707	0.000	-
Active (secs)	0.177	0.968	-
Unique Zones	-0.685	0.251	-
<i>% variance explained</i>	52.63	33.34	
<i>Cum % variance explained</i>	52.63	95.97	
Aggression			
Biting	0.525	0.058	-0.702
Social Calls	0.564	0.039	-0.001
Charging	0.629	0.059	-0.001
N Wins	-0.031	0.707	0.240
Bout Duration	0.097	-0.701	0.219
<i>% variance explained</i>	34.94	28.60	15.68
<i>Cum % variance explained</i>	34.94	65.54	79.22
Exploration (Hole board)			
Total Dips	0.707	-	-
Active (secs)	0.707	-	-
<i>% variance explained</i>	79.29		
<i>Cum % variance explained</i>	79.29		
Exploration (Maze)			
Mean Duration (Arm 1)	-0.116	0.411	-0.768
Mean Duration (Arm 2)	-0.423	-0.687	0.053
Mean Duration (Arm 3)	0.515	-0.131	-0.060
Mean Duration (Arm 4)	-0.178	0.574	0.624
Mean Duration (Center)	0.554	-0.045	0.049
Total Duration	0.452	-0.107	0.106
<i>% variance explained</i>	25.08	22.53	18.87
<i>Cum % variance explained</i>	25.08	47.61	66.48

Using the explanatory variables described above, unadjusted repeatabilities were calculated for each trial type. Three of the four personality axes showed moderate to high repeatabilities (activity = 0.204, hole board exploration = 0.592, maze exploration = 0.276) (Dochtermann and Jenkins 2007, Bonnet et al 2015). Alternatively, aggression exhibited a low repeatability of 0.055. Adjusted repeatabilities (i.e. with bootstrapping analysis) were also calculated for all trial types and were as follows: activity = 0.411, hole board exploration = 0.579, maze exploration = 0.385, aggression = 0.189). All four trial types exhibited minimal

variance in the adjusted repeatability (Table 1.2). None of the fixed effects (replicate, day) or random effects (subgroup, bat ID, opponent) were significant for any of the behavioral trials when calculating unadjusted or adjusted repeatabilities.

Table 1.2. Adjusted repeatabilities for each trial type. Bolded numbers indicate significant correlations between personality axes.

	Activity	Hole board	Aggression	Maze	Adjusted Repeatability
Activity	1.000	0.552	0.253	-0.070	0.411
Hole board	0.552	1.000	-0.013	-0.088	0.579
Aggression	0.253	-0.013	1.000	-0.065	0.189
Maze	-0.070	-0.088	-0.065	1.000	0.385

1.3.2. Behavioral Syndromes

Generalized linear mixed models (GLMM) analysis were used to assess between- and within-individual correlations among behavioral measures of personality (Dingemanse and Dochtermann 2012). The limited level of skew in the distribution could most likely be attributed to uncontrolled social or environmental factors. Since the radial arm maze was substantially less repeatable than the hole board trial for assessing exploration, this trial type was not used for behavioral syndrome analyses. To summarize, open field trials were reflective of the activity axis, dyadic competition trials were reflective of the aggression axis, and hole board trials were reflective of the exploration axis.

GLMMs were used to examine correlations across personality axes within individuals and to assess variation in these correlations (Table 1.2; Figure 1.1). Only exploration and activity showed a strong correlation (0.552). Alternatively, activity and aggression were weakly correlated (0.253) while exploration and aggression were negatively and even more weakly correlated (-0.013).

