

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. In this
19 chapter I investigated the influence of social group composition on consistent individual differences in multiple
20 behavioral traits in the nectar-feeding bat species *Glossophaga mutica*. Four social groups, of six female
21 bats each, were confronted with a foraging context consisting of two flower patches. The short-term and
22 long-term consistency of individual differences in five behavioral traits were quantified: Foraging activity,
23 spread evenness of flower visits, agonistic behavior, sampling of the unrewarding patch and the latency to
24 switch to a newly available patch. After assigning individuals to new social groups, individual behavior was
25 reassessed in order to quantify the influence of social group composition on the consistency of individual
26 differences in behavior. All three repeatable behavioral traits were consistent across social groups and
27 differences between individuals also did not increase with time spent in the same social group. However,
28 social group composition had an effect on individual foraging performance. These results indicate that social
29 niche construction plays only a minor role in shaping consistent individual differences in the behavior of *G.*
30 *mutica*.

31 Lay summary

32 Keywords:

33 , bat, *Glossophaga*

34 1. Introduction

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

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

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

109 performance.

110 2. Materials and methods

111 (a) Subjects and housing

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

120 (b) Experimental set-up

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

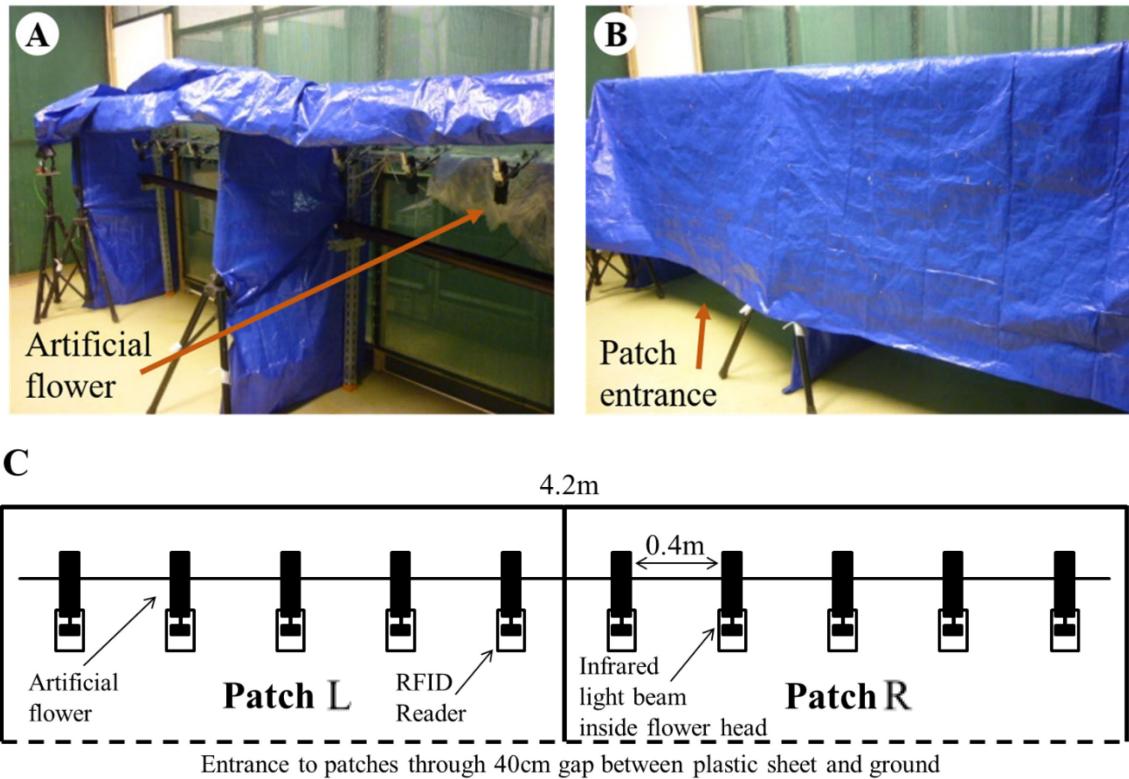


Figure 1: Experimental set-up consisting of two spatially separated patches of five flowers each. (A) The ten flowers were mounted 1.2m above ground. They were divided into two patches, L and R. (B) During experiments the patches were separated by plastic sheets. To make it more demanding for bats to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

134 (c) General procedure

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

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

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

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

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

162 **(d) Experimental schedule**

163 Each experimental run lasted for seven nights. The rewarding patch during the first part of the night (clumped
164 resource condition) was chosen pseudo-randomly so that the same first rewarding patch was never repeated on
165 more than two consecutive nights. The duration of the clumped resource condition varied between four and
166 eight hours to avoid habituation to a specific time. The sequence of the first active patch and the duration of
167 the clumped resource condition were determined for the first experimental run and then kept constant for all
168 subsequent runs (details see Table 5.1).

