1 **Behavioral repeatability and foraging performance in wild free-flying**
2 **nectarivorous bats (*Glossophaga commissarisi*)**
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17 **ABSTRACT**

18 Animal individuals show patterns of behavior that are stable within individuals but

19 different among individuals. Such individual differences are potentially associated with

20 differences in foraging efficiency and in fitness. Furthermore, behavioral responses may be

21 correlated in specific suites of so called behavioral syndromes that are consistent across

22 different contexts and with time. Here we present a field investigation on individual

23 differences between wild, free-flying nectarivorous bats (*Glossophaga commissarisi*) in the

24 foraging context. We further investigated how individual differences effect foraging

25 performance, and we examined their interdependence within hypothesized behavioral

26 syndrome structures. Free-ranging bats were individually identified as they visited an array of

27 24 artificial flowers with nectar of high or low sugar concentration. We found that three

28 behavioral measures of foraging behavior were individually stable over the two-month

29 observation period. We investigated the link between individual behavioral measures and

30 measures of foraging performance using generalized linear mixed models. Individual

31 measures of foraging performance showed significant repeatability, and we found evidence

32 that bats making more visits per bout tend to be slower in learning to avoid unprofitable

33 flowers. We used a multi-response generalized linear mixed model to estimate between-

34 individual correlations and compare hypothesized syndrome structures. There were no clear

35 patterns of between-individual correlations among the behavioral measures in our study,

36 despite the measures exhibiting significant repeatability. This may indicate that foraging

37 performance depends on multiple individual behavior dimensions that are not adequately

38 described by simple models of behavior syndromes.

39

40   ***Keywords: personality traits, behavioral syndromes, foraging, nectarivory, bats.***
41

42   **INTRODUCTION**
43   Findings from the diverse fields of comparative behavioral biology, neurobiology, and

44   psychology (Gosling 2001; Sih, Bell, and Johnson 2004; Dingemanse and Réale 2005; Bell

45   2007; Réale et al. 2007; Roche, Careau, and Binning 2016) demonstrate that intra-specific

46   behavioral variation is sometimes maintained in behavioral types: individual differences in

47   behavioral responses remain stable with time and are consistent across various contexts. Such

48   differences are referred to as 'animal personalities' (Roche, Careau, and Binning 2016),

49   'temperaments' (Réale et al. 2007), 'coping styles' (Koolhaas et al. 2007), or

50   'endophenotypes' (Gould and Gottesman 2006). When several different measures of

51   behavioral traits correlate with each other in their individual expression then such between-

52   individual correlations of behavioral traits are referred to as 'behavioral syndromes' or

53   'personality dimensions' (Sih et al. 2004; Réale et al. 2007; Dingemanse et al. 2012;

54   Dingemanse and Dochtermann 2013; but also see Beekman and Jordan 2017). It has been

55   suggested that different behavioral types can be maintained in natural populations via

56   frequency-dependent selection because different behavioral responses have similar fitness

57   payoffs but are better adapted to slightly different environmental conditions (Benus et al.

58   1991; Sih et al. 2004; Dingemanse and Réale 2005; Penke et al. 2007; Wolf et al. 2007; Wolf

59   et al. 2008; Guilette et al. 2011). However, in addition to the genetic contribution to

60   behavioral variability (Dochtermann, Schwab, and Sih 2015), individual differences may also

61   arise from a state-behavior positive feedback loops (Sih et al. 2015), for example from

62   conditions or events during brain maturation.

63   The idea that individuals tend to exhibit only a limited range of behavioral responses

64   compared to the full behavioral repertoire of the species is interesting from an evolutionary

65   perspective. On the other hand, models of decision making and resource use will remain

66   incomplete if they do not take the constraints and consequences arising from individual

67   differences into account.

68   Here we present a study on the foraging behavior of a population of wild nectar-

69   feeding bats (*Glossophaga commissarisi* Gardner). Bats from the genus *Glossophaga* exhibit

70   considerable individual variation in foraging behavior (Winter and Stich 2005; Thiele 2006).

71   Compared to other members of the Glossophaginae subfamily (e.g. *Hylonycteris* or

72   *Choeronycteris*) they are less specialized nectarivores with a broader diet (Tschapka 2004),

73   which may result in a variety of foraging strategies adapted to different seasonal and local

74   habitat conditions. Working with *Glossophaga soricina* in the laboratory we have performed

75   pilot exploratory analyses searching for personality traits that satisfy the conditions of being

76   different among individuals but stable with time. We have noticed that individuals on average

77   maintain the same level of activity (daily number of visits to flowers) and tend to exploit a

78   similar number of feeding locations (daily number of different flowers visited) over

79   observation periods lasting for several months. Visit duration (time spent in hovering flight in