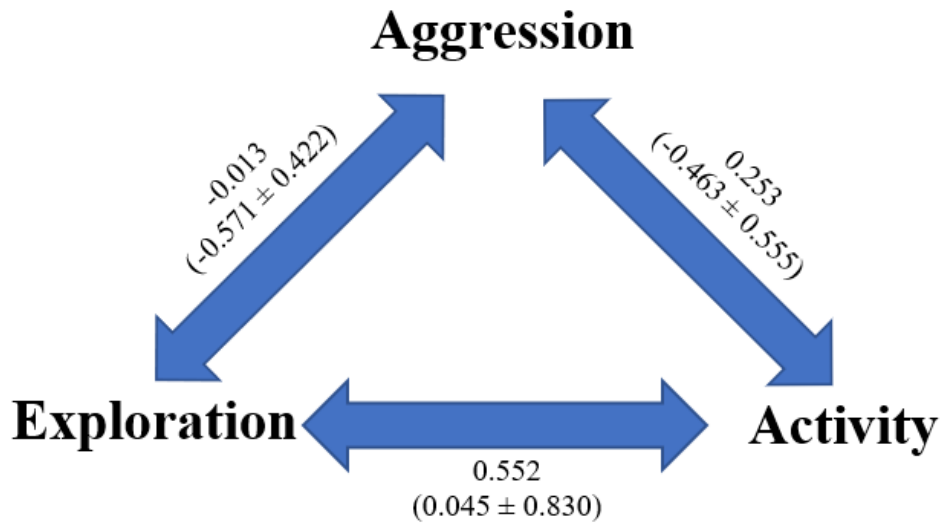


Figure 1.1. Behavioral syndrome relationships between activity, exploration (hole board arena only), and aggression. Shown are the estimated correlation and associated confidence intervals for the relationship between each set of the variables.

1.4. Discussion

Adjusted repeatabilities were moderate to high for three of the behavioral trials, each of which were reflective of a personality axis (exploration or activity). The activity trial arena showed distance moved was the most explanatory variable, which was similar to other studies (Herde & Eccard 2013; Montiglio et al 2013; Dochtermann & Nelson 2014). Interestingly, Bell et al (2009) conducted a meta-analysis and found that the least repeatable type of behavior was activity, which contradicts our findings. Additionally, the two trial arenas designed for exploration (hole board and maze) produced moderate to high repeatabilities. Overall, these results indicate that some bat behaviors are consistent over time, at least over moderate temporal periods (1-2 months). Only dyadic trials, which were reflective of aggression, showed little repeatability (0.055). This finding may indicate that, in general, aggressive behavior is a more plastic trait that is responsive to a variety of other factors, such as environmental quality,

reproductive status, potential opponents, or food availability (Hollander et al 2008; Briffa et al 2015; Courtenes-Jones et al 2014; Herde & Eccard 2013; McRobert et al 2015; Santoro et al 2015).

Our results are similar to the two other studies focused on assessing personality in bats. Menzies et al (2013) showed that little brown bats, *Myotis lucifugus*, exhibited high repeatability in explorative (0.34) and activity (0.29) measures. Kilgour and Brigham (2013) assessed a variety of behavioral traits in big brown bats; although they did not explicitly calculate individual repeatability, they did repeatedly test bats in the same arenas, and found significant interrelatedness between some behavioral traits within the population. Results from our study suggest that these interrelationships may be driven by personality differences in activity or exploratory behaviors among individuals and a behavioral syndrome between these two axes (see below). Our study adds to this current literature due to the time period over which we assessed repeatability in behavior – Menzies et al (2013) conducted their study over a 24-hour period, while Kilgour and Brigham (2013) repeatedly measured behaviors over a maximum period of 11 days. Hence, our results indicate that high short-term repeatabilities in bats have a strong potential to carry over through longer periods of time (1-2 months). Interestingly, studies in other taxa have suggested that repeatability can decrease with the interval between measurements because the ‘same’ phenotypic trait may be influenced by different sets of genes at different ages. Therefore, increasing the interval between measurements to even longer time periods (i.e. years) could decrease repeatability of the phenotypic traits if the two measures do not represent the exact same trait at the genetic level (Bell et al 2009).

Analysis for behavioral syndromes resulted in only one strong correlation, between activity and exploration. This is one of the most commonly observed behavioral syndromes in

the literature (Dingemanse et al 2012; Massen et al 2013; Dochtermann & Nelson 2014; Bonnot et al 2015). However, due to the use of different definitions and variables to define the same personality axis (Dochtermann & Nelson 2014), it is difficult to accurately assess how common this syndrome is across a wide variety of taxa. A continued effort to clearly distinguish amongst personality axes will not only benefit understanding of within and among individual variation, but also the ability of researchers to answer more advanced proximate and ultimate questions focused on animal personality. Our finding of weak or essentially no correlations of activity and exploration to aggression is not surprising given the low repeatability of aggression.

Based on our research, we suggest that future studies test behavioral responses in modified arenas that more appropriately reflect the natural movement patterns of bats. Specifically, bats primarily move by flight or crawling along vertical surfaces. Test arenas converted into three-dimensional spaces would be ideal for permitting movement across vertical and horizontal axes. Menzies et al (2013) used an arena design that allowed for vertical movement, which is a significant improvement over horizontal movement alone; yet, providing both orientations for movement has the potential to be even more informative.

