

<sup>1</sup> Changes in social group composition do not disrupt individual  
<sup>2</sup> behavioral differences in female nectar-feeding bats

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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 In recent years, great attention has been given to research showing that individuals differ in animal personality  
35 traits like activity, exploration and aggressiveness (A. M. Bell 2007; Wolf and Weissing 2012; Dall and  
36 Griffith 2014). In general, these individual differences in behavior are consistent across contexts and/or time  
37 (A. Bell, Hankison, and Laskowski 2009). Moreover, personality traits can be correlated and thereby form  
38 behavioral syndromes (Sih, Bell, and Johnson 2004), for example delicate skinks (*Lampropolpis delicata*)  
39 that are more active tend to be faster explorers and are also more social (Michelangeli, Chapple, and Wong  
40 2016). However, individuals of a given species can also consistently differ in other aspects of behavior like  
41 foraging (Alcalay, Scharf, and Ovadia 2015), dispersal behavior (Hogan et al. 2014) or habitat selection  
42 (Ehlinger 1990). Finding consistent individual differences in social environments is interesting because social  
43 interactions are thought to be highly dynamic. There are at least two non-mutually-exclusive hypotheses  
44 that can explain why consistent individual differences in behavior in a social environment emerge and persist  
45 (Laskowski and Bell 2014). The behavioral type hypothesis predicts that individuals differ in their behavior  
46 in a social environment because differences reflect individual behavior in other contexts due to common  
47 underlying mechanisms (e.g. pleiotropic genes) that reduce behavioral plasticity (Sih, Bell, and Johnson  
48 2004). In accordance with the behavioral type hypothesis, changes in the social environment should not  
49 influence individual behavior. However, since individuals behave according to their behavioral type, the  
50 behavioral composition of the group could influence individual and group performance (Jolles et al. 2017).  
51 For example, a study with sticklebacks showed that individual differences in behavior were not influenced  
52 by group familiarity whereas the average social foraging behavior of group members was predicted by the  
53 behavioral composition of the group (Laskowski and Bell 2014). Nevertheless, the social environment itself  
54 might play a role in shaping consistent individual differences in behavior.  
55 The social niche specialization hypothesis states that individual differences in behavior can emerge within

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

<sup>109</sup> **2. Materials and methods**

<sup>110</sup> **(a) Subjects and housing**

<sup>111</sup> Experiments were conducted from March to October 2015 with 24 females of the nectarivorous bat species  
<sup>112</sup> *Glossophaga mutica* (formerly *Glossophaga soricina*, Pallas's long-tongued bat). Bats came from our captive  
<sup>113</sup> colony and were older than one year as judged by finger joint ossification [@brunet-rossini\_methods\_2009].  
<sup>114</sup> They carried radio frequency identification (RFID) tags attached to cable tie collars (total weight of collar  
<sup>115</sup> with tag = 0.2g, max. 2.4% of the body weight) that were removed after the experiment. Additionally,  
<sup>116</sup> bats had numbered plastic split rings (A C Hughes Ltd., Middlesex, UK) around the forearm for visual  
<sup>117</sup> identification. Temperature in the experimental and colony room was kept at 20-25°C, air humidity at 65-75%,  
<sup>118</sup> and light conditions were 12:12 LD (light off at 16h).