80   front of or clinging to a flower) is another trait that showed individual consistency and it also

81   tended to correlate negatively with activity, i.e. bats that make few visits make longer-lasting

82   visits and vice versa. We hypothesized that the number of visits and visit duration might both

83   be a part of a general *activity* personality dimension (Réale et al. 2007). The measure of

84   different flower locations visited we interpreted as an indicator of how much an animal

85   invests in information-gathering while foraging or, for the case of low numbers, its tendency

86   to form behavioral routines. This can be considered as the exploration-exploitation balance in

87   theoretical treatments of reinforcement learning (Daw et al. 2006). It must not be confused

88   with the behavioral tendency to explore novel environments or objects. This latter concept is

89   referred to as the *exploration-avoidance* continuum (Réale et al. 2007) i.e. the conflict

90   between the motivation to explore novel contexts vs. the anxiety of an unknown that may be

91   harmful. In our experiments bats were tested on a daily basis in a familiar environment, which

92   eliminated the element of novelty. Furthermore, studies in rodents (Benus et al. 1991;

93   Koolhaas et al. 2007; Coppens et al. 2010) and theoretical analyses of responsiveness (Wolf et

94   al. 2008) indicate that routine formation and cue dependency are correlated with a tendency

95   for aggression and that individual differences in aggressive behavior may reflect more general

96   differences in how animals cope with environmental challenges. Consequently, the measure

97   of number of different flowers visited can be taken as an indicator of an animal's *proactivity-*

98   *reactivity* coping style (Koolhaas et al. 2007; Coppens et al. 2010; or *shyness-boldness*

99   personality dimension, Réale et al. 2007). However, in the absence of measures of other

100   behaviors from this dimension, this interpretation is tentative.

101   We tested these hypotheses by investigating the foraging behavior of the species *G.*

102   *commissarisi* in its natural habitat. The goals of this study were to: (*i*) confirm that previously

103   identified behavioral traits in the foraging context exhibit consistency within individuals, (*ii*)

104   investigate the potential link between personality traits and individual measures of foraging

105   performance, and (*iii*) test whether the correlational patterns between these behavioral traits

106   are consistent with previously hypothesized syndrome structures. We reanalyzed data from a

107   field study in which free flying, individually tagged bats visited an array of computer operated

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108   flowers that provided nectar differing in sugar concentration (Nachev and Winter 2012). From

109   the individual records of flower visitation, we determined the behavioral parameters *number*

110   *of visits per bout*, *visit duration*, and *flowers visited during nightly foraging*. We then used

111   these parameters to construct multi-response multivariate generalized linear mixed models

112   (glmm), which allowed us to assess the within and between-individual correlations of the

113   three parameters (Dingemanse and Dochtermann 2013). We used generalized linear mixed

114   models to investigate whether foraging performance measures were correlated with these

115   other behavioral measures. Finally, we compared hypothesized syndrome structures using the

116   observed correlation pattern of the behavioral measures and deviance information criterion

117   (DIC)-based model comparison (Dingemanse and Dochtermann 2013).

118   **METHODS**

119   We analyzed the behavior of 51 adult *G. commissarisi* bats (21 females and 30 males)

120   at La Selva Biological Station, Province Heredia, Costa Rica. The data were originally

121   collected for a different study (Nachev and Winter 2012), and reanalyzed here because of the

122   rarity of field data on a large number of individuals over a longer time period (over two

123   months). Bats were caught by mist-netting, marked with 100 mg radiofrequency identification

124   tags, measured, and released at the site of capture. As an indicator of a bat's size, we

125   measured forearm length with calipers. Bats had free access to a patch of artificial flowers – a

126   rectangular array of 24 computer-controlled artificial flowers suspended horizontally under a

127   steel frame canopy (Fig. 1 in Nachev et al 2017). The distance between flowers in the same

128   row was about 40 cm and the distance between rows, about 60 cm. The flowers delivered

129   rewards of 55-60 µL on every visit. Repeated visits to the same flower were always rewarded.

130   Each artificial flower was connected via valves to two independent nectar pumps containing

131   different concentration sugar solutions. This allowed us to program the experimental system

132   such that half of the flowers provided a higher sugar concentration and the other half a lower

133   sugar concentration. During a single night an individual flower's concentration was fixed, but

134   between nights, flower concentrations were systematically varied throughout the experiment.

135   Thus bats had to relearn the quality of the flower locations each night. The data set consisted

136   of series of two-alternative choice tests, with 12 flowers per option. The extent to which bats

137   discriminate between two options of different food quality depends on both the difference

138   between the two concentrations, and the average of the concentration pair (Nachev and

139   Winter 2012; Nachev et al. 2013). Thus, for every night we calculated this relative intensity

140   measure from the two sugar concentrations (Eq. 4 with $\beta = 1.4$ in Nachev et al. 2013). We

141   then used this measure as a fixed predictor variable in further analyses.

