

¹ Sex-dependent resource defense in a nectar-feeding bat

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8 Abstract

9 Aggressive resource defense spans from the transient monopolization of a resource up to the long-term
10 maintenance of a territory. While such interference competition is common in nectar-feeding birds, reports in
11 nectar-feeding bats are rare. *Glossophaga* bats have been observed to temporarily defend flowers but the
12 extent of this monopolization, its effects on nectar intake, and underlying sexual differences remain unknown.
13 We investigated resource defense behavior of *Glossophaga mutica* in the laboratory. We presented bats with
14 two patches of computer-controlled artificial flowers and tracked individual nectar intake. Furthermore, we
15 established an automated method for detecting aggressive interactions at the artificial flowers. Theoretical
16 models of interference competition predict more aggressive interactions when resources are spatially more
17 clumped. To test this, we varied resource distribution across two patches from clumped to dispersed and
18 monitored bats' interactions in one male, one female, and four mixed-sex groups. Males engaged in aggressive
19 interactions more often than females and in each group some individuals defended clumped artificial flowers
20 against others. Subordinate males experienced a substantial decrease in nectar intake, while females were
21 only marginally affected by male aggression. These results suggest that aggressive interactions and their effect
22 on nectar intake are sex-dependent in *G. mutica*. Furthermore, aggressive interactions were more frequent
23 and resource defense was only successful when resources were clumped. Our experimental set-up allowed
24 us to perform an automated test of models of interference competition with a mammal under controlled
25 laboratory conditions. This approach may pave the way for similar studies with other animals.

26 Lay summary

27 Males bully other males to get more food, but only when food is easy to defend. When flowers are spread
28 out nectar-feeding bats rarely engage in fights. However, when there are rich flowers in one spot and no
29 flowers elsewhere, some males start attacking others, denying them access to the nectar. Females do not seem
30 bothered by such male bullies, but when there are no males around, some females become bullies themselves.

31 Keywords:

32 resource defense, economic defendability, bat, *Glossophaga*

33 1. Introduction

34 Competition for limited resources like food or mates is a ubiquitous phenomenon in the animal kingdom.
35 Such competition can be indirect by exploiting a common resource and preventing others from benefiting
36 from it (Paton and Carpenter 1984); or it can be direct by aggressively defending a resource. The latter is
37 known as interference competition (Amarasekare 2002). Aggressive resource defense by excluding competitors
38 leads to priority of access to those resources and thus establishes dominance. One individual is dominant
39 over another if it directs aggressive behavior towards it (chasing, threatening, biting, etc.) while receiving
40 little or no aggression from the other (Chase et al. 2002). In the extreme, dominance behavior can lead to
41 exclusive territoriality. Territoriality is a concept belonging to an indivisible continuum starting with the
42 transient monopolization of a preferred feeding opportunity to the longer-term defense of an area as exclusive
43 territory. The rules of economic defendability (Brown 1964) determine the adaptive compromise to which
44 a species' dominance behavior will evolve and develop along this continuum. The establishment of feeding
45 territories is well known for nectar-feeding birds (Boyden 1978; Carpenter and Macmillen 1976; Ewald and
46 Carpenter 1978; Gill and Wolf 1975).

47 The cost of defense, a key parameter in the economic defendability equation, is likely much higher for a
48 nocturnal, echolocating bat than for a diurnal, visually oriented bird. The successful resource defense is only
49 possible after the competition is detected. Visual detection in the daylight works well over long distances.
50 In contrast, for a nocturnal, echolocating bat, especially for phyllostomid bats that are able to echolocate
51 with whispering calls (Howell 1974; Hörmann et al. 2020; Yoh et al. 2020), detecting intruders at a feeding
52 territory's boundary would require expensive patrolling flights.

53 Within bats, the flower visitors have an advantage compared to insect-hunting bats if they are intimately
54 familiar with their feeding area. Bats feeding on insects must continually scan for elusive prey by active
55 echolocation, whereas flower visitors can approach a target with minimal echolocation when seeking specific
56 flowers at known locations (Thiele and Winter 2005; Winter and Stich 2005; Gonzalez-Terrazas et al. 2016;
57 Rose et al. 2016). Thus, it is not surprising that the longer-term defense of extensive feeding territories
58 as commonly observed in nectar-feeding birds is not known for glossophagine, nectar-feeding bats (but see
59 Watzke 2006 for nectar-feeding flying foxes). Nonetheless, several observations have documented aggressive
60 food defense by glossophagine bats. The inflorescences of *Agave desmettiana* with their copious nectar
61 (Lemke 1985) may be defended by males or females of *Glossophaga soricina* against conspecifics but only
62 during some hours of the night (Lemke 1984, 1985). When left unguarded, intruders quickly exploited the
63 opportunity to feed from the previously defended plants. The Costa Rican bat *Glossophaga commissarisi*
64 occasionally defends and temporarily monopolizes single inflorescences of the understory palm *Calyptrogyne*
65 *ghiesbreghtiana* against other hovering bats, perching bats and katydids (Tschapka 2003). A commonality in
66 these reports was that the defense did not cover the area of a typical feeding range but was restricted to a
67 single or a few flowering plants and was also limited to a small number of hours during the night. Still, these
68 reports demonstrate that glossophagine bats can show aggressive resource defense.

