

¹ Changes in social group composition do not disrupt individual
² behavioral differences in a nectar-feeding bat

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9 Abstract

10 Even in highly dynamic social environments, individuals can differ consistently in their behavior. There are at
11 least two hypotheses that propose mechanisms that can explain how consistent individual differences emerge
12 and persist despite of the unpredictability of social interactions. The behavioral type hypothesis states that
13 consistent individual differences in behavior in a social environment reflect individual differences in other
14 contexts and thus, social group composition should have no influence on individual behavior. The social
15 niche construction hypothesis on the other hand predicts that repeated social interactions and competition
16 avoidance promote individual differences in behavior and as a consequence individual behavior should change
17 depending on the social environment. However, these two hypotheses are non-mutually exclusive and different
18 behavioral traits could be influenced to different degrees by changes in the social environment. We investigated
19 the influence of social group composition on consistent individual differences in multiple behavioral traits
20 in the nectar-feeding bat species *Glossophaga mutica*. Four social groups, of six female bats each, were
21 confronted with a foraging context consisting of two flower patches. The short-term and long-term consistency
22 of individual differences in five behavioral traits were quantified: Foraging activity, spread evenness of flower
23 visits, agonistic behavior, sampling of the unrewarding patch and the latency to switch to a newly available
24 patch. After assigning individuals to new social groups, individual behavior was reassessed in order to quantify
25 the influence of social group composition on the consistency of individual differences in behavior. All three
26 repeatable behavioral traits were consistent across social groups and differences between individuals also did
27 not increase with time spent in the same social group. However, social group composition had an effect on
28 individual foraging performance. These results indicate that social niche construction plays only a minor role
29 in shaping consistent individual differences in the behavior of *G. mutica*.

30 Lay summary

31 Keywords:

32 , bat, *Glossophaga*

33 1. Introduction

34 Animals show consistent individual differences in a wide variety of behaviors. In recent years, great attention
35 has been given to research showing that individuals differ in animal personality traits like activity, exploration
36 and aggressiveness (A. M. Bell 2007; Wolf and Weissing 2012; Dall and Griffith 2014). In general, these
37 individual differences in behavior are consistent across contexts and/or time (A. Bell, Hankison, and Laskowski
38 2009). Moreover, personality traits can be correlated and thereby form behavioral syndromes (Sih, Bell,
39 and Johnson 2004), for example delicate skinks (*Lampropolitis delicata*) that are more active tend to be
40 faster explorers and are also more social (Michelangeli, Chapple, and Wong 2016). However, individuals of
41 a given species can also consistently differ in other aspects of behavior like foraging (Alcalay, Scharf, and
42 Ovadia 2015), dispersal behavior (Hogan et al. 2014) or habitat selection (Ehlinger 1990). Finding consistent
43 individual differences in social environments is interesting because social interactions are thought to be
44 highly dynamic. There are at least two non-mutually-exclusive hypotheses that can explain why consistent
45 individual differences in behavior in a social environment emerge and persist (Laskowski and Bell 2014).
46 The behavioral type hypothesis predicts that individuals differ in their behavior in a social environment
47 because differences reflect individual behavior in other contexts due to common underlying mechanisms
48 (e.g. pleiotropic genes) that reduce behavioral plasticity (Sih, Bell, and Johnson 2004). In accordance with
49 the behavioral type hypothesis, changes in the social environment should not influence individual behavior.
50 However, since individuals behave according to their behavioral type, the behavioral composition of the group
51 could influence individual and group performance (Pruitt and Riechert 2011). For example, a study with
52 sticklebacks showed that individual differences in behavior were not influenced by group familiarity whereas
53 the average social foraging behavior of group members was predicted by the behavioral composition of the
54 group (Laskowski and Bell 2014). Nevertheless, the social environment itself might play a role in shaping
55 consistent individual differences in behavior. The social niche specialization hypothesis states that individual

56 differences in behavior can emerge within a social context through repeated social interactions (Bergmüller
57 and Taborsky 2010; Montiglio, Ferrari, and Réale 2013). In order to avoid competition, individuals might
58 develop different behavioral strategies and as a consequence settle in different social niches. These individual
59 differences in behavior could be maintained through negative-frequency dependent pay-offs, which means
60 that the benefit of inhabiting a certain social niche is higher the less individuals occupy it (game-theoretic
61 dynamics). Individual differences in behavior that have been established through social niche construction
62 should be strongly influenced by changes of the social environment. For example, nutmeg mannikins differ
63 consistently in their tactic use in a producer-scrounger foraging game but these individual differences were not
64 stable across social groups (Morand-Ferron, Wu, and Giraldeau 2011). Furthermore, social niche specialization
65 also implies that initial differences between individuals in non-familiar groups should increase the longer
66 individuals remain in the same social environment. However, social niche construction and innate behavioral
67 differences could interact in order to shape consistent individual differences in behavior within a social
68 environment and different behaviors might be affected to different extents by changes in the social group
69 composition. For example, recently it has been shown that the amount of between-individual variation in
70 agonistic behavior depends on how sociable a shrew species is whereas individual differences in activity did
71 not change between social and less social species (Merten, Zwolak, and Rychlik 2017).