142 *Behavioral measures*

143   The behavioral data collected during the experiments were the time stamped events

144 (including starting time and duration) of individually identified bats visiting specific flowers

145 that delivered rewards of known amount and sugar concentration. We present data from the

146 51 bats (out of a total number of 63 tagged bats) that made at least 24 flower visits per night

147 on at least three nights. The number of repeated measures per focal individual was 22 ± 13

148 (mean ± SD; range: 3-44). Our sample of females consisted of 21 individuals, eight of which

149 were pregnant. Due to the smaller sample size and potential confounding factor in females we

150 mainly focus on the behavior of the 30 male individuals. Three behavioral measures were

151 calculated for each bat for every experimental night. We analyzed the complete record of

152 nightly events, in contrast to the analysis presented in Nachev and Winter (2012), where only

153 events between 20:00h and 3:00h were analyzed. The behavioral measures we analyzed were:

154   **Visits per bout** – the total number of flower visits divided by the number of bouts

155 made by an individual bat during a single night. We split the foraging behavior of bats into

156 bouts using an interval of 120 seconds duration without flower visits as a bout break criterion

157 (Figure 1). If a bat made fewer visits during a night than the number of flowers on the

158 experimental array ($N = 24$), we excluded this day from the data set of this bat, in order to

159 avoid a spurious positive correlation between number of visits per bout and number of flowers

160 visited (see below).

161   **Visit duration** – the mean of all visit durations made by a bat during a single night.

162 Longer durations of several seconds indicate a tendency to make clinging visits instead of the

163 brief hovering visits, which normally lasted less than a second. However, there is no clear

164 threshold duration value that separates the two behaviors.

165   **Flowers visited** – the total number of different flowers visited by an individual bat

166 (ranging from 1 to 24) during a single night.

167 *Behavioral consistency*

168   Based on prior experiments in the laboratory, we expected the individual differences

169 between bats to remain stable over time. In order to test this, we performed repeatability

170 analyses (Bell et al. 2009; Nakagawa and Schielzeth 2010) separately for males ($N = 30$) and

171 females ($N = 21$). We used a multivariate random intercept and random slope model with

172 *intensity* as a fixed effect and with visits per bout, visit duration, and flowers visited as

173 independent variables (Hadfield 2009; Dingemanse and Dochtermann 2013; *MCMCglmm*

174 package in R 3.4.3, R Development Core Team 2018). We used the Gaussian family for the

175 parameters visits per bout and visit duration, and the Poisson family for flowers visited. For

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176   this, and each further analysis unless otherwise specified, we used 130,000 iterations with a

177   thinning interval of 100 and a burn-in phase of 30,000, obtaining 1,000 samples for each

178   estimate. Different priors (inverse Wishart, flat covariances, and parameter expanded;

179   Hadfield 2009; Mutzel et al. 2013) did not result in qualitative changes in the output. From

180   the output of these models we calculated the adjusted repeatabilities, that is the repeatabilities

181   after controlling for confounding effects (Nakagawa and Schielzeth 2010).

182

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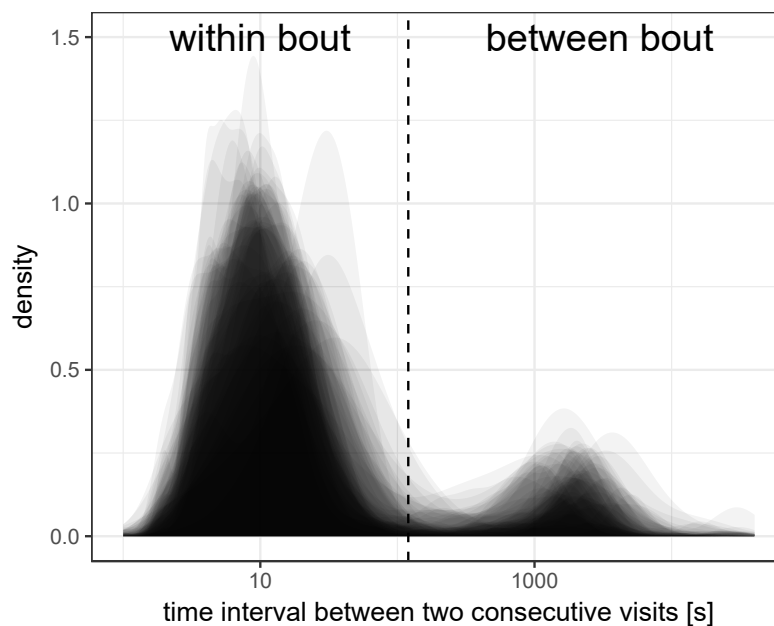
184   **Fig. 1** Bats' foraging behavior was organized in clear bouts. The time intervals between two
185   visits at a flower had a bimodal distribution when logarithmically transformed. Each
186   transparent curve is based on the cumulative visits of an individual tagged bat. We selected
187   the time interval of 120 seconds (vertical dashed line) as a criterion to distinguish visits within
188   a bout from visits between bouts.