1.5. Conclusion

In conclusion, our results highlight that big brown bats exhibit moderate to high repeatability along common personality axes, as well as a single behavioral syndrome. To our knowledge, this is the third published study on personality in bats, indicating a knowledge gap that still needs to be filled, as there are more than 1,300 species of bats. As a highly social group of animals with extensive diversity in social structure, feeding ecology, and roosting behavior, bats could serve as an excellent system for comparative studies of personality. Specifically, comparative analyses incorporating phylogeny and ecology would be valuable for understanding

the factors that drive the evolution of repeatability in behavior (Dall and Griffith 2014). Understanding personality may even be important in the battle against white-nose syndrome, a disease caused by a fungal pathogen that has killed more than 6 million hibernating bats in North America (USFWS, 2018). Specifically, social interactions between colony members may mediate the spread of the fungus, and understanding these social dynamics may provide insight into patterns of disease transmission.

2. IMPACTS OF SOCIAL GROUP COMPOSITION ON PERSONALITY IN *EPTESICUS FUSCUS*

2.1. Introduction

Over long and short time scales, animals are likely to encounter a variety of social, behavioral, and ecological scenarios, making it improbable that a single behavioral response will be optimal under all possible conditions. As a result, many species demonstrate behavioral plasticity, with individuals adapting their responses to varying conditions. Despite the potential advantages of high plasticity, a growing body of work on behavioral repeatability, known as personality, has shown that animals often exhibit limits to behavioral flexibility, with an individual's range of variation only covering a portion of the range observed across the entire population (Dingemanse et al 2012; Dingemanse et al 2010; Santoro et al 2015; Garamszegi et al 2015). As the evolutionary implications of repeatability along behavioral axes (i.e. activity, exploration) are increasingly studied (Dammhahn 2012; Herde & Eccard 2013; Alpin et al 2015), it is important to understand behavioral flexibility across different conditions and over long time periods.

Many of the model species used in behavioral studies, and particularly those of personality, are social in nature (e.g. sticklebacks, great tits, guppies); hence, it is important to understand how sociality and group dynamics impact the stability of personality. Sociability has itself been examined as an axis of animal personality, with previous studies measuring grouping tendencies, such as preferred group size and proximity to nearest neighbors within a group (Best et al, 2015; Briard et al 2015). Sociability is also reflected in the number of animals with whom an individual associates and the strength of those associations (Best et al 2015). In turn, an

individual's personality can impact patterns of interaction, level of familiarity among conspecifics, and preferred group size (Aplin et al 2015).

Two hypotheses have been proposed regarding the repeatability of individual behavior under changing social conditions. The social niche specialization hypothesis states that behavior is relatively plastic, with individuals modifying their behavioral patterns based on the composition of their social group and the availability of different social niches (Modlmeier et al 2014; Koski et al 2011; Pinter-Wollman et al 2015). An alternative idea is the behavioral type hypothesis, which posits that behavior is relatively fixed with little plasticity, such that animals maintain similar patterns of behavior despite changing social group composition (Laskowski & Bell 2014; McCune et al 2014; von Merten et al 2017). Here, we test which of these hypotheses is supported in a social bat species, the big brown bat, *Eptesicus fuscus*.

Bats are an ideal system to investigate links between personality and social interactions, as most species are highly social and there is substantial variation across species in social structure (Kerth & Konig 1999). Some bat species have been shown to exhibit a fission-fusion social structure in which individuals within a colony divide into several smaller roosting groups that regularly change composition (Willis & Brigham 2007; Kerth & Reckardt 2003). Similarly, other taxa exhibiting fission-fusion, (e.g., elephants, dolphins, primates), have been shown to maintain tangible social links among colony members despite frequent splitting and merging of groups (Best et al 2015; Dinis et al 2018; Ramos-Fernandez et al 2018; Loretto et al 2017). To date, relatively little is known about repeated social interactions amongst bats sharing a roost or how dynamics of group formation are impacted by the behavioral characteristics of individual animals. In this study, we hypothesized that big brown bats, one of the species exhibiting a fission-fusion social structure, exhibit changes in behavior in response to social group

composition, as per the social niche specialization hypothesis. In turn, we predict that animals exhibiting shifts in the composition of their social group will exhibit lower repeatability in behavior compared to animals that remain with the same social group.