72 In this study, we investigated the role of repeated social interactions and the influence of changes in the
73 social environment on individual differences in multiple behavioral traits in the nectar-feeding bat species
74 *Glossophaga mutica*. Consistent individual differences in behavior were assessed in a social foraging regime
75 similar to the simultaneous patch regime introduced in a study that investigated the influence of repeated
76 social interactions on individual behavioral differences in sticklebacks (Laskowski and Bell 2013). In this
77 experimental schedule only one out of two food patches is rewarding at the beginning of a trial. After a
78 certain time, a second food patch becomes rewarding without increasing the total amount of available food.
79 Rewards are now distributed equally across the two patches. As a consequence, as soon as the second patch
80 becomes active, the amount of food available in the first patch drops. Therefore, the competition increases in
81 this patch and individuals start to distribute themselves across the two patches. In the current experiment,
82 each patch consisted of five artificial flowers that delivered nectar rewards with a fixed time interval schedule.
83 In order to keep the amount of available food constant, the time interval between rewards doubled without
84 increasing the reward volume as soon as the second flower patch became active. In this experimental regime,
85 multiple behavioral traits were investigated in four social groups of six female bats and the consistency of
86 individual differences was assessed short-term (across seven nights) and long-term (across three months).
87 Thereafter, bats were reassigned to new social groups in order to investigate the influence of the social
88 environment on individual behavior. The following five behavioral traits were assessed in this experiment:
89 Foraging activity, spread evenness of flower visits, agonistic behavior, sampling of the unrewarding patch and
90 the latency to switch to a newly available patch. We expected that individuals which sample the unrewarding
91 patch more often might also switch faster to the newly rewarding patch because they should be more likely
92 to detect changes in the status of the second patch. Furthermore, similar to the results of the experiment
93 with sticklebacks, individual differences in the latency to switch to the newly rewarding patch should increase
94 the longer individuals remain in the same social group. With increasing time spent within the same social
95 group, individuals might become familiar with the individual strategies of their groupmates and therefore
96 some individuals might not switch to the new patch at all and others might switch faster. Thereby individual
97 differences would increase with time and individual latency to switch should depend on social group
98 composition. Glossophagine bats have been shown to aggressively chase other bats away from artificial flowers
99 (Wintergerst, Winter, and Nachev 2021). Although, females rarely chased other individuals in mixed sexed
100 groups, agonistic behavior in female-only groups has been shown to be as high as in male groups. Since
101 agonistic behavior inherently has a social component, we expected that individual differences in agonistic
102 behavior change depending on social group composition. Additionally, more aggressive individuals might be
103 more likely to concentrate their flower visits on a smaller subset of flowers (Milinski 1984). Therefore, the
104 distribution of individual visits across the flowers should also depend on social group composition. On the
105 other hand, foraging activity, which is related to energy intake, is expected to be independent of repeated
106 social interactions and social group composition. In addition to assess how the social group composition
107 influences individual behavior, we explored how the behavioral composition of a social group affects foraging
108 performance.

¹⁰⁹ **2. Materials and methods**

¹¹⁰ **(a) Subjects and housing**

¹¹¹ Experiments were conducted from March to October 2015 with 24 females of the nectarivorous bat species
¹¹² *Glossophaga mutica* (formerly *Glossophaga soricina*, Pallas's long-tongued bat). Bats came from our captive
¹¹³ colony and were older than one year as judged by finger joint ossification [@brunet-rossini_methods_2009].
¹¹⁴ They carried radio frequency identification (RFID) tags attached to cable tie collars (total weight of collar
¹¹⁵ with tag = 0.2g, max. 2.4% of the body weight) that were removed after the experiment. Additionally,
¹¹⁶ bats had numbered plastic split rings (A C Hughes Ltd., Middlesex, UK) around the forearm for visual
¹¹⁷ identification. Temperature in the experimental and colony room was kept at 20-25°C, air humidity at 65-75%,
¹¹⁸ and light conditions were 12:12 LD (light off at 16h).