<sup>119</sup> **(b) Experimental set-up**

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

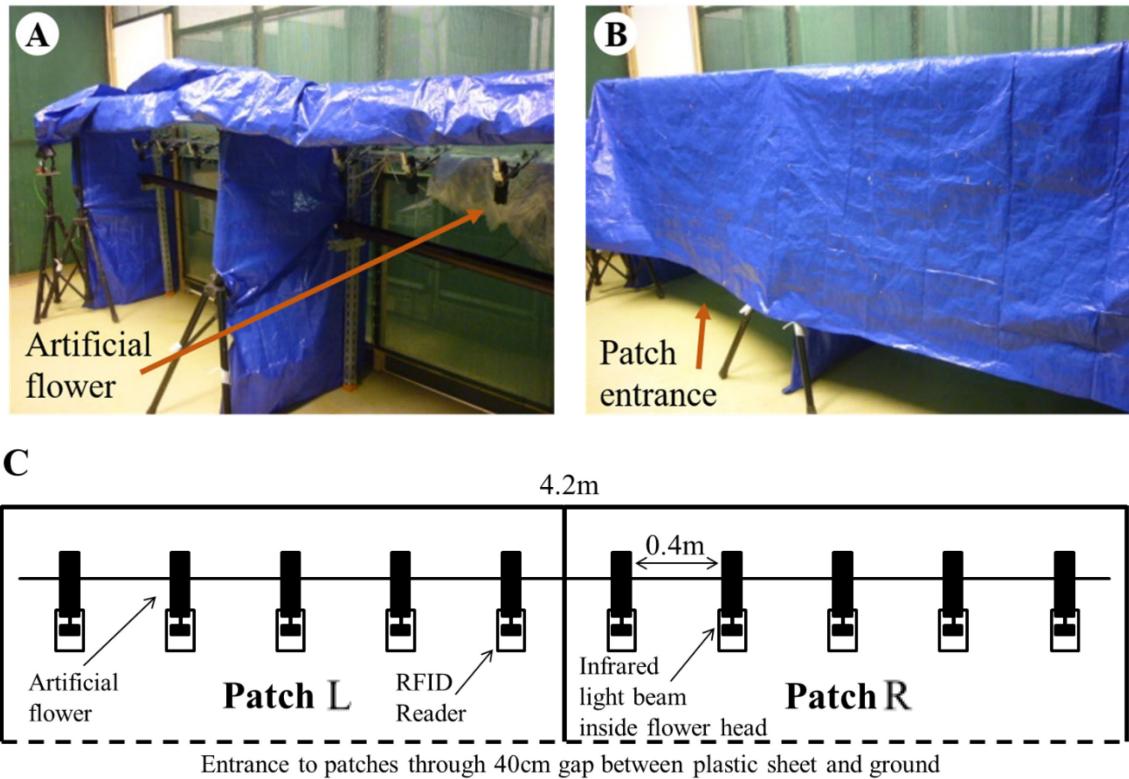


Figure 1: Experimental set-up consisting of two spatially separated patches of five flowers each. (A) The ten flowers were mounted 1.2m above ground. They were divided into two patches, L and R. (B) During experiments the patches were separated by plastic sheets. To make it more demanding for bats to 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.

133 (c) General procedure

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

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

138 During the nightly experiments, in addition to the nectar provided by artificial flowers, bats had access to  
139 pollen and water and to 6mL of additional food containing 1.2g NektarPlus (Nekton, Keltern, Germany) and  
140 1.8g milk powder (Milasan Folgemilch 2, Sunval Baby Food GmbH, Mannheim, Germany) dissolved in water.  
141 Rewards at flowers consisted always of 30 $\mu$ L nectar (15% w/w sugar concentration, sucrose: fructose 1:2 [no  
142 glucose, ask Sabine??]). Before the experimental schedule started, individuals were allowed to familiarize  
143 themselves with the set-up and the artificial flowers. Since during this training phase the plastic cover was  
144 removed, the two flower patches were not spatially separated and every flower visit was rewarded. This phase  
145 lasted for one to four nights until each bat visited the flowers regularly, which took 1-4 nights. In total six  
146 individuals (belonging to three different experimental groups) did not visit the artificial flowers at all and  
147 were therefore replaced by six new females from the colony after the first night of habituation.

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

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).