169 Every individual experienced this experimental schedule three times (Fig. 5.1). During the first and the
170 second experimental run (“Test” and “Retest”) individuals remained in the same social group consisting
171 of six females. The time between test and retest was three months. These two experimental runs were
172 conducted to assess the long-term repeatability of individual differences in behavior. Directly after the retest
173 individuals were assigned to new experimental groups (“New social group”) to assess the influence of the
174 social environment on the consistency of behavior. Between experimental runs, all individuals returned to
175 the housing colony. One female became pregnant after the retest and could therefore not participate in the
176 last experimental run during which individuals were assigned to new social groups. For this reason, another
177 female was assigned to two new social groups. The individual data of this female during this last experimental
178 run was only included once (data of the experimental group that was tested first) whereas group means were
179 calculated using the data of this individual in both groups, so that every 1group consisted of six individuals.

180 **(e) Behavioral traits**

181 **Agonistic behavior**

182 Individual agonistic behavior was assessed by quantifying how often an individual was chasing other individuals
183 away from artificial flowers. These chasing events were indicated by a special sequence of events automatically
184 recorded by the experimental system. For more details see Chapter 4. Furthermore, females rarely chased
185 other bats in the presence of males (Wintergerst, Winter, and Nachev 2021). However, the frequency of chasing
186 in a group that only consisting of females was as high as in mixed sex groups. Notably, in contrast to males,
187 females never succeeded in successfully monopolizing a flower patch by excluding other individuals. Since
188 individuals that make more visits to artificial flowers also have more possibilities to chase other individuals
189 away from artificial flowers we used the proportion of chasing events from the total number of visits as a
190 measure for agonistic behavior.

191 **Foraging activity**

192 Foraging activity was quantified as the number of visits at artificial flowers. Activity specifically during the
193 clumped or uniformly distributed resource condition was calculated as the number of visits per hour since the
194 duration of each condition differed between nights.

195 **Spread evenness index**

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

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

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

204 **Latency to utilize new food patch**

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

209 **Sampling behavior**

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

215 **Efficiency**

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

219 **Nectar intake rate**

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

222 **Mean spatial overlap**

223 As previously proposed (Ohashi and Thomson 2009), spatial overlap between foraging bats was calculated
 224 using Pianka's symmetrical index of niche overlap (Pianka 1973). This index quantifies the spatial overlap of
 225 two individuals. In order to get one daily measurement for each bat, the spatial overlap between one bat
 226 and the five other bats of the respective group was calculated and then the mean of these five values was
 227 determined. The following equation was used to calculate Pianka's index *PI* between for example bat 1 and
 228 2:

$$PI = \frac{\sum_{i=1}^{10} p_{i1}p_{i2}}{\sqrt{\sum_{i=1}^{10} p_{i1} \sum_{i=1}^{10} p_{i2}}}$$

229 p is the proportion of visits to the ith flower made by bat 1 and 2 respectively. The value of *PI* lies between
 230 1 and 0. The higher the value of *PI* calculated for two bats, the higher the spatial overlap between them.