¹¹⁹ **(b) Experimental set-up**

¹²⁰ In the experimental room ten artificial flowers with automated nectar delivery (Winter and Stich 2005;
¹²¹ Wintergerst, Winter, and Nachev 2021) were mounted along a 4.2m bar at the height of 1.2m (Fig. 1). The
¹²² distance between flowers was 0.4m. Flowers were divided into two groups of five to simulate two flower
¹²³ patches. Each patch was enclosed by a sheet-covered frame around the four sides and at the top to separate
¹²⁴ the groups of flowers spatially (Fig. 1). The only entrance to the patches was a 0.4m gap between the
¹²⁵ ground and the bottom end of this enclosure (Fig. 1, dashed line). From this entrance bats had to fly up
¹²⁶ vertically to reach the flowers, which increased the costs of moving between patches. A stepper-motor syringe
¹²⁷ pump delivered nectar via tubes and pinch valves to the artificial flowers. Nectar rewards were triggered
¹²⁸ by the interruption of an infrared light barrier at the flower opening. The RFID reader below the flower
¹²⁹ head identified a bat's ID code. Flower visits (infrared light barrier interruptions) and ID sensor events were
¹³⁰ recorded during every experimental night. The reward schedule was configured using PhenoSoft Control
¹³¹ (Phenosys GmbH, Berlin, Germany). Every detected event at a flower (including date, time, individual ID,
¹³² duration of the event and amount of nectar delivered) was recorded for data analysis.

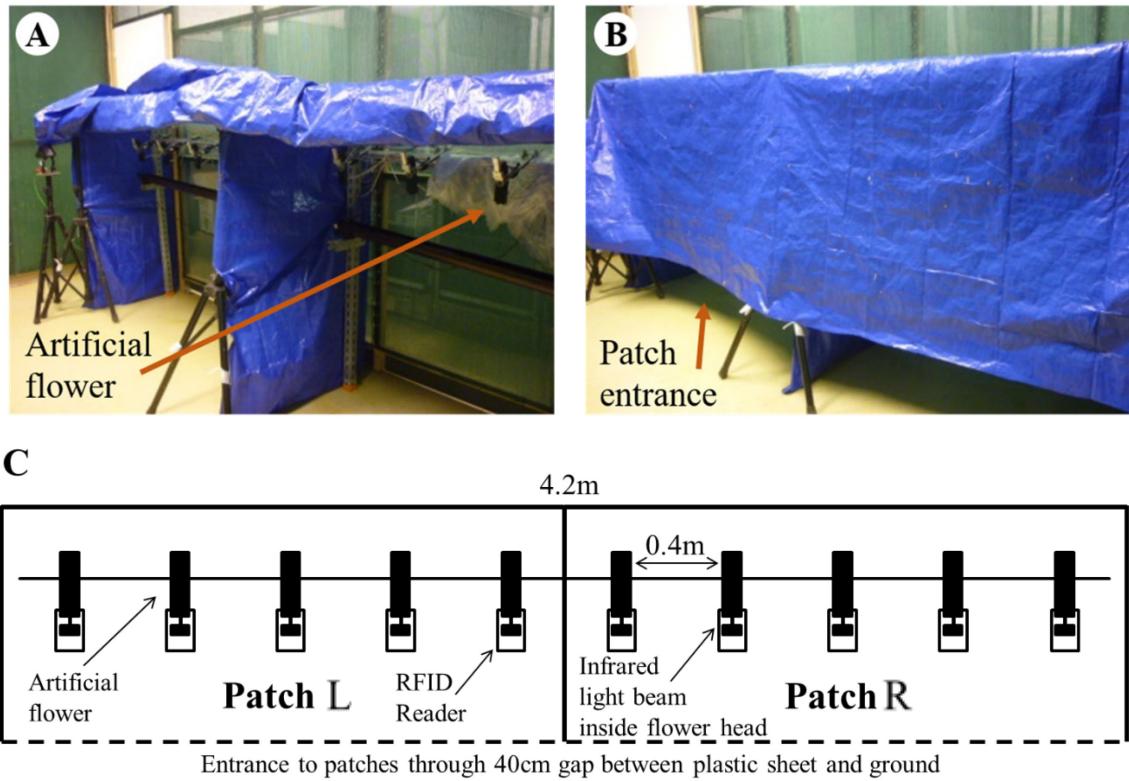


Figure 1: Experimental set-up consisting of two spatially separated patches of five flowers each. (A) The ten flowers were mounted 1.2m above ground. They were divided into two patches, L and R. (B) During experiments the patches were separated by plastic sheets. To make it more demanding for bats to enter a patch, the only entrance was through a 0.4m gap above the ground. (C) Schematic drawing of the experimental set-up from above. The dashed line indicates the side with the patch entrance.

(c) General procedure

The general procedure was as described in (Wintergerst, Winter, and Nachev 2021), reproduced below for clarity.

Each experimental group consisted of six female bats randomly caught from the colony. All bats were weighed before the experiment.