69 In this study, we investigated for a nocturnal, nectar-feeding mammal, the flower-visiting bat *Glossophaga*
70 (*mutica* (previously *G. soricina*, Calahorra-Oliart, Ospina-Garcés, and León-Paniagua (2021)), the role of
71 aggressive interactions for gaining access to nectar food. We tested the predictions of models of resource
72 defense (Grant et al. 2002) and interference competition (Grant 1993) using a naturalistic foraging paradigm
73 in the laboratory. The occurrence of resource defense is predicted to be highest at intermediate levels of food
74 abundance (Grant et al. 2002). In line with this prediction, the transient nature of nightly defense behavior
75 observed in the field suggests that changes in food-abundance or food-requirements that occur within the
76 night affected the strength of the observed behavior. To mimic the natural situation of chiropterophilous
77 flowers which often replenish their nectar more or less continuously throughout a night (e.g. Tschapka and
78 Helversen 2007) we programmed artificial flowers to provide nectar with a fixed interval reward schedule.
79 Once a nectar reward had been taken by any bat, the fixed interval had to pass before the next reward was
80 available at this flower. Theoretical models of interference competition predict that clumped resources lead to
81 more agonistic behavior and resource defense than evenly dispersed resources (Grant 1993). To include a test
82 of this prediction in our experimental design, we spatially subdivided our flower field into two patches and
83 programmed them to automatically change the spatial distribution of available nectar resources during the
84 night. We performed our study with 36 individuals of male and female *G. mutica*. By using artificial flowers
85 in a closed environment, we could track all flower visits and total nectar consumption of every individual in
86 the group. Each individual carried an electronic ID tag and flowers were equipped with ID sensors. This
87 also enabled us to detect and quantify a typical class of aggressive interactions between pairs of individuals
88 directly at the artificial flowers fully automatically.
89 Our novel experimental set-up thus allowed us to perform a mostly automated experimental test of models
90 of interference competition and resource defense with a mammal under the controlled conditions of the
91 laboratory. This new approach may pave the way for further such studies with other groups of organisms.

92 2. Materials and methods

93 (a) Subjects and housing

94 Experiments were conducted with 54 (36 females and 18 males) individuals of the small, (9-10g) neotropical
95 nectarivorous bat species formerly identified as *Glossophaga soricina* (Pallas's long-tongued bat). In view
96 of the recent taxonomic revision of the *G. soricina* species complex (Calahorra-Oliart, Ospina-Garcés, and
97 León-Paniagua 2021), it is relevant to note that the founders of our colony used in this and all our previous
98 studies were caught at the Cueva de las Vegas, Municipio de Tenampulco, Mexico and transported to Germany
99 in 1988 by Otto von Helversen. Thus they belong to the species *G. mutica*. Bats came from our captive colony
100 and were older than one year as judged by finger joint ossification (Brunet-Rossini and Wilkinson 2009). They
101 carried radio frequency identification (RFID) tags attached to cable tie collars (total weight of collar with
102 tag = 0.2g, max. 2.4% of the body weight) that were removed after the experiment. Additionally, bats had
103 numbered plastic split rings (A C Hughes Ltd., Middlesex, UK) around the forearm for visual identification.

104 Temperature in the experimental and colony room was kept at 20-25°C, air humidity at 65-75%, and light
 105 conditions were 12:12 LD (light off at 16h).