2.2. Methods

2.2.1. General Trial Setup

An established colony of *E. fuscus* housed at the NDSU Research and Conservation Facility (Red River Zoo) in Fargo, ND (Photo A2) was used for this study (23 animals in 2017, 21 animals in 2018). While it would have been ideal to use different sets of animals for each replicate, this was not possible due to limitations on the number of animals that could be brought into captivity. Despite the same animals being used across years, treatment and group assignment were randomly reassigned in the second year of the study. Each summer, bats were randomly divided into 6 groups of 4-5 bats, with each group housed in a 2.5m x 2.5m x 2.5m flight cage that contained one bat house. After groups were formed and placed in housing, animals were given 2-5 days to acclimate prior to the start of the experiment. Three treatment groups were established, which differed only in the number of social group shuffles that occurred over the 6-week experimental period (Figure 2.1.). Control groups (2 in 2017; 1 in 2018) experienced no alteration in their subgroup throughout the 6-week period. Single mix treatment groups (2 in each year) experienced one mixing event after 2 weeks, with social groups remaining stable for the remaining four weeks. Finally, the double mix treatment groups (2 in each year) had subgroup composition altered at both weeks 2 and 4. All other external factors and parameters (diet, housing conditions, time of trials) were kept consistent across groups and years.

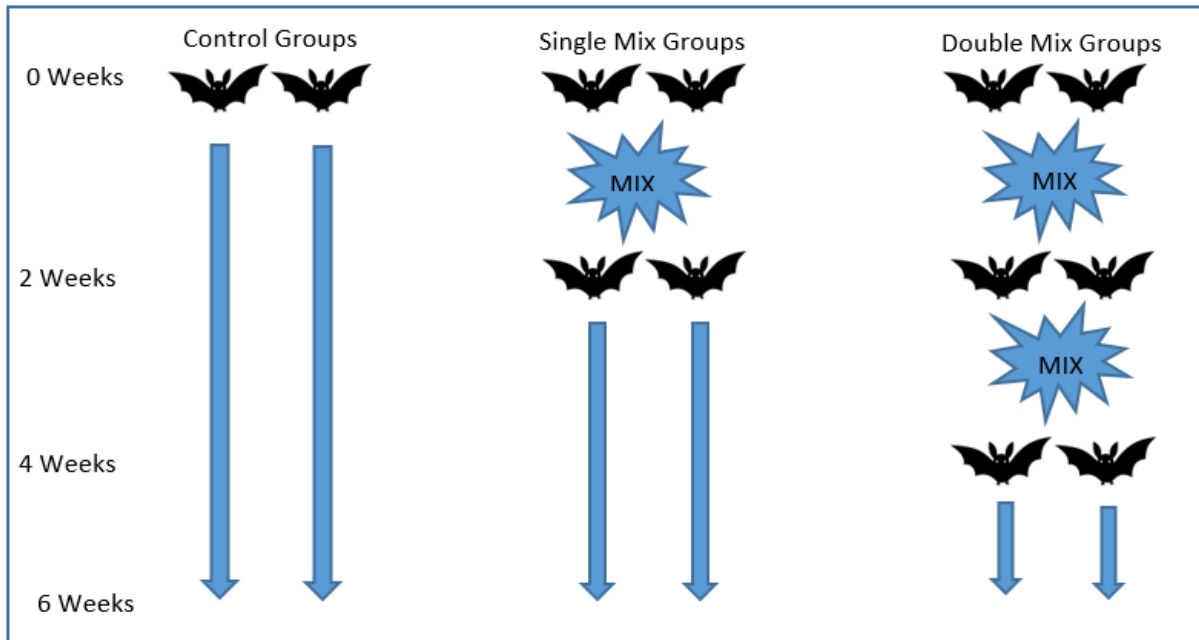


Figure 2.1. Experimental design depicting mixing scenarios for control, single mix, and double mix groups

Individuals were run through behavioral trials twice a week during weeks 2, 4, and 6 (any group shifts occurred at the end of weeks 2 and 4 following the last trial day of the week; Figure 2.1). For each trial type, this resulted in a total of six replicates for each animal over the 6-week study period. Due to video loss, some trial data could not be analyzed, but information was retained for each individual for at least 4 trials (a minimum of one of the two trials for each of the three sampling periods). Behavioral trials assessed two different behavioral axes (exploration and activity) and allowed calculation of behavioral repeatability. Within a testing week, the order animals were run through each trial was randomized and individuals were given at least 48 hours between the two replicates of a given trial type.

2.2.1.1. Activity Trials

Activity was assessed using a standard open field trial (Bierbach et al 2015; Dingemanse et al 2012; Boon et al 2007). The 0.5m x 0.35m x 0.15m arena was divided into 12 separate

zones using electrical tape (Photo A5). At the beginning of a trial, an animal was placed in the lower right corner, corresponding to Zone 1. A given trial began when the animal was released from the hand and a Plexiglass cover was positioned over the arena; each trial lasted three minutes. Based on tracking the location of an individual throughout the duration of the behavioral trial (see analysis below), the following parameters were collected: cumulative time spent in each zone, total time spent active, total time spent inactive, number of unique zones visited, and the total number of zones visited (including revisits).