During the nightly experiments, in addition to the nectar provided by artificial flowers, bats had access to pollen and water and to 6mL of additional food containing 1.2g NektarPlus (Nekton, Keltern, Germany) and 1.8g milk powder (Milasan Folgemilch 2, Sunval Baby Food GmbH, Mannheim, Germany) dissolved in water. Rewards at flowers consisted always of 30 μ L nectar (15% w/w sugar concentration, sucrose: fructose 1:2 [no glucose, ask Sabine??]). Before the experimental schedule started, individuals were allowed to familiarize themselves with the set-up and the artificial flowers. Since during this training phase the plastic cover was removed, the two flower patches were not spatially separated and every flower visit was rewarded. This phase lasted for one to four nights until each bat visited the flowers regularly, which took 1-4 nights. In total six individuals (belonging to three different experimental groups) did not visit the artificial flowers at all and were therefore replaced by six new females from the colony after the first night of habituation.

During the experiment, the two flower patches were covered and spatially separated (Fig. 1). Experimental nights were divided into two phases. During the first phase of the night only one of the two flower patches was rewarding, and therefore the resources were spatially clumped at a single location. The fixed time interval between rewards at each flower was 60s. During the second phase of the night both patches gave rewards, resources were evenly distributed across the two patches, and the fixed time interval between two rewards at

153 a flower was increased to 120s. Therefore, the amount of food available per unit time did not change during
 154 the whole night; only the spatial distribution of food changed from the clumped resource condition with one
 155 patch rewarding (five flowers) during the first phase of the night to the distributed resource condition with
 156 two patches rewarding (ten flowers) during the second phase of the night. With this experimental schedule,
 157 the maximal amount of nectar the bats could collect was $108mL$, which corresponds to $18mL$ nectar per
 158 individual per night, roughly 150% of their daily requirement (Winter and Helversen 2001). The side of the
 159 rewarding patch during the first phase of the night was chosen pseudo-randomly and the same patch was
 160 never chosen in more than two consecutive nights.

161 (d) Experimental schedule

Table 1: Sequence of the first active patch and the duration of the
clumped resource condition during each experimental run.

night	initial active patch ^a	duration of clumped resource condition [h]
1	1	6
2	2	8
3	1	5
4	1	7
5	2	4
6	2	6
7	1	8

Note: Every night the experiment started with the clumped resource condition.

Patch 1 included flowers 1-5, and patch 2 - flowers 6-10^a

162 Each experimental run lasted for seven nights. The rewarding patch during the first part of the night (clumped
 163 resource condition) was chosen pseudo-randomly so that it was never repeated on more than two consecutive
 164 nights. The duration of the clumped resource condition varied from 4 to 8 hours to avoid habituation to a
 165 specific time. All experimental runs used the same sequence of initial active patches and durations of the
 166 clumped resource condition (Table 1).

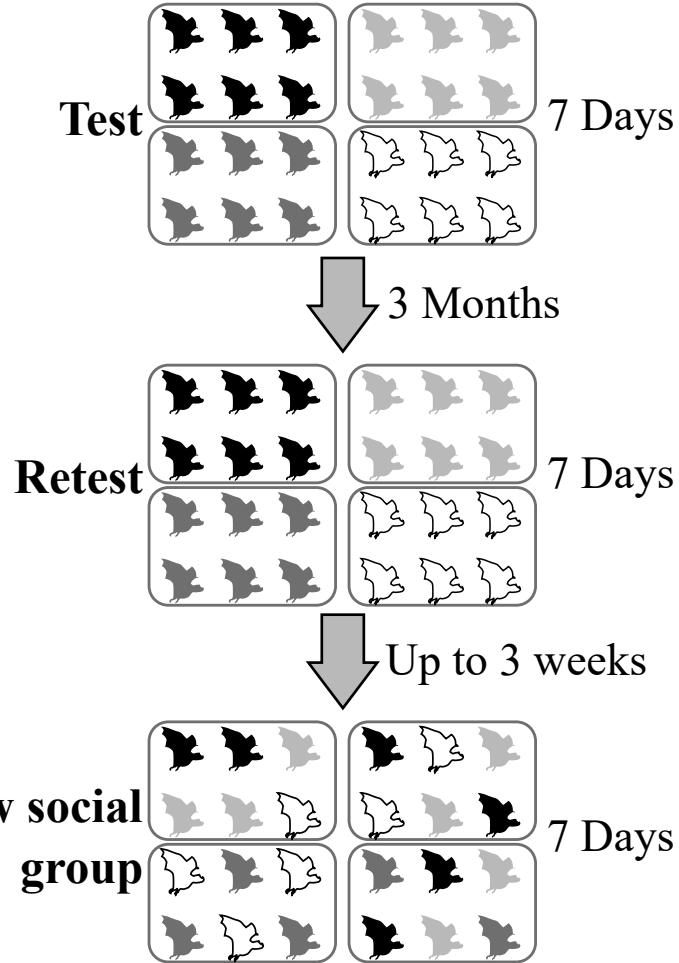


Figure 2: Each experimental run for the four groups of six female bats lasted for seven nights. During the first experimental run (“Test”), we assessed individual differences in multiple behavioral traits in a foraging task with two patches of artificial flowers. We then assessed the long-term consistency of individual behavior within the same social group by repeating the same experimental procedure three months later (“Retest”). Finally, we reassigned individuals pseudo-randomly to new social groups and performed the last experimental run (“New social group”) to assess the consistency of individual differences in behavior across different social groups.