106 (b) Experimental set-up

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

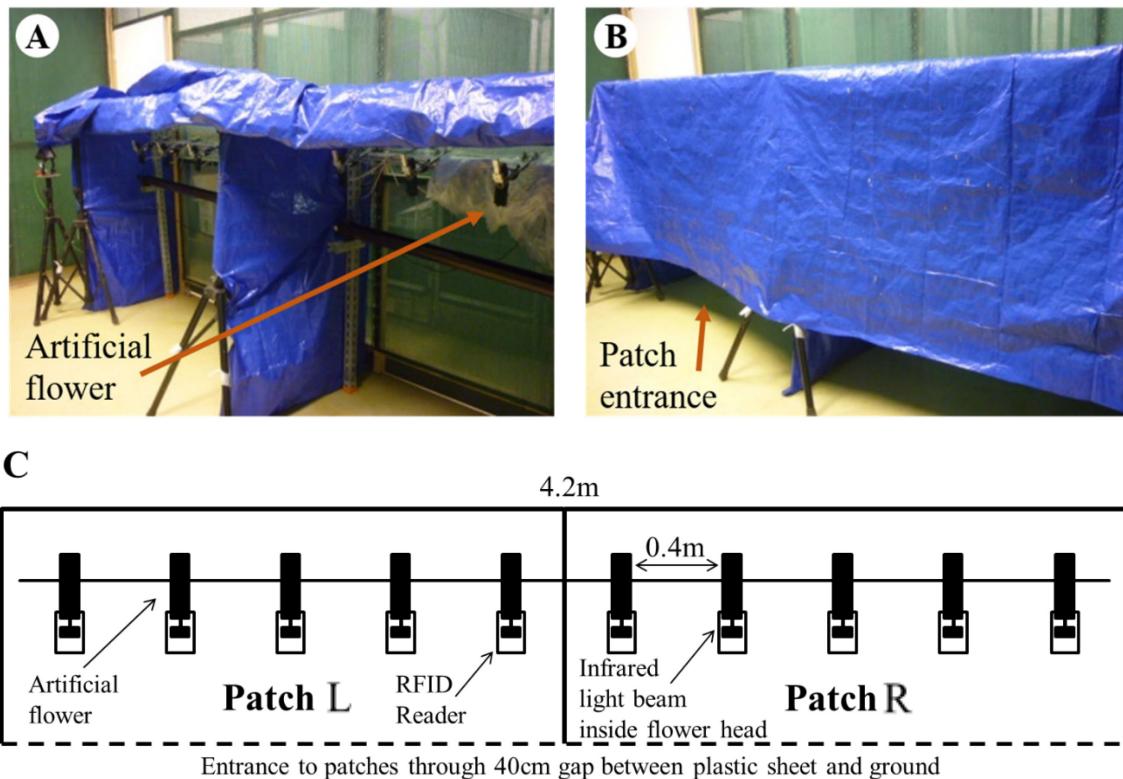


Figure 1: Experimental set-up consisting of two spatially separated patches of five flowers each. (A) The ten flowers were mounted 1.2m above ground. They were divided into two patches, L and R. (B) During experiments the patches were separated by plastic sheets. To make it more demanding for bats to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

120 **(c) Experimental procedure**

121 Six bats were randomly selected from the colony (out of the total of ca. 150 individuals) and were tested
122 simultaneously as a group. Four experimental groups consisted of three males together with three females
123 (mixed groups), whereas one group consisted of six males, and four others of six females. No bats were re-used
124 between experiments. We weighed all bats before the experiment.

125 During the nightly experiments, in addition to the nectar provided by artificial flowers, bats had access to
126 pollen and water and to 6mL of additional food containing 1.2g NektarPlus (Nekton, Keltern, Germany)
127 and 1.8g milk powder (Milasan Folgemilch 2, Sunval Baby Food GmbH, Mannheim, Germany) dissolved in
128 water. Rewards at flowers consisted always of 30 μ L nectar (15% w/w sugar concentration, sucrose: fructose
129 1:2). Before the experimental schedule started, individuals were allowed to familiarize themselves with the
130 set-up and the artificial flowers. Since during this training phase the plastic cover was removed, the two
131 flower patches were not spatially separated and every flower visit was rewarded. This phase lasted for one to
132 four nights until each bat visited the flowers regularly. One female of the first mixed group did not visit any
133 artificial flower during the first night and was replaced by another female.

134 During the experiment, the two flower patches were covered and spatially separated (Fig. 1. Experimental
135 nights were divided into two phases. During the first phase of the night only one of the two flower patches was
136 rewarding, and therefore the resources were spatially clumped at a single location. The fixed time interval
137 between rewards at each flower was 60s. During the second phase of the night both patches gave rewards,
138 resources were evenly dispersed across the two patches, and the fixed time interval between two rewards at a
139 flower was increased to 120s. Therefore, the amount of food available per unit time did not change during
140 the whole night; only the spatial distribution of food changed from the clumped resource treatment with one
141 patch rewarding (five flowers) during the first phase of the night to the dispersed resource treatment with two
142 patches rewarding (ten flowers) during the second phase of the night. With this experimental schedule,
143 the maximal amount of nectar the bats could collect was 108mL, which corresponds to 18mL nectar per
144 individual per night, roughly 150% of their daily requirement (Winter and Helversen 2001). The side of
145 the rewarding patch during the first phase of the night was chosen pseudo-randomly and the same patch
146 was never chosen in more than two consecutive nights. For the mixed groups, the duration of the clumped
147 resource treatment was six hours and the experiment lasted nine nights (seven nights for the first mixed
148 group). For the same-sex groups, the duration of the first part of the night was variable (range = 4-8h, mean
149 = 6h) and the experiment lasted eight nights for the male group and seven nights for the female groups.