2.2.1.2. Exploration Trials

Exploration was assessed using a hole-board arena, with minor modifications from the standard vertical design (Boisser and Simon 1962; Menzies et al 2013) (Photo A6). The 0.6m x 0.4m x 0.15m arena was constructed of a plywood base with transparent Plexiglass walls and lid. Within the arena, six, evenly spaced holes were cut into the plywood. These holes were shallow enough for a bat to investigate the contents of the hole. A given trial began when the bat was released into the arena through a small opening and the lid of the opening replaced. Trials lasted 3 minutes. Calculated parameters included the proportion of time spent moving, frequency of head dips into holes, and latency to head dip into the first hole.

2.2.2. Behavioral and Statistical Analysis

All videos were coded in Noldus Observer and Ethovision using a behavioral analysis template. Noldus Observer allows the observer to break down each trial by coding pre-determined variables, and ultimately calculating averages, durations, and totals of all coded variables. Results from the coded videos were then uploaded to JMP 13 and R version 3.3.1, and used in a principal component analysis (PCA). PCA reduced the number of measured behavioral traits into composite, synthetic variables, principal component (PC) scores, which are

independent of each other. Additionally, a Bartlett test was used to determine which variables significantly contributed to each PC score. Based on the factor loadings from the retained PC scores, we designated a single explanatory variable for each trial type (i.e. “Total Distance Moved” for open field trials), which was then the basis of additional analyses.

Repeatabilities were calculated for each experimental group using the selected explanatory variables. Repeatability was defined as the ratio of among-individual variation over the sum of among- and within- individual variance of the individual. Additionally, scores were run through a generalized linear mixed-effects model (GLMM) to determine the presence and strength of correlations (i.e. behavioral syndromes) . For the GLMM analysis, date and replicate were fixed variables while bat ID, subgroup, (and opponent for aggression) were assigned as random effects. ANOVA tests were used to examine whether the explanatory variables were significantly different across treatment groups for the three sampling periods, in two sampling years being analyzed separately.

2.3. Results

Analysis of the open field data showed “Total Distance Moved” had the highest loading in both 2017 (0.942) and 2018 (0.949); hence, it was used as the explanatory variable for this trial type. For the hole board arena, “# Head Dips” had the strongest loading in 2017 (0.933) and 2018 (0.924) and was selected as the explanatory variable.

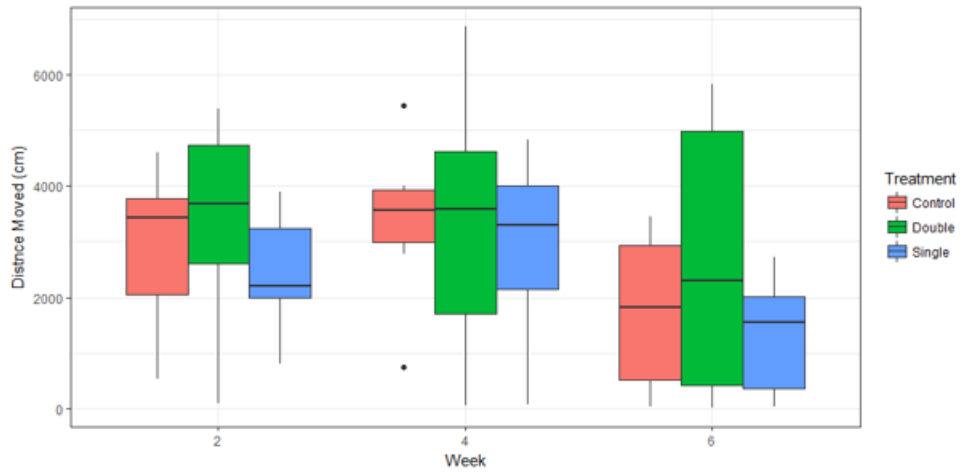
In 2017, exploration data showed the highest repeatability for the single mix groups (0.596) followed by the double mix groups (0.493) and control groups (0.286). For activity data from the 2017 season, only the double mix treatment groups had high repeatability (0.451), with the control and single mix treatments showing essentially no repeatability (control = 0.013, single = 0.037). In 2018, both activity and exploration trials exhibited moderate to high

repeatability. Repeatability of activity was highest for the control group (0.815), followed by the single mix group (0.593) and the double mix group (0.354), aligning with experimental predictions. Repeatability of exploratory behavior was highest for the control group (0.513), followed by the double mix (0.440) and single mix groups (0.413; Table 2.1). For both years, none of the fixed effects (replicate, day) or random effects (switch, subgroup, bat ID) were significant for either type of behavioral trial when calculating repeatabilities for each year. When examining differences across weeks, there were no significant differences for any of the conditions in 2017 or 2018, indicating that repeatability remained stable across the study period for all groups (2017 exploration; control = 0.515, single mix = 0.231, double mix = 0.878: 2018 exploration; control = 0.477, single mix = 0.296, double mix = 0.341: 2017 activity; control = 0.415, single mix = 0.704, double mix = 0.416: 2018 activity; control = 0.378, single mix = 0.596, double mix = 0.607).