167 Every individual experienced this experimental schedule three times (Fig. 2). During the first and the second
 168 experimental run (“Test” and “Retest”) individuals remained in the same social group consisting of six females.
 169 The time between test and retest was three months. These two experimental runs were conducted to assess
 170 the long-term repeatability of individual differences in behavior. Directly after the retest individuals were
 171 assigned to new experimental groups (“New social group”) to assess the influence of the social environment on
 172 the consistency of behavior. Between experimental runs, all individuals returned to the housing colony. Due
 173 to pregnancy after the retest, one female had to be replaced with another individual, in order to keep group
 174 sizes constant. As the replacement female had already participated in a complete experimental run, its data
 175 in the second new social group were only used to calculate the group means, but not individually analyzed.

176 **(e) Behavioral traits**

177 **Agonistic behavior**

178 Individual agonistic behavior was assessed by quantifying how often an individual chased others away from
179 artificial flowers. These detection of these chasing events occurred automatically, as previously described
180 (Wintergerst, Winter, and Nachev 2021). In our previous observations females rarely chased other bats
181 in the presence of males, but in single-sex groups the frequency of chases were similar between males and
182 females (Wintergerst, Winter, and Nachev 2021). Notably, in contrast to males, females never succeeded in
183 successfully monopolizing a complete flower patch by excluding all other individuals. Since individuals that
184 make are more frequently detected at artificial flowers also have more possibilities to chase other individuals
185 away from artificial flowers we used the proportion of chasing events from the total number of detections as a
186 measure for agonistic behavior.

187 **Foraging activity**

188 Foraging activity was quantified as the number of visits [perhaps also better to take total detections here?] at
189 artificial flowers. Activity specifically during the clumped or uniformly distributed resource condition was
190 calculated as the number of visits per hour since the duration of each condition differed between nights.

191 **Spread evenness index**

192 The calculation of the spread evenness index was based on Simpson's Equitability (E_D , Simpson 1949) which
193 can be used as a measure of how well an animal distributes its visits across the available artificial flowers
194 (Ohashi and Thomson 2009). The following equation was used to calculate the spread evenness index:

$$E_D = \frac{1}{\sum_i^S (\frac{n_i}{N})^2} \times \frac{1}{S}$$

195 where n_i is the number of visits a bat made at feeder i , N is the total number of visits and S is the number
196 of available flowers. This index can take values between 0 and 1. The higher the spread evenness index the
197 more evenly a bat distributes its visits across the available flowers. The daily individual spread evenness
198 index was only calculated during the uniformly distributed resource condition when both patches and all ten
199 flowers were rewarding.

200 **Latency to utilize new food patch**

201 To assess if individuals differ in how fast they switch to the newly available patch during the uniformly
202 distributed resource condition, the latency to utilize the new food patch was quantified as the number of
203 seconds between the activation of the second patch and the first visit an individual made at the newly
204 available patch.

205 **Sampling behavior**

206 Sampling was defined as the proportion of visits to the non-rewarding patch during the clumped resource
207 condition. Since the position of the rewarding patch changed between nights, bats had to learn the new
208 position of the rewarding patch at the beginning of each night. Sampling was only quantified after a bat
209 reached the asymptotic phase of its performance curve. Details about the calculation of the individual
210 sampling rate can be found in Chapter 2.

211 **Efficiency**

212 One way to quantify individual foraging performance is efficiency. Here we measured efficiency by dividing
213 the total amount of nectar intake by the number of visits during the uniformly distributed resource condition.
214 With this calculation efficiency is a measure of the average amount of nectar a bat received per visit.

215 **Nectar intake rate**

216 Nectar intake during the uniformly distributed resource condition was calculated as milliliters of nectar
217 obtained per hour since the duration of conditions differed between nights.