150 **(d) Chasing behavior**

151 We took the frequency of individuals chasing each other at the artificial flowers as an indicator of the intensity
152 of aggressive interactions between group members. We developed a method to automatically detect and score
153 chasing events using the computer-collected animal identification data from the RFID sensors and flower
154 sensors. In a previous pilot study (Wintergerst 2018), three mixed groups of bats were video recorded for 24h
155 over 14 nights, and the video data were synchronized to the computer-collected data. During this pilot study
156 flowers were not covered by plastic sheets so that all flowers and the surrounding room were visible on video.
157 From the analysis of the combined data we were able to identify the following pattern of visitation events
158 that reliably indicated a chasing event between two identified individuals: (i) an identified bat visited a
159 flower and (ii) its visit was instantaneously followed by the detection of a second bat, the chaser, that was
160 detected very briefly (<200ms) and only by the ID sensor (detection range 5-7cm). Importantly, this second
161 bat never attempted to drink and therefore did not insert its nose into the artificial flower and interrupt the
162 light barrier inside the flower head. This distinguished such a chase from the occasional quick succession
163 of two feeding visits by two bats at the same flower. This automated detection of chasing events not only
164 saves considerable time for the experimenter, but also avoids human observer bias, a common drawback in
165 video analysis. For the 24 hours of combined video data and automatically logged data, all 89 chasing events
166 detected in the computer-logged data were confirmed by video (Wintergerst 2018). Therefore, we consider
167 the algorithm for detecting chasing events in the logged data to be highly reliable. Of course, chases did
168 not only occur at the artificial flowers. Thus, our chase numbers are only an indicator of chasing intensity
169 between pairs of bats. For example, in one hour of video we observed 61 chasing events, but only five of
170 those occurred during flower visits and were also automatically detected. However, since with our algorithm
171 (see below) we detected a total of 2597 chasing events (35.8 ± 16.6 events per night during the experiment

172 and only 4.1 ± 2.8 during the training nights, mean \pm SD) for the 36 participating bats, we considered the
173 automated approach adequate for quantifying within-group dominance relationships. The total number of
174 individual detections per night constrains the number of chasing opportunities detectable with our method.
175 Therefore, we calculated a *chase score* and a *chased score* by dividing the number of observed chases (directed
176 to others or received from others, respectively) for each bat by the total number of detections for that bat on
177 each night.

178

179 (e) Statistical analysis

180 To investigate the difference in chasing behavior between males and females and between the resource
181 treatments (one versus two rewarding patches) a Bayesian generalized linear mixed model (MCMCglmm,
182 Hadfield 2010) with a binomial error structure and a parameter expanded prior was used. Body weight as an
183 approximation of size and the full interaction between resource treatment and sex were included as fixed
184 effects and the influence of these fixed effects on the proportion of chasing events was assessed. Experimental
185 group and individual were included as random effects. The same model structure was used to address the
186 question whether the proportion of visits on which the visitor was chased was influenced by these independent
187 variables. If one or more individuals start to defend flowers and thus exclude others from drinking, nectar
188 consumption should increasingly differ between individuals since the successful chaser should gain a higher
189 nectar intake thus reducing the intake of the chased individuals. Therefore, the between-individual difference
190 in nectar consumption over the course of the experiment was compared between experimental groups and
191 resource treatments (clumped vs. dispersed). First, each individual's total nectar consumption standardized
192 by the number of hours of foraging during the clumped (one rewarding patch) and dispersed (two rewarding
193 patches) resource treatment was determined for each experimental night. Then these data were used to
194 calculate group standard deviations, separately for the males and females of each group. In order to assess
195 the influence of resource defense on the individual differences in nectar consumption (standard deviation
196 of nectar intake) we fit a MCMCglmm model with a Gaussian error structure and the following fixed effects:
197 sex, experimental night (centered), and resource treatment (clumped or dispersed), as well as all two-way
198 interactions. Again, we included group and individual as random effects.