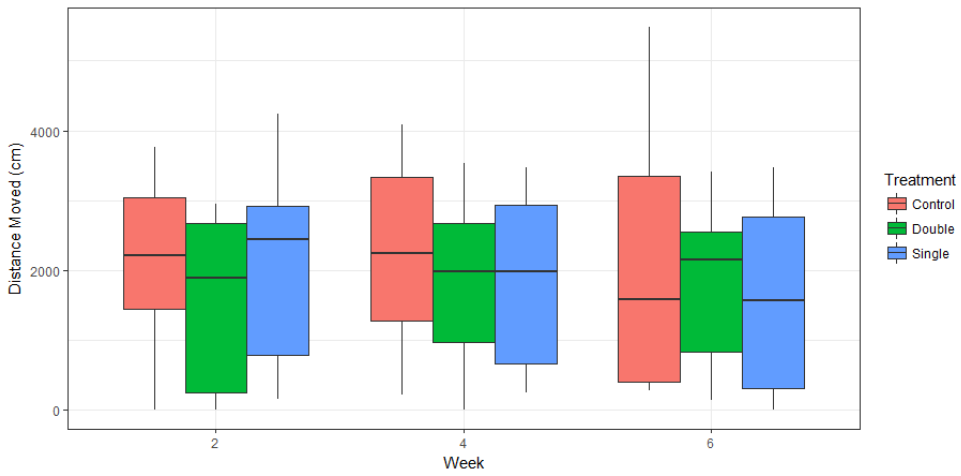
Table 2.1. Principle component loadings for each trial type. Loadings greater than 0.4 are bolded to indicate significance in explaining each PC factor.

	2017		2018	
	PC1	PC2	PC1	PC2
Activity (2017)				
Total Distance Moved	0.942	0.165	0.949	0.231
Active (secs)	0.893	0.363	0.938	0.279
Unique Zones	-0.685	0.795	-0.603	0.797
<i>% variance explained</i>	<i>68.23</i>	<i>26.37</i>	<i>71.49</i>	<i>25.57</i>
<i>Cum % variance explained</i>	<i>68.23</i>	<i>94.61</i>	<i>71.49</i>	<i>97.06</i>
Exploration (2017)				
Total Dips	0.933	-	0.924	-
Active (secs)	0.933	-	0.924	-
<i>% variance explained</i>	<i>86.01</i>	-	<i>85.41</i>	-
<i>Cum % variance explained</i>	<i>86.01</i>	-	<i>85.41</i>	-

For 2017 activity data, there were significant differences in behavior across the sampling weeks for the control ($F_{2,33} = 4.73$, $p = 0.016$) and single mix groups ($F_{2,25} = 3.90$, $p = 0.0336$), while the double mix group exhibited no significant differences across weeks ($F_{2,27} = 0.349$, $p = 0.709$; Figure 2.2A). In 2018, there were no significant changes in activity level across weeks for any treatment groups (control: $F_{2,27} = 0.024$, $p = 0.977$, single mix: $F_{2,45} = 4.73$, $p = 0.578$, double mix: $F_{2,45} = 0.2665$, $p = 0.767$; Figure 2.2B). For exploration data, there were no significant differences across weeks for any treatments in 2017 (control: $F_{2,37} = 0.0529$, $p = 0.949$, single mix: $F_{2,32} = 0.0127$, $p = 0.9874$, double mix: $F_{2,37} = 0.091$, $p = 0.9132$; Figure 2.3A) or 2018 (control: $F_{2,24} = 2.579$, $p = 0.089$, single mix: $F_{2,37} = 3.172$, $p = 0.059$, double mix: $F_{2,39} = 0.069$, $p = 0.933$; Figure 2.3B).



A.



B.