189

190   From the same models we also obtained estimates for the between-individual and

191   within-individual correlations of the three behavioral measures, along with their 95% credible

192   intervals. We compared the observed between-individual correlation pattern with *a priori*

193   hypotheses about behavioral syndrome structures (Figure 2; Dochtermann and Jenkins 2007;

194   Dingemanse et al. 2010). Credible intervals that do not overlap with zero indicate statistical

195   significance for paths between behavioral measures. We used credible intervals to distinguish

196   between models 2 through 4 (Figure 2). Additionally, we tested if the three measures were

197   independent from each other by running models in which the betindividual covariances were

198   fixed at zero, but with the within-individual covariances left as free parameters. We compared

199   the two models (model 1 and model 5, Figure 2) using the deviance information criterion

200   (DIC; Spiegelhalter et al. 2002). A lower DIC score indicates higher explanatory power after

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201   penalizing for the number of free parameters. We considered models with ΔDIC>2 (i.e. with

202   DIC scores differing by more than two from the model with the lowest DIC score) to be

203   statistically unsupported.

204   In order to test which of the three behavioral parameters visits per bout, visit duration,

205   and flowers visited were influenced by intensity, sex, and body size, we also ran three

206   univariate random intercept and random slope models with intensity, sex, and forearm length

207   as fixed factors, and bat individual as random factor on the pooled data set for males and

208   females (*MCMCglmm* package in R 3.4.3, R Development Core Team 2018). For these tests

209   we corrected the *P* values using the Benjamini & Hochberg (a.k.a. false discovery rate)

210   correction.

211
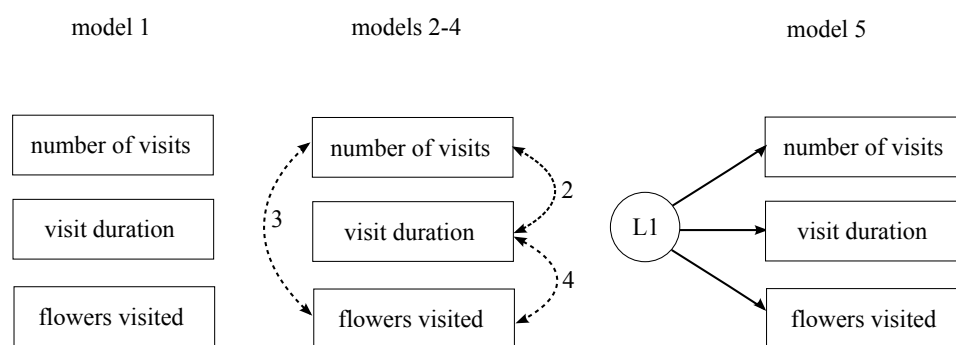
212   **Fig. 2** Models (1-5) of different syndrome structures. See *Methods* for model descriptions.
213   Continuous unidirectional lines represent a causal relationship from a latent variable (L1) to
214   behavioral measures. Dashed bidirectional arrows represent correlations between behavioral
215   measures expressed in particular syndrome structures. In model 2 only path '2' is active, in
216   model 3 only path '3' is active and in model 4 only path '4' is active.

217

218   ***Behavioral syndrome structure***

219   *Model 1.* Behavioral independence. This was the null model with assumed lack of

220   relationship between the three behavioral parameters.

221   *Model 2.* A link between visits per bout and visit duration (Figure 2, only path 'a'

222   activated), both interpreted as indicators of the *activity* dimension (Réale et al. 2007). Flowers

223   visited is independent from the other two measures.

224   *Model 3.* A link between visits per bout and flowers visited (Figure 2, only path 'b'

225   activated). In this model visit duration is independent from the other variables and not an

226   indicator of any particular personality dimension, whereas visits per bout and flowers visited

227   both reflect the *activity* dimension.

228   *Model 4.* A link between flowers visited and visit duration and (Figure 2, only path 'c'

229   activated), both interpreted as probable indicators of the *proactivity-reactivity* dimension

230   (Koolhaas et al. 2007). The rationale behind this hypothesis is that an animal might make

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231   visits to a higher number of different flowers to sample their nectar concentration and abort

232   the visits prematurely when the concentration is of the lower type. In this model visits per

233   bout is the sole indicator of the *activity* dimension.