199 By plotting individual nectar consumption during the last two nights of the experiment against the chase
200 scores, two non-overlapping groups of males were obtained, which were labeled dominant and subordinate
201 males, respectively. Such a clear pattern was not observed in females. The identification of dominant
202 individuals was also supported by calculating the individual Glicko ratings (Glickman 1999; So et al. 2015)
203 from all chasing events over the last two experimental nights in each group. In the Glicko Rating algorithm
204 individuals gain or lose ranking points based on their wins or losses and the rating of their opponent (Glickman
205 1999; So et al. 2015). Glicko ratings were analyzed using the `PlayerRatings` package in R (Stephenson and
206 Sonas 2020). Based on nectar consumption, the frequency of chasing events and the individual Glicko group
207 ranks (from 1 to 6, with 1 corresponding to the highest Glicko rating), each group contained individuals
208 belonging to one of three different types of social status: female, dominant male, and subordinate male. To
209 address the question whether nectar consumption varied depending on social status during the early and
210 late stages of the experiment we used Welch's tests and adjusted the p values using the Holms method for
211 multiple comparisons.

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

213 3. Results

214 (a) Behavioral observations

215 The goal of our experiment was to investigate the sex-specific effects of resource defense in *Glossophaga*
216 *mutica*, in addition to the potential influence of interference competition on individual nectar intake. Quali-
217 tative behavioral observations of four hours of video recordings revealed several behaviors that seem to be
218 characteristic for some males, which according to further analyses (see below) we designated as dominant
219 males. Instead of just visiting the flowers and leaving the patch as the other individuals did, dominant males
220 remained hanging between the flowers within the patch for a significant amount of time (Fig. S1). When

221 other individuals came close due to visits of directly adjacent flowers, dominant males often spread one wing
222 in the direction of the other individual which could be interpreted as a threatening posture. Some individuals
223 were attacked and chased away by dominant males while visiting artificial flowers. In this case, dominant
224 males mostly attacked from above with their mouth wide open, and followed the intruder for a short distance.
225 Sometimes the chasing escalated into fighting with both bats tumbling towards the ground and resuming
226 their flight only shortly above the floor. In rare cases, these fights might have led to small injuries. One
227 subordinate male had several fresh scratches on its wing that were not present before the experiment and
228 that were possibly caused by bites (Fig. S2). After a successful flower defense, the dominant male normally
229 visited most of the five flowers within the patch before returning to its hanging position between the flowers.

230 **(b) Example of nectar intake in one experimental group**

231 One of the first striking observation we made was the uneven distribution of nectar consumed between the
232 sexes and individuals. For example, in the first mixed group of bats tested, after only two nights the nectar
233 consumption of two males was nearly reduced to zero, whereas the third male increased its consumption
234 substantially (Fig. 2A). However, this pattern occurred mostly for males during the clumped resource
235 treatment (Fig. @ref(fig: overview)). Nectar consumption of females was rarely as divergent as in males,
236 especially in the mixed groups (Fig. @ref(fig: overview)). Later on the same nights when resources were
237 dispersed over two patches, nectar consumption of males and females generally converged by the end of the
238 experiment (Fig. 2B, Fig. @ref(fig: overview)).

239 **(c) Differences between sexes in frequency of chasing (chase score) and being
240 chased (chased score)**

241 In all mixed groups males chased other bats in front of flowers significantly more often than females did
242 (Fig. 3A, Table 1). Notably, the frequency of females as active chasers in female-only groups was higher
243 than chasing by females in the mixed groups (Fig. 3A). Although the rate of nectar availability remained
244 constant throughout the night and only the spatial distribution of the resources changed, chase frequencies
245 were significantly lower during the dispersed resource treatment when rewards were available at both patches
246 (Table 1). There was no significant difference between the sexes in how often a bat was chased by another
247 individual (Fig. 3B) but individuals were chased less during the dispersed resource treatment (Table 1).
248 Weight as an indicator of size had no significant effect on either the chase score or the chased score (Table 1).