231 (f) Statistical analysis

232 Individual differences in five behavioral traits were analyzed: agonistic behavior, foraging activity, sampling
233 behavior, spread evenness index and latency to utilize a new food patch. Since foraging conditions changed
234 between the clumped (one rewarding patch) and the distributed resource condition (two active patches),
235 individuals might have adjusted their level of foraging activity and agonistic behavior accordingly. Thus,
236 repeatability estimates might change between these two parts of the night. However, initial analyses failed to
237 show an effect of resource condition on individual differences in foraging activity (Table A3.1; Figure A3.3)
238 and proportion of chasing events (Table A 3.1; Figure A 3.4). Thus, foraging activity and agonistic behavior
239 were estimated over whole nights in all further analyses, without discriminating between the clumped and
240 distributed resource condition. A Bayesian Markov chain Monte Carlo generalized linear-mixed models
241 (MCMCglmm package version 2.24, (Hadfield 2010)) was used to calculate repeatability of the five behavioral
242 traits. In each model, the individual behavioral trait was used as a dependent variable and individual and
243 experimental group were included as random effects. Day was initially included as a fixed effect to assess if
244 behavioral traits were changing with time within each experimental run. However, estimates of repeatability
245 only changed marginally with day as fixed effect and therefore I calculated repeatability estimates without
246 any fixed effects which usually leads to a more conservative measure of repeatability. Sampling and agonistic
247 behavior were quantified as proportions and therefore the multinomial2 family was used in these models.
248 Latency to utilize a new food patch was assumed to have a Poisson error structure and Gaussian error
249 structure was assumed for foraging activity. The spread evenness index takes values between 0 and 1 and can
250 be considered as a rate, but not a proportion. Usually a beta regression can be used to analyze rates. However,
251 beta regressions are not yet implemented in the MCMCglmm package and to my best knowledge packages
252 that include beta regressions with random effects are not available. Thus, in order to be able to assume a
253 Gaussian error structure, I used the z-transformation on the spread evenness index. The z-score quantifies
254 the distance in terms of standard deviation of an individual value from the group mean and it was calculated
255 daily and within each experimental group. The repeatability of individual z-scores would therefore provide
256 information of how consistently individuals remained at their relative position within an experimental group.
257 As priors, I used an inverse-Wishart distribution for the residual variance and a parameter expanded prior for
258 random effects. Analysis of autocorrelation, effective sample size and visual inspection of trace plots were used
259 to assess the models. Repeatability, the proportion of variance that can be explained by between-individual
260 differences, was calculated following Nakagawa and Schielzeth (2010). Since each experimental run lasted for
261 seven days, behavioral traits were measured seven times for each individual for each run and repeatability
262 of behavioral traits was calculated for each experimental run (“Test,” “Retest after three months,” “New
263 social group”). Additionally, to assess the potential change of between-individual differences, repeatability
264 estimates were also calculated for the first three days and last three days of each experimental run. Spearman
265 rank correlation coefficients were calculated to explore possible between-individual correlations of behavioral
266 traits which would indicate a behavioral syndrome. To investigate the long-term consistency of individual
267 differences in behavioral traits and the consistency of individual behavior across social groups the individual
268 mean behavior was calculated for each experimental run. Linear (foraging activity and agonistic behavior)
269 and beta regressions (spread evenness index) were used to assess the correlations of individual mean behavior.
270 To explore the influence of consistent individual differences on individual and group foraging performance I
271 calculated the mean nectar intake rate, Pianka’s index and foraging efficiency during the uniformly distributed
272 resource condition. However, the mean spatial overlap of foraging individuals was highly collinear with the
273 measure of individual spread evenness index (Spearman’s $\rho = 0.95$, $p < 0.001$) and therefore was dropped
274 from further analysis. Linear models were used to explore potential correlations. All analysis was performed
275 in R version 3.3.2 (Team R Core 2016). All linear mixed-effects models were performed using the R package
276 “nlme” version 3.1-128 (Pinheiro et al. 2007), all linear models were performed using the R package “lme4”
277 version 1.1-12 (Bates et al. 2014) and beta regressions were performed using the R package “betareg” version
278 3.1-0 (Cribari-Neto and Zeileis 2009).

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

280 **3. Results**

281 **4. Discussion**

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

299 **(a) Influence of social environment on foraging activity**

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

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

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

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

322 Agonistic behavior and spread evenness index of flower visits were correlated across individuals (Table 5.2)
323 In accordance with the result that the social environment had only a minor effect on individual agonistic
324 behavior, individual spread evenness index was also correlated across social groups. How individuals distribute
325 their visits across flowers could have been a consequence of differences in aggressiveness associated with

326 competitive ability. However, individuals differed in their spread evenness index already during the first three
327 days of the first experimental run (Table 5.3) indicating that aggressive individuals might have a tendency to
328 visit less flowers even before they could demonstrate their competitive ability. This is in line with results
329 from a previous study that has shown that *G. commissarisi* differ consistently in the number of flowers they
330 visit in an flower array independent of aggressive interactions (Nachev and Winter 2019).

331 (d) The role of repeated social interactions

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

342 (e) Latency to switch to a newly available flower patch

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

357 (f) Sampling of unrewarding patch

358 Although, individuals of the closely related species *G. commissarisi* have been shown to differ in how much
359 they sample unrewarding flowers, in the present experiment the repeatability of sampling behavior was very
360 low and did not even differ from zero during the last experimental trial with new social groups (Fig. 5.2).
361 Contrary to the previous experiment with *G. commissarisi* (Chapter 2), in this experiment the same five
362 spatially concentrated artificial flowers were rewarding for all bats instead of two single rewarding flowers per
363 individual distributed among ten unrewarding flowers. This indicates that individual differences in sampling
364 might be only present in more challenging situations. In line with this proposition, individual differences in
365 learning in great tits have been shown to be also only present in difficult tasks (Titulaer, Oers, and Naguib
366 2012).

367 (g) Influence of behavioral group composition on foraging performance

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

373 spatial overlap the higher the mean individual foraging efficiency was. Since the individual spread evenness
374 index correlated significantly with agonistic behavior, individual efficiency was higher in groups consisting of
375 individuals with higher mean agonistic behavior.

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

384 (h) Conclusion

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

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

399 Supplementary material

400 **Authors' contributions**

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

406 **Competing interests**

407 We declare we have no competing interests.

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415 **Data Availability**

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

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