234   *Model 5.* Full domain-general syndrome with all measures indicators of the same

235   dimension, (e.g. *activity*).

236   ***Foraging performance***

237   Foraging tasks are often modeled using temporal difference (TD) learning. Here, the

238   expectations about finding a positive reward in an environment with resource locations of yet

239   unknown quality are continually updated with ongoing experience. Choice performance then

240   depends primarily on the learning rate (Glimcher 2011) and also the balance between

241   exploration and exploitation, i.e. the sampling of locations with uncertain quality vs. the

242   visitation of locations with a recently experienced positive outcome (Daw et al. 2006; Mathot

243   et al. 2012). Consequently, we used two different measures of foraging performance, bouts to

244   criterion and error rate (see below), both calculated from the seven nights on which the most

245   extreme differences in sugar concentrations were presented to the bats (5% vs. 20%, 10% vs.

246   25%, and 15% vs. 30%). These pairs of sugar concentrations were chosen because they were

247   associated with the highest, nearly perfect discrimination performance by bats (Nachev and

248   Winter 2012). Under these conditions the effect of individual differences in perception of

249   sugar concentrations is minimized, so that differences in learning rates and non-perceptual

250   error rates (e.g. due to exploration) can be better estimated. For these measures the sample

251   size was $N = 23$ bats, because we only analyzed males and not all bats were detected on more

252   than two of these seven nights. Again, if a bat made fewer than 24 visits on a given night, this

253   data point was not included.

254   **Visits to criterion** – the number of visits a bat made on a particular night, until the

255   average proportion of visits to the higher sugar concentration flowers (discrimination

256   performance) reached 0.8 or higher. In order to calculate this parameter, we used a change

257   point algorithm (Gallistel et al. 2004; Nachev 2018) that separates a sequence of visits into

258   chunks with significantly different choice preferences. We considered only chunks of at least

259   ten visits. The visits to criterion measure was taken as the number of the first visit of the

260   chunk in which the bat reached the criterion. Most males reached this criterion on every night

261   on which they were detected, except for three bats, each on only a single night. Thus, the

262   average number (± SD) of repeated measures per bat for this parameter in our data set was 5.7

263   nights ± 1.7. All else being equal, a high value for this measure indicates that a bat was faster

264   in avoiding options with lower sugar concentrations and therefore gained a higher energy

265   intake per visit. The probability of making a mistake and the overall number of visits needed

266   to obtain a reliable estimate of the flower quality for each flower both scale with the total

267   number of flowers visited. Therefore, we expected that bats visiting overall a smaller number

268   of different flowers to reach criterion within a lower number of visits. On the other hand, we

269   expected, all else being equal, for bats to reach the criterion just as fast, regardless of how

270   they distributed their visits between bouts. In other words, we expected a bat making 50 visits

271   in a single bout and a bat making ten bouts of five visits each (but visiting the exact same

272   flowers in the exact same sequence) both to reach the criterion in the same number of visits.

273   Therefore, we expected a lack of correlation between visits per bout and visits to criterion.

274   Finally, we did not have a prior expectation for a relationship between visits to criterion and

275   visit duration

276   **Error rate** – a measure of the relative frequency of errors (in this case, visits to low

277   concentration flowers) due to factors of a non-perceptual nature, e.g. information-gathering or

278   exploratory behavior. Error rate was calculated from the data after a bat had reached its

279   nightly asymptotic choice behavior phase. The error rate is the proportion of visits to low

280   concentration flowers after the last change point (Gallistel et al. 2004; Nachev 2018) in

281   preference. We expected our stable experimental conditions (fixed sugar concentrations and

282   volumes during a night) to favor bats with more routinized behavior. Once several

283   advantageous flowers had been found a bat did not gain from further exploration. |Therefore,

284   bats visiting only a few different flowers were expected to have lower error rates. Since we

285   measured error rate from asymptotic behavior, we expected error rate to be unaffected by

286   visits per bout. We had no prior expectation for the relationship with visit duration. As

287   mentioned above, error rate was only determined from those experimental conditions where

288   concentration differences were of high salience.

289   We ran another multivariate random intercept and random slope model as the one

290   described in *Behavioral consistency*, but added visits to criterion and error rate as dependent

291   variables (*MCMCglmm* package in R 3.4.3, R Development Core Team 2018). We used the

292   Poisson family for visits to criterion and the multinomial family for the error rate. This

293   allowed us to estimate the repeatabilities for the two measures of foraging performance, as

294   well as the between and within-individual correlations for all behavioral measures. Because of

295   the larger number of estimated parameters, we used 1,300,000 iterations with a thinning

296   interval of 1000 and a burn-in phase of 30,000, obtaining 1,000 samples for each estimate.