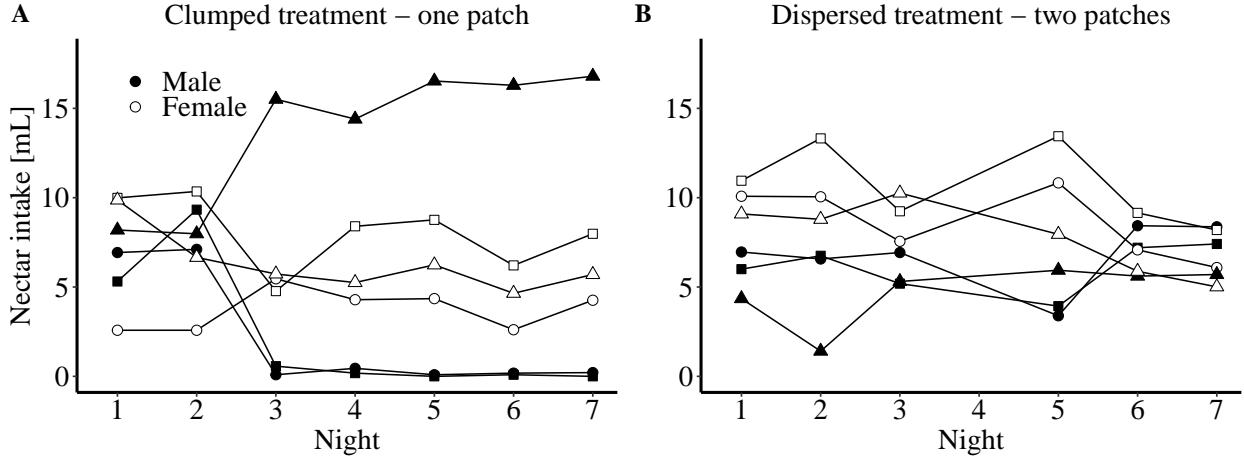


Figure 2: Change of individual nectar consumption from the clumped treatment (A) to the dispersed treatment (B) during an experiment of one mixed group (3 males, 3 females, symbols show different individuals). (A). During the clumped resource treatment (first part of the experimental night) rewards were only available at one patch. The nectar consumption of two subordinate males approached zero after only two nights, whereas the third, dominant, male greatly increased nectar intake during the experiment (males filled symbols). Females (open symbols) on the other hand maintained a stable level of nectar intake. (B) During the dispersed resource treatment (second part of the experimental night) rewards were available at both patches. Under this treatment, individuals nearly equalized their level of nectar intake over the course of the experiment. The second part of night 4 was excluded due to technical problems.

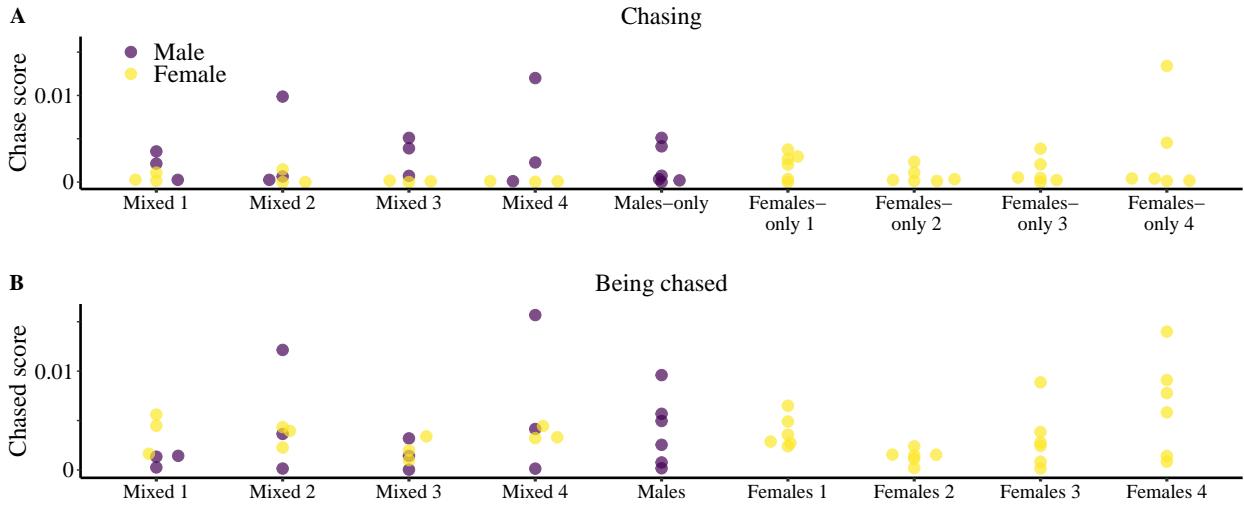


Figure 3: Sexes differed in the frequency of chasing or being chased during the clumped resource treatment. (A) Males (dark symbols) chased others significantly more than females did (light symbols, Table 1). Shown are the individual proportions of chasing events (chase scores) over the whole experiment. Notably, in the females-only groups some females chased more than any female in the mixed groups. (B) Being chased by other bats did not differ significantly between sexes (Table 1).

Table 1: Summary of fixed effects from generalized linear mixed-effects models of chasing frequency and the frequency of being chased.