218 **Mean spatial overlap**

219 As previously proposed (Ohashi and Thomson 2009), spatial overlap between foraging bats was calculated
220 using Pianka's symmetrical index of niche overlap (Pianka 1973). This index quantifies the spatial overlap of
221 two individuals. In order to get one daily measurement for each bat, the spatial overlap between one bat
222 and the five other bats of the respective group was calculated and then the mean of these five values was
223 determined. The following equation was used to calculate Pianka's index *PI* between for example bat 1 and
224 2:

$$PI = \frac{\sum_i^{10} p_{i1}p_{i2}}{\sqrt{\sum_i^{10} p_{i1} \sum_i^{10} p_{i2}}}$$

225 *p* is the proportion of visits to the *i*th flower made by bat 1 and 2 respectively. The value of *PI* lies between
226 1 and 0. The higher the value of *PI* calculated for two bats, the higher the spatial overlap between them.

227 **(f) Statistical analysis**

228 Individual differences in five behavioral traits were analyzed: agonistic behavior, foraging activity, sampling
229 behavior, spread evenness index and latency to utilize a new food patch. Since foraging conditions changed
230 between the clumped (one rewarding patch) and the distributed resource condition (two active patches),
231 individuals might have adjusted their level of foraging activity and agonistic behavior accordingly. Thus,
232 repeatability estimates might change between these two parts of the night. However, initial analyses failed to
233 show an effect of resource condition on individual differences in foraging activity (Table A3.1; Figure A3.3)
234 and proportion of chasing events (Table A 3.1; Figure A 3.4). Thus, foraging activity and agonistic behavior
235 were estimated over whole nights in all further analyses, without discriminating between the clumped and
236 distributed resource condition. A Bayesian Markov chain Monte Carlo generalized linear-mixed models
237 (MCMCglmm package version 2.24, (Hadfield 2010)) was used to calculate repeatability of the five behavioral
238 traits. In each model, the individual behavioral trait was used as a dependent variable and individual and
239 experimental group were included as random effects. Day was initially included as a fixed effect to assess if
240 behavioral traits were changing with time within each experimental run. However, estimates of repeatability
241 only changed marginally with day as fixed effect and therefore we calculated repeatability estimates without
242 any fixed effects which usually leads to a more conservative measure of repeatability. Sampling and agonistic
243 behavior were quantified as proportions and therefore the multinomial2 family was used in these models.
244 Latency to utilize a new food patch was assumed to have a Poisson error structure and Gaussian error
245 structure was assumed for foraging activity. The spread evenness index takes values between 0 and 1 and can
246 be considered as a rate, but not a proportion. Usually a beta regression can be used to analyze rates. However,
247 beta regressions are not yet implemented in the MCMCglmm package and to my best knowledge packages
248 that include beta regressions with random effects are not available. Thus, in order to be able to assume a
249 Gaussian error structure, we used the z-transformation on the spread evenness index. The z-score quantifies
250 the distance in terms of standard deviation of an individual value from the group mean and it was calculated
251 daily and within each experimental group. The repeatability of individual z-scores would therefore provide
252 information of how consistently individuals remained at their relative position within an experimental group.
253 As priors, we used an inverse-Wishart distribution for the residual variance and a parameter expanded prior for
254 random effects. Analysis of autocorrelation, effective sample size and visual inspection of trace plots were used
255 to assess the models. Repeatability, the proportion of variance that can be explained by between-individual
256 differences, was calculated following Nakagawa and Schielzeth (2010). Since each experimental run lasted for
257 seven days, behavioral traits were measured seven times for each individual for each run and repeatability
258 of behavioral traits was calculated for each experimental run ("Test," "Retest after three months," "New
259 social group"). Additionally, to assess the potential change of between-individual differences, repeatability

estimates were also calculated for the first three days and last three days of each experimental run. Spearman rank correlation coefficients were calculated to explore possible between-individual correlations of behavioral traits which would indicate a behavioral syndrome. To investigate the long-term consistency of individual differences in behavioral traits and the consistency of individual behavior across social groups the individual mean behavior was calculated for each experimental run. Linear (foraging activity and agonistic behavior) and beta regressions (spread evenness index) were used to assess the correlations of individual mean behavior. To explore the influence of consistent individual differences on individual and group foraging performance we calculated the mean nectar intake rate, Pianka's index and foraging efficiency during the uniformly distributed resource condition. However, the mean spatial overlap of foraging individuals was highly collinear with the measure of individual spread evenness index (Spearman's $\rho = 0.95$, $p < 0.001$) and therefore was dropped from further analysis. Linear models were used to explore potential correlations. All analysis was performed in R version 3.3.2 (Team R Core 2016). All linear mixed-effects models were performed using the R package "nlme" version 3.1-128 (Pinheiro et al. 2007), all linear models were performed using the R package "lme4" version 1.1-12 (Bates et al. 2014) and beta regressions were performed using the R package "betareg" version 3.1-0 (Cribari-Neto and Zeileis 2009).

All statistical analyses were conducted using R (Team 2021).