Figure 2.2. Average (\pm SE) activity score (Total Distance Moved) across weeks and treatments in 2017 (A) and 2018 (B)

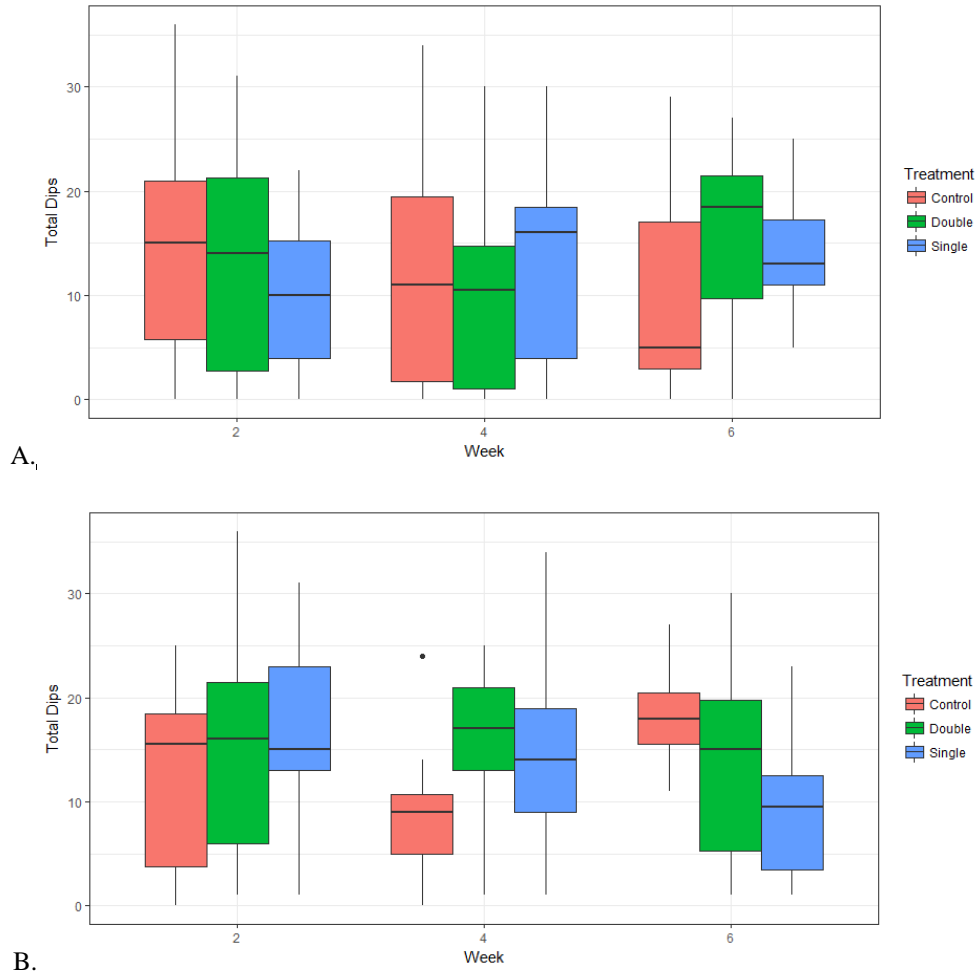


Figure 2.3. Average (\pm SE) exploratory score (# Head Dips) across weeks and treatments in 2017 (A) and 2018 (B)

2.4. Discussion

Across both field seasons, there was moderate to high repeatability for the activity personality axis. However, exploration was only repeatable for the double mix treatment in 2017 and all treatment groups for 2018. Despite some patterns in the data suggesting lower repeatability for animals that experienced shifting social group composition, particularly from our 2018 season, these differences were not significant. Further, our ANOVA results did not indicate substantial shifts in variation across weeks for any of the treatment groups.

Cumulatively, these results suggest that repeatability of exploratory behavior and activity level is independent of social group composition, lending support to the behavioral type hypothesis.

Although differences within years were not significant, it is unclear why we appeared to see different patterns of repeatability across our two study years. For the 2018 season, study animals had already been in captivity for a full year and had spent the winter months in hibernation with a larger group of animals from the colony (10-12 animals per cage). In 2017, animals struggled with high parasite loads from their site of capture. In late summer 2017, all individuals were treated with fenbendazole, which effectively treated the high parasite load, with no additional high loads observed through the second season. It is plausible that stress from the move into captivity and carrying a high parasite load in 2017 may have impacted the repeatability of behavior. Webber et al (2015) examined the impacts of ectoparasite prevalence on behavior of little brown bats, *Myotis lucifugus*, finding mixed results depending upon the sex and age of individuals. Further research exploring how animal health and baseline stress levels are correlated to individual behavior and personality would be valuable for understanding behavioral repeatability in bats.