Model	term	estimate	95% credible interval	pMCMC
Chase score	(Intercept)	-5.20	(-11.54, 0.64)	0.0970
	sex (female)	-1.33	(-2.53 , -0.2)	0.0290
	phase	-0.46	(-0.76 , -0.17)	0.0050
	weight	-0.11	(-0.75, 0.5)	0.7470
	sex (female):phase	-0.06	(-0.46, 0.34)	0.7490
Chased score	(Intercept)	-5.24	(-10.06 , -0.41)	0.0300
	sex (female)	0.72	(-0.12, 1.62)	0.1060
	phase	-0.95	(-1.22 , -0.67)	0.0005
	weight	-0.07	(-0.58, 0.41)	0.7810
	sex (female):phase	-0.11	(-0.44, 0.21)	0.5340

Note: Fixed estimates whose credible intervals do not span zero are shown in bold. pMCMC = posterior probability

249 (d) Differences in nectar intake over time and between sexes and treatments

250 Resource defense should lead to a larger between-individual difference in nectar consumption (Brown 1964).
 251 Differences in nectar consumption were quantified as the standard deviation of nectar intake in each group,
 252 separately for males and females. During the clumped resource treatment, the standard deviation was higher
 253 for males than for females (Table 2, Fig. S24) and increased significantly over time for males but not for
 254 females (Table 2, Fig. S24). For females in the clumped resource treatment the increase in standard deviation
 255 was significantly smaller than in males (significant interaction between sex and night, Table 2), and was not
 256 itself significant (estimate = 0.02, 95% CI = 0, 0.06). Compared to the clumped resource treatment, in the
 257 dispersed resource treatment the effect of experimental night was significantly lower for males (interaction
 258 between treatment and night, Table 2), but not for females (estimate = 0, 95% CI = -0.02, 0.02). Moreover,
 259 in the dispersed resource treatment there was no significant increase in standard deviation over the course of
 260 the experiment in males (estimate = 0.02, 95% CI = -0.01, 0.05) nor in females (estimate = 0.03, 95% CI =
 261 0, 0.06). Overall, for both males (significant effect of treatment) and females (estimate = -0.11, 95% CI =
 262 -0.16, -0.06) the standard deviations were generally higher in the clumped than in the dispersed resource
 263 treatments.

Table 2: Summary of fixed effects from a generalized linear mixed-effects model of the standard deviation of nectar intake over time.

term	estimate	95% credible interval	pMCMC
(Intercept)	0.55	(0.45, 0.65)	0.000
sex (female)	-0.17	(-0.24, -0.12)	0.000
treatment (dispersed)	-0.22	(-0.28, -0.16)	0.000
night	0.06	(0.03, 0.1)	0.001
sex (female):treatment (dispersed)	0.11	(0.04, 0.19)	0.004
sex (female):night	-0.03	(-0.06, -0.01)	0.007
treatment (dispersed):night	-0.04	(-0.07, -0.02)	0.001
sex (female):treatment (dispersed):night	0.05	(0.01, 0.08)	0.006

Note: Fixed estimates whose credible intervals do not span zero are shown in bold. pMCMC = posterior probability

264 (e) Social status and its effects on nectar intake

265 When plotting chasing events against nectar consumption the data for males fell into two non-overlapping
 266 groups. The males of one cluster (Fig. 4A, inside dashed oval) chased other individuals and consumed more
 267 nectar than the other males. This cluster included only one male from each of the four mixed groups but
 268 two males from the single males-only group. These six males were categorized as “dominant”. The second
 269 cluster of males (Fig. 4A, outside and below dashed oval) was characterized by a low frequency of chasing
 270 and low nectar consumption. These males were categorized as “subordinate”. In females such a pattern
 271 did not emerge (Fig. 4B). This classification was also supported by the highest social dominance scores as
 272 estimated by Glicko ratings in each group (Figs. S25, S26) and the observation that there was generally an
 273 inverse relationship between the frequency of chasing and the frequency of being chased (Fig. S27). While in
 274 the females-only groups some females chased other females more frequently, only three of these females (one
 275 in group 1 and two in group 4) would be classified as dominant using the same cut-off criteria we used for the
 276 males (Fig. 4B). While in females-only group 4 the two females were the individuals with the highest Glicko
 277 ratings, in females-only group 1 the female with the highest nectar consumption and chase score did not have
 278 the highest Glicko rating (Figs. S25, S26). During the last two nights of the experiment in the clumped
 279 resource treatment, the highest nectar intake was observed in dominant males, with an intermediate intake
 280 in females, and lowest nectar intake in subordinate males (Fig. 5). In contrast, in the dispersed resource
 281 treatment there were no detectable differences between the nectar intake of dominant and subordinate males
 282 at any stage of the experiment (Fig. 5), while the subordinate males had a significantly lower nectar intake
 283 than females in the first two, but not in the last two experimental nights (Fig. 5). Finally, the subordinate
 284 males increased their nectar intake from the clumped to the dispersed treatment, but the difference was
 285 only significant for the last two experimental nights (Fig. 5). While there was a correspondent decrease in
 286 the nectar intake of dominant males, it was not significant, most likely due to the small sample size ($n = 6$,
 287 Fig. 5). In females there were no significant differences in nectar intake from the clumped to the dispersed
 288 resource treatment at any stage of the experiment (Fig. 5)