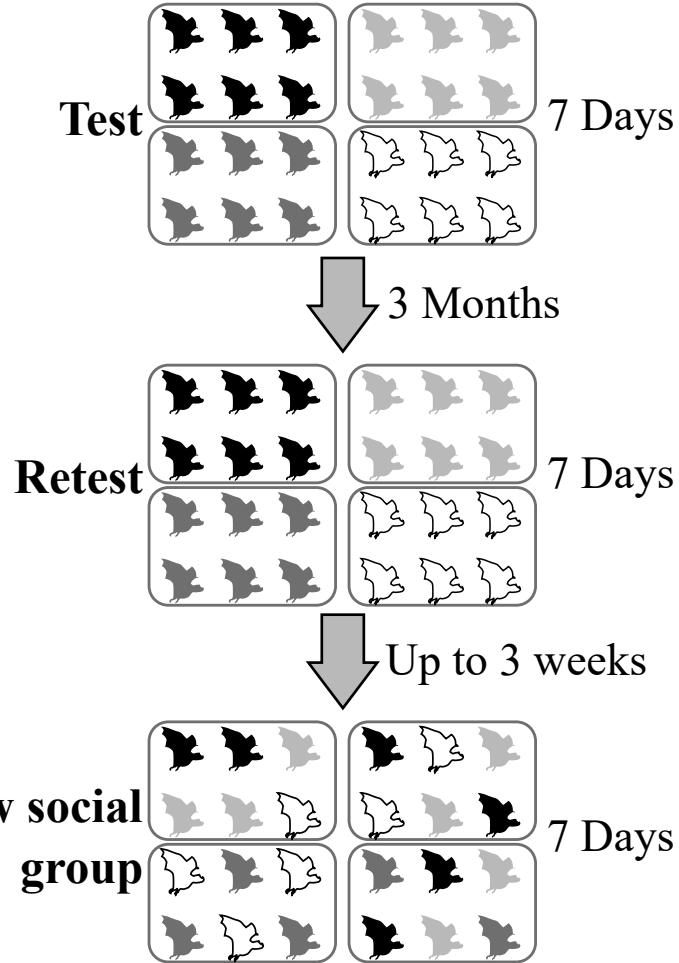


Figure 2: Each experimental run for the four groups of six female bats lasted for seven nights. During the first experimental run (“Test”), we assessed individual differences in multiple behavioral traits in a foraging task with two patches of artificial flowers. We then assessed the long-term consistency 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). We calculated the spread evenness index as:

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

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 forage in new food patch**

201 To assess if individuals differed in how fast they switched to the newly available patch during the uniformly  
202 distributed resource condition, the latency to forage in the new food patch was calculated as the number of  
203 seconds between the activation of the second patch and the first visit at that patch.

204 **Sampling behavior**

205 Sampling was defined as the proportion of visits to the non-rewarding patch during the clumped resource  
206 condition. Bats had to learn the new position of the rewarding patch at the beginning of each night. Sampling  
207 was only quantified after a bat reached the asymptotic phase of its performance curve. We assumed that  
208 all visits made to non-rewarding flowers during the asymptotic phase were for exploration and collecting  
209 information about the current state of these flowers, i.e. sampling. For the analysis, we grouped individual  
210 visits in blocks of 20. The beginning of the asymptotic phase was determined as the second of two consecutive  
211 blocks with a number of visits to the rewarding flowers higher than the daily mean [Nachev et al., in prep.].

212 **Efficiency**

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

216 **Nectar intake rate**

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

219 **Mean spatial overlap**

220 As previously proposed (Ohashi and Thomson 2009), spatial overlap between foraging individuals was  
221 calculated using Pianka's symmetrical index of niche overlap (Pianka 1973). In order to obtain one daily  
222 measurement for each bat, the mean of the spatial overlaps between each focal bat and the five other bats  
223 of the respective group was calculated, using this general equation for Pianka's index *PI* between two  
224 individuals:

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

225 where *p* is the proportion of visits to the *i*th flower made by individual 1 and 2, respectively. *PI*'s values  
226 range between 1 and 0, with higher values corresponding to higher the spatial overlap between individuals.

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 a 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  
260 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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