2.5. Conclusion

In conclusion, our results demonstrate that big brown bats have moderate to high repeatability along common personality axes and that individual behavior is primarily independent of the composition of an animal's social group. These results support the behavioral type hypothesis (Laskowski and Bell 2014). Given these findings, it is likely that when tree-roosting populations of big brown bats regularly switch subgroups across nights (i.e. fission-fusion) that individuals are not altering their behavior in a substantial way. The implications of this are not clear. If group functionality, and in turn, individual fitness, are relatively unaffected

by the composition of the social group (i.e. most animals have similar personalities vs a mix of personality types), then it is logical that high behavioral plasticity would not be selected for. In some birds, personality type is correlated with individual fitness (Dingemanse et al. 2004, Both et al. 2005, Smith and Blumstein 2008, Chira 2014) and, in great tits, *Parus major*, assortative mating based on exploratory behavior (fast vs slow phenotypes) can have substantial impacts on fitness (Both et al 2005). Further studies assessing the relationship between composition of bat social groups and individual fitness would be valuable. In addition, examining patterns of repeatability in bat species that exhibit different types of social structure is also critical to understanding if patterns of repeatability and social group composition vary between species.

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APPENDIX. GENERAL SETUP AND ARENA PICTURES



Figure A1. Control subgroup of *E. fuscus* from 2017 field season



Figure A2. NDSU Conservation Research Facility at the Red River Zoo in Fargo, ND



Figure A3. Customized bat house provided to study animals



Figure A4. Aggression trial arena.

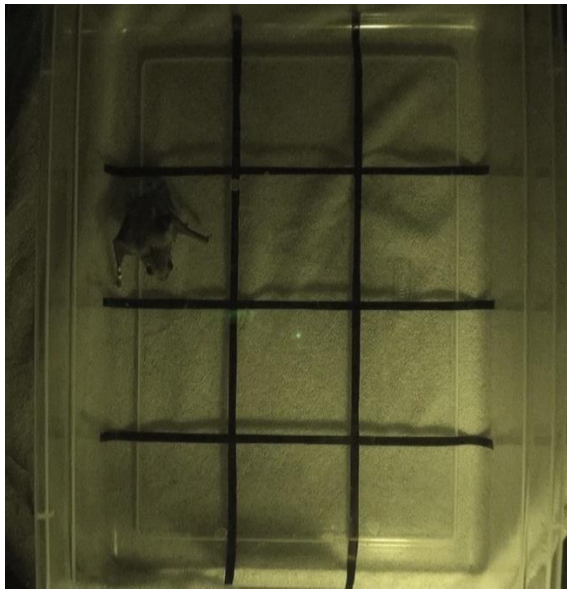


Figure A5. Open field arena

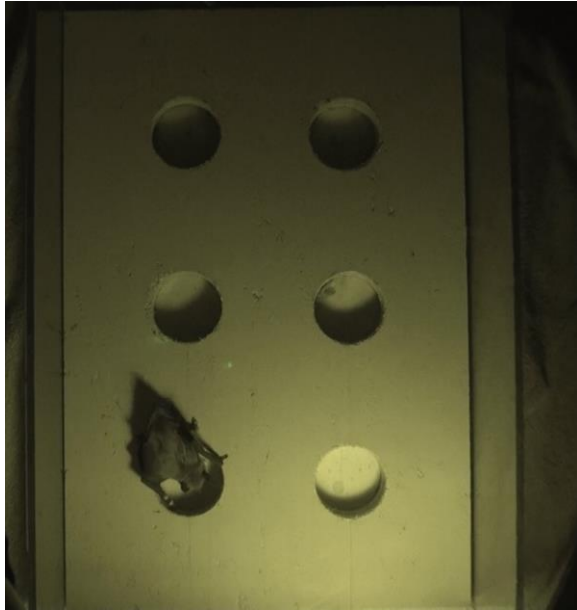


Figure A6. Hole board arena

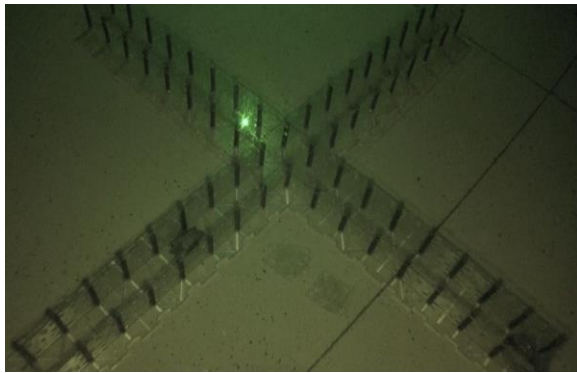


Figure A7. Radial arm maze arena