3. Results

4. Discussion

Both the behavioral type and the social niche construction hypothesis propose mechanisms that can explain how individual behavioral differences emerge and persist in a highly dynamic social environment (Sih et al. 2004; Bergmüller and Taborsky 2010). The social niche construction hypothesis predicts that repeated social interactions and competition avoidance can promote individual differences in behavior. On the other hand, the behavioral type hypothesis states that individual differences in behavior in a highly dynamic social environment reflect individual behavior in other contexts and therefore individual differences in behavior should not be affected by changes in the social environment. These two hypotheses are non-mutually exclusive and therefore they could influence different behavioral traits to different degrees. In this chapter, we assessed the consistency of individual behavior in a social foraging context across different social groups in order to investigate the role of the social environment in shaping individual behavioral differences in the nectar-feeding bat species *Glossophaga mutica*. Three behavioral traits, agonistic behavior, foraging activity and spread evenness of flower visits, were highly repeatable short-term within experimental runs and long-term over three months. In accordance with the behavioral type hypothesis, individual behavior was consistent across social group. Therefore, we explored how the behavioral composition of the group could influence the performance during foraging. We could show that the average spread evenness index (which is negatively correlated with agonistic behavior across individuals) influenced the average foraging efficiency of individuals and also individual nectar intake was influenced to some extent by changes in the social group composition.

(a) Influence of social environment on foraging activity

As predicted, individual foraging activity was independent of social group composition. This result is in line with a previous finding showing that the level of individual differences in activity did not differ between social and non-social shrew species (Merten, Zwolak, and Rychlik 2017). Foraging activity measured as the number of flower visits is related to individual nectar consumption and food intake determines how much energy an individual can spend. In Chapter 3, we could show that individuals of the closely related species *G. commissarisi* differ consistently in their daily energy expenditure and individual differences in energy metabolism have been proposed to correlate with different life-history strategies (Careau et al. 2008; Réale et al. 2010). Therefore, in line with the behavioral type hypothesis, individual differences in foraging activity and consequently energy intake might reflect individual differences in other contexts independent of the social environment.

306 **(b) Influence of social environment on agonistic behavior**

307 Contrary to foraging activity, absolute values of individual agonistic behavior did not correlate across social
308 groups. However, individuals that showed high agonistic behavior relative to the group average were also
309 more likely to show higher than average agonistic behavior in new social groups as shown by the correlation
310 of z-scores (Figure 5.2 E and F). Individual agonistic behavior was quantified as the proportion of chasing
311 events at artificial flowers on the total number of visits. However, the number of chasing possibilities does
312 not only depend on the individual aggressive tendency but also on the behavior of other group members. For
313 example, other individuals might have avoided proximity to aggressive individuals and therefore diminished
314 their amount of chasing opportunities independent of their individual aggressive tendency. Since the relative
315 amount of agonistic behavior was consistent across social groups, social niche construction seems to play also
316 only a minor role in shaping individual differences in aggressiveness.

317 **(c) Influence of social environment on spread evenness index**

318 Agonistic behavior and spread evenness index of flower visits were correlated across individuals (Table 5.2)
319 In accordance with the result that the social environment had only a minor effect on individual agonistic
320 behavior, individual spread evenness index was also correlated across social groups. How individuals distribute
321 their visits across flowers could have been a consequence of differences in aggressiveness associated with
322 competitive ability. However, individuals differed in their spread evenness index already during the first three
323 days of the first experimental run (Table 5.3) indicating that aggressive individuals might have a tendency to
324 visit less flowers even before they could demonstrate their competitive ability. This is in line with results
325 from a previous study that has shown that *G. commissarisi* differ consistently in the number of flowers they
326 visit in an flower array independent of aggressive interactions (Nachev and Winter 2019).

327 **(d) The role of repeated social interactions**

328 Although individual behavior was consistent across social groups in all three repeatable behavioral traits
329 (agonistic behavior, foraging activity and spread evenness index), repeated social interactions could have
330 still played a role in shaping differences between individuals by reducing within-individual variation [find
331 a citation]. However, repeatability estimates did not change with time (Table 5.3) in any of the three
332 behavioral traits, supporting the hypothesis that differences in behavior of bats in a social foraging context
333 were the result of individual differences in other contexts rather than the result of repeated social interactions.
334 However, since the confidence intervals of these repeatability estimates were very wide, the failure of showing
335 an increase could also be due to low statistical power. Nevertheless, repeatability estimates during the first
336 three days are already significantly greater than zero showing that individuals already differed consistently at
337 the beginning of each experimental run.