297

298 *Data availability*

299   The datasets generated during and/or analysed during the current study, including all

300 statistical tests are available in the Zenodo repository:

301 https://doi.org/10.5281/zenodo.1230548.

302 **RESULTS**

303   Some 50–80 *G. commissarisi* bats foraged simultaneously during the course of the

304 two-alternative choice experiment, making on average one visit per minute per individual.

305 The average number ($\pm$ SD; range) of flower visits by individual tagged bats per night was

306 2900 $\pm$ 1600 (400-9700). The three univariate glmm models revealed no significant

307 differences between males and females in visit duration (estimate = -11.8, credible interval = -

308 41.0, 20.9, hereafter reported as $-41.0 \leq -11.8 \leq 20.9$, $P = 0.55$, all P values corrected for false

309 discovery rate; Table 1). However, males made on average fewer visits per bout ($-1.66 \leq -0.95$

310 ≤ -0.16, $P = 0.024$; Table 1) and visited fewer different flowers than females did ($-1.67 \leq -$

311 $1.55 \leq -1.42$, $P = 0.005$; Table 1). Forearm length did not significantly affect visits per bout ($-$

312 $0.53 \leq -0.07 \leq 0.32$, $P = 0.86$), or flowers visited ($-0.05 \leq 0.00 \leq 0.05$, $P = 0.94$), but bats with

313 longer forearms on average made visits with shorter durations ($-35 \leq -18 \leq -1.3$, $P = 0.045$).

314 On average, visits per bout increased with the relative intensity of the difference in available

315 concentrations ($4.59 \leq 9.74 \leq 14.79$, $P = 0.005$), but visit duration ($-561 \leq -288 \leq -28.9$, $P =$

316 0.072) or the number of flowers visited did not significantly depend on relative intensity of

317 the sugar concentration difference ($-1.20 \leq 1.34 \leq 2.46$, $P = 0.435$).

318   The individual behavioral consistency of all three measures in the 51 tagged

319 individuals was high, as indicated by the individual repeatability estimates for visits per bout

320 (males: adj.$R = 0.40$, 95% credible interval = 0.26, 0.54, $N = 30$; hereafter reported as $0.26 \leq$

321 $0.40 \leq 0.54$; females: $0.26 \leq 0.39 \leq 0.58$, $N = 21$), visit duration (males: $0.59 \leq 0.69 \leq 0.81$, N

322 $= 30$; females: $0.37 \leq 0.57 \leq 0.70$, $N = 21$), and flowers visited (males: $0.29 \leq 0.46 \leq 0.61$, $N =$

323 30; females: $0.34 \leq 0.49 \leq 0.71$, $N = 21$).

324

325 *Relationship between behavioral measures and measures of foraging performance*

326   The two measures of foraging performance were both significantly repeatable within

327 individuals (visits to criterion: $0.18 \leq 0.30 \leq 0.54$, $N = 23$; error rate: $0.32 \leq 0.49 \leq 0.71$, $N =$

328 23). The glmm revealed that bats that made more visits per bout on average took more visits

329 to reach the criterion of 80% discrimination performance (Table 2). However, there were no

330 other significant between-individual correlations between the two measures of foraging

331 performance and any of the other three behavioral measures (Table 2). Within individuals,

10

332   there was a significant negative correlation only between error rate and visit duration (Table

333   2).

334 **Table 1** Phenotypic correlation (Pearson's *r*) coefficients for behavioral parameters of the 51
335 bats.

	Visits per bout	Visit duration (ms)	Flowers visited
Males (N = 30)			
Visits per bout	7.73 (3.13)[a]		
Visit duration (ms)	0.05 (0.80)[b]	659 (214)	
Flowers visited	0.33 (0.08)	**0.37 (0.04)**	8.28 (3.09)
Females (N = 21)			
Visits per bout	8.86 (3.83)		
Visit duration (ms)	**-0.64 (0.002)**	662 (150)	
Flowers visited	0.18 (0.42)	0.24 (0.29)	13.10 (3.70)

336
337 [a] Values on main diagonals give mean measures with standard deviations in parentheses.
338 These mean measures are calculated from the individual means.
339 [b] Correlations are based on individual means calculated over the whole data set, excluding
340 nights in which bats made less than 24 visits, and bats that were detected on fewer than three
341 nights. The corresponding two-tailed p values are given in parentheses. Significant
342 correlations are shown in bold.
343
344 **Table 2.** Between-individual and within-individual correlation coefficients for behavioral
345 parameters and measures of foraging performance.

	Between individuals		Within individuals	
Males (N = 23)				
	Visits to criterion	Error rate	Visits to criterion	Error rate
Error rate	$-0.45 \leq 0.05 \leq 0.49$		$-0.22 \leq 0.13 \leq 0.39$	
Visits per bout	**$0.03 \leq 0.58 \leq 0.83$**	$-0.47 \leq -0.09 \leq 0.47$	$-0.21 \leq 0.11 \leq 0.36$	$-0.51 \leq -0.11 \leq 0.20$
Visit duration	$-0.53 \leq 0.08 \leq 0.45$	$-0.61 \leq -0.13 \leq 0.35$	$-0.31 \leq -0.10 \leq 0.19$	**$-0.58 \leq -0.35 \leq -0.01$**
Flowers visited	$-0.20 \leq 0.21 \leq 0.60$	$-0.41 \leq 0.05 \leq 0.46$	$-0.20 \leq 0.32 \leq 0.60$	$-0.32 \leq -0.02 \leq 0.34$

346
347 Note.- Correlations are based on 1000 posterior samples per individual. The values are given
348 as lower 95% credible interval ≤ posterior mode ≤ upper 95% credible interval. Between-
349 individual correlations are given to the left and within-individual correlations are given to the
350 right. Values in bold do not overlap with 0.
351
352 ***Analysis of behavioral syndrome structure***

353   The between-individual correlations for the three behavioral parameters did not

354 support any of the path connections between the different behavioral measures in males

355 (models 2-4; Figure 2; Table 3), but in females there was support for model 2 (Figure 2; Table

356 2). The model in which the between-individual correlations were fixed to zero (model 1) and

357 the model in which the correlations were left as free parameters (model 5) could not be

358 distinguished from each other neither in males (model 1: DIC = 14627.03; model 5 DIC =

359   14626.55; ΔDIC = -0.48) nor in females (model 1: DIC = 11644.12; model 5: DIC =

360   11644.61; ΔDIC = 0.49).

361   Even though there was no support for any of the between-individual correlations in

362   males, there was a significant positive within-individual correlation between visits per bout

363   and flowers visited (Table 3). In females all the within-individual correlations were significant

364   and positive (Table 3).

365

366   **Table 3** Between-individual and within-individual correlation coefficients for behavioral
367   parameters of the 51 bats.

	Visits per bout	Visit duration	Flowers visited
Males (N = 30)			
Visits per bout		–0.15 ≤ -0.09 ≤ 0.00	**0.52 ≤ 0.61 ≤ 0.67**
Visit duration	–0.35 ≤ 0.07 ≤ 0.38		–0.04 ≤ 0.09 ≤ 0.17
Flowers visited	–0.18 ≤ 0.23 ≤ 0.56	–0.01 ≤ 0.42 ≤ 0.67	
Females (N = 21)			
Visits per bout		**0.03 ≤ 0.13 ≤ 0.21**	**0.49 ≤ 0.59 ≤ 0.66**
Visit duration	**–0.88 ≤ -0.73 ≤ -0.39**		**0.18 ≤ 0.29 ≤ 0.42**
Flowers visited	–0.42 ≤ 0.11 ≤ 0.48	–0.24 ≤ 0.07 ≤ 0.59	

368
369   Note.- Correlations are based on 1000 posterior samples per individual. The values are given
370   as lower 95% credible interval ≤ posterior mode ≤ upper 95% credible interval. Between-
371   individual correlations are given to the left and below the main diagonal and within-individual
372   correlations are given to the right and above. Values in bold do not overlap with 0.
373

374   **DISCUSSION**

375   Consistent with our observations from the laboratory, the wild *G. commissarisi* in this

376   study exhibited individual behavioral consistency in the number of visits per bout they made

377   to a patch of artificial flowers, their mean visit duration, and the number of different flowers

378   they visited. Except for visit duration, there was no evidence that the individual behavioral

379   differences were related to differences in body size (from forearm length).

380   This individual behavioral consistency of the three parameters could not be explained

381   by their interdependence within a full domain-general syndrome. We found no clear patterns

382   of between-individual correlations, neither in males nor in females (Table 3). The mostly low

383   and non-significant between-individual correlations suggest that the behavioral consistency

384   most likely results from three independent dimensions. The only consistent finding in both

385   male and female bats was that on nights on which bat individuals made a higher number of

386   visits per bout, they were also more likely to visit a higher number of flowers. It was not the

387   case, however, that bats that on average made more visits per bout also visited a higher

388   number of different flowers on average, as indicated by the lack of significant between-

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389 individual correlations in either sex. The only significant between-individual correlation in

390 females suggests that females either visit many flowers per bout but hovering very briefly in

391 front of them, or they visit a smaller number of flowers per bout but make visits with longer

392 durations. Surprisingly, the within-individual correlation between visits per bout and visit

393 duration was significant, but in the opposite direction compared to the between-individual

394 correlation. All in all, our findings demonstrate that phenotypic correlations between different

395 behaviors (Table 1) are not necessarily indicators of behavioral syndromes (Table 3;

396 Dingemanse et al. 2012; Dingemanse and Dochtermann 2013).

397 Without significant between-individual correlations between the three behavioral

398 measures from our study and without knowing what other behaviors these correlate with, it is

399 not possible to determine the mechanisms leading to the observed behavioral consistency. In

400 the following, we provide some tentative interpretations and ideas for future studies.