338 **(e) Latency to switch to a newly available flower patch**

339 Contrary to results of a study with sticklebacks that used the same experimental design, individual bats did
340 not differ in their latency to switch to a newly rewarding patch. The experiment with sticklebacks showed
341 that individual fish differed consistently in their latency to switch to a newly available patch and that these
342 differences increased the longer individuals remained in the same social group (Laskowski and Bell 2013).
343 However, a subsequent experiment showed that switch latency was predicted by individual differences in other
344 behaviors measured in different contexts like the tendency to shoal with other individuals. This showed that
345 not only repeated social interactions played a role in shaping individual differences in switch delay (Laskowski
346 and Bell 2014). In the present experiment with nectarivorous bats, the main reason for the lack of individual
347 differences in switch delay might have been the close proximity of the two patches and consequently the very
348 low costs of switching to the newly available patch. Additionally, every time an artificial flower delivered
349 a reward, the valve controlling the nectar flow was audible which could have served as a signal indicating
350 the availability of the new patch as soon as one bat started to exploit it. In this case leaving the first flower
351 patch might have not been due to competition avoidance but due to an audible signal and the benefit of
352 being the first to switch was therefore very low.

353 **(f) Sampling of unrewarding patch**

354 Although, individuals of the closely related species *G. commissarisi* have been shown to differ in how much
355 they sample unrewarding flowers, in the present experiment the repeatability of sampling behavior was very
356 low and did not even differ from zero during the last experimental trial with new social groups (Fig. 5.2).
357 Contrary to the previous experiment with *G. commissarisi* (Chapter 2), in this experiment the same five
358 spatially concentrated artificial flowers were rewarding for all bats instead of two single rewarding flowers per
359 individual distributed among ten unrewarding flowers. This indicates that individual differences in sampling
360 might be only present in more challenging situations. In line with this proposition, individual differences in
361 learning in great tits have been shown to be also only present in difficult tasks (Titulaer, Oers, and Naguib
362 2012).

363 **(g) Influence of behavioral group composition on foraging performance**

364 In accordance with the behavioral type hypothesis, individual differences in all three repeatable behavioral
365 traits were consistent across social groups. Since individuals did not change their behavior in response to
366 changes in social environment, individual foraging performance might be influenced by the behavior of its
367 group members (Bleakley, Parker, and Brodie 2007). An exploratory analysis showed that average 89 group
368 spread evenness index indeed influenced the mean spatial overlap of group members and the lower the mean
369 spatial overlap the higher the mean individual foraging efficiency was. Since the individual spread evenness
370 index correlated significantly with agonistic behavior, individual efficiency was higher in groups consisting of
371 individuals with higher mean agonistic behavior.

372 Individuals did not adapt their foraging activity to changes in social group composition, individual nectar
373 intake could be influenced by changes in the social environment. The analysis showed that individual mean
374 nectar intake rate during the uniformly distributed resource condition, was significantly correlated between
375 the test and the retest after three months ($t = 2.87$, $p = 0.009$, Figure 4.5A). This indicates that the individual
376 nectar intake rate was stable within the same social group. However, individual mean nectar intake during
377 both the first test and the retest after three months were only poor predictors of the individual mean nectar
378 intake rate during the experimental run with new social groups (Figure 5.5 B and C) which indicates that
379 the foraging performance measured as nectar intake might indeed be influenced by social group composition.

380 **(h) Conclusion**

381 In the present experiment, we confronted *G. mutica* with a social foraging design in which individual foraging
382 decisions influenced the experience of other members of the group. In their natural environment however,
383 *Glossophaga* have been observed to forage mainly independently instead of in social flocks (Heithaus, Opler,
384 and Baker 1974). The lack of evidence for social niche construction in the behavioral traits measured in these
385 bats is therefore in line with the hypothesis that the importance of the social niche construction on shaping
386 consistent individual differences in behavior should depend on the sociability of the species (Merten, Zwolak,
387 and Rychlik 2017). However, recently it has been shown that *G. mutica* are capable of using social information
388 to learn new profitable flower positions (Rose et al. 2016) indicating that there is a social component in their
389 foraging behavior. Additionally, even though individual differences in behaviors might be innate they can still
390 be influenced by group composition and habitat, like it has been shown for individual differences in boldness
391 of perches (Magnhagen and Staffan 2005).

392 Further studies that investigate the role of social niche construction in shaping between-individual variation
393 of behavioral traits in various species can contribute to the understanding of the ecological conditions that
394 favor consistent individual differences due to social niche construction.

395 **Supplementary material**

396 **Authors' contributions**

397 S.W. Conceptualization, Methodology, Software, Data collection, Formal Analysis, Video Analysis, Writing—
398 original draft. V.N. Conceptualization, Methodology, Software, Formal Analysis, Data curation, Writing—
399 review and editing, Visualization, Supervision, Project Administration.
400 Y.W. Conceptualization, Resources, Methodology, Software (data acquisition), Writing—review and editing,
401 Supervision, Funding.

402 **Competing interests**

403 We declare we have no competing interests.

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411 **Data Availability**

412 All data and code are available in the Zenodo repository: xxx

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