401 Concerning the pattern of resource exploitation, some bats consistently visited only a few of

402 the available flowers, whereas others spread their activity over more than half of the flower

403 array (range of mean number of flowers visited: 4–20; Table 1). We suggest that this

404 difference may be a difference in the degree of behavior routinization (Koolhaas et al. 2007;

405 see also Wolf et al. 2008). Our flowers always delivered rewards and the sugar concentrations

406 of their nectars were stable within nights and only varied from night to night, thus favoring

407 the development of stable choice patterns and penalizing unnecessary information-gathering.

408 It remains to be shown that number of flowers visited is linked to known behaviors from the

409 *proactivity-reactivity* (Koolhaas et al. 2007, e.g. aggressive interactions with conspecifics) or

410 *shyness-boldness* continuum (responses to non-novel risk situations, Réale et al. 2007, e.g.

411 delay to resume foraging after a perceived predator attack).

412 The distance bats travelled from their (night-time) roosts to the flower array is a

413 potential uncontrolled confounding factor that could account for the repeatability of the

414 number of visits per bout and potentially other behavioral measures. However, we first

415 became aware of the repeatability of visits per bout in our laboratory studies, where all bats

416 were kept in the same room with the flowers and considerations of travel distances were not

417 applicable.

418 Our results provide some support to the hypothesis that different behavioral types may

419 be better adapted to different environmental conditions (Guillette et al. 2011), more

420 specifically, to different resource qualities and distributions. Though we did not assess fitness

421 directly, differences in foraging efficiency can be positively correlated with fitness (Ritchie

422 1990; Lemon 1991; Jeanniard-du-Dot et al. 2017). The differences in both measures of

14

423   foraging performance were significantly repeatable and the measure visits to criterion was

424   significantly correlated with visits per bout, also a repeatable measure. Although this

425   correlation was unexpected, we had based our prediction on the assumption that bats differing

426   in visits per bout do not also differ in the spread of visits over the flower array *per bout*.

427   However, if we define a new measure, flowers per bout, as the average number of different

428   flowers a bat visits per bout during a single night, we can see that there is a significant

429   correlation between flowers per bout and visits per bout (between-individual $r = 0.20 < 0.62 <$

430   0.80, within-individual $r = 0.76 < 0.73 < 0.79$). Thus, when bats make more visits within a

431   bout, they tend to visit a higher number of different flowers, which seems to slow learning

432   down and affect visits to criterion. Under conditions of higher reward uncertainty, we would

433   expect bats that invest more in information-gathering to have better chances of detecting the

434   locations of more profitable sources of nectar. On the other hand, especially at flowers with

435   high nectar secretion rates, a more routinized behavior may confer fitness benefits through

436   'defense by exploitation' (Paton and Carpenter 1984; Ohashi and Thomson 2005). Foragers

437   employing this strategy maintain high activity rates and exploit a limited number of

438   replenishable food sources therefore keeping the mean resource standing crops low. This can

439   reduce resource competition, because competitors using different strategies may perceive the

440   shared food sources as unprofitable and leave to forage elsewhere. In our experiments the

441   behavior of males seems consistent with defense by exploitation. Alternatively, the smaller

442   numbers of visits per bout and flowers visited compared to females might also be an

443   indication of agonistic interactions at the flowers.

444   Realistic models of bat foraging need to take into account the observed repeatable

445   differences in frequency and distribution of flower visits. However, these differences also

446   have important implications for the fitness of the plants that bats pollinate. For example, bats

447   with different propensities to make revisits to the same plant or flower can exert very different

448   selection pressures on plants, especially if the plants are self-incompatible. On the other hand,

449   bats that make more visits per bout probably remove and deposit more pollen from flowers,

450   since pollen can be ingested during grooming in the pauses between bouts. Finally, although

451   hovering flight duration has been shown to be uncorrelated with pollen transfer (Muchhala

452   and Thomson 2007), it may be that clinging visits result in higher pollen transfer than

453   hovering visits. Thus, both the quality and quantity of pollination service provided by a

454   pollinator may depend on its foraging strategy.

15

455 **Acknowledgments**

460 **Conflict of Interest**

461   The authors declare that they have no conflict of interest.

462 **Ethical Standards**

463   Treatment of the experimental animals complies with the national laws on animal care

464 and experimentation.

465

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