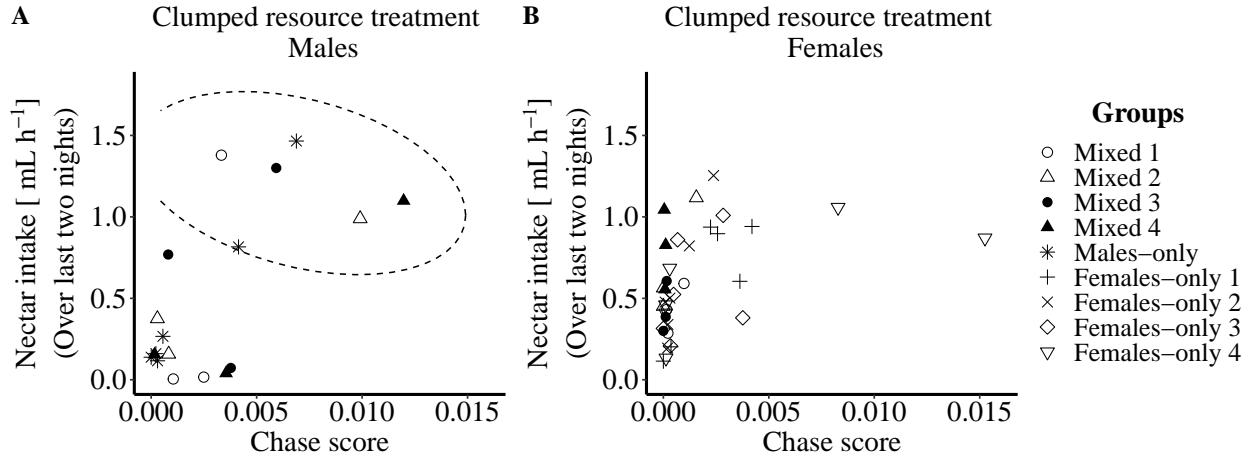


Figure 4: Influence of chasing frequency (chase score) on nectar intake in the clumped resource treatment during the last two nights of the experiment. (A) Males that more often chased other males also consumed more nectar. Males were divided into two non-overlapping groups by considering the chasing frequency and the amount of nectar an individual received during the clumped resource treatment at the end of the experiment. Dominant males (inside dashed line oval) met two criteria: they chased other individuals at flowers more frequently (>0.003) and received more nectar ($>0.75mL\ h^{-1}$) during the clumped resource treatment. Individuals outside the dashed line oval were categorized as subordinate males. (B) Nectar consumption of females did not generally depend on the chase score during the clumped resource treatment and non-overlapping groups did not emerge.

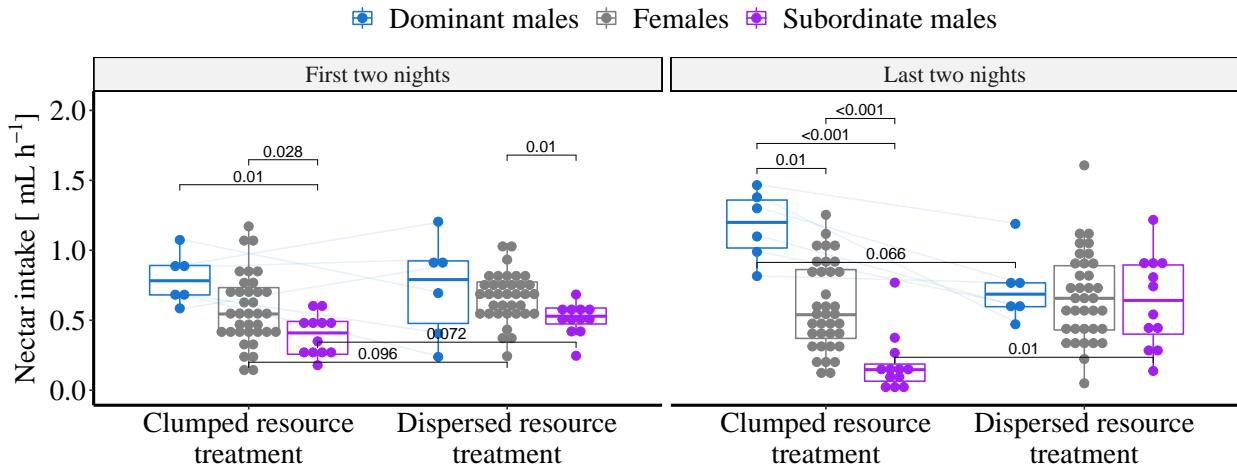


Figure 5: Comparison of nectar intake during the first and last two nights of the experiment depending on sex and social status. During the clumped resource distribution (left in each panel), already at the beginning of the experiment (left panel) subordinate males collected significantly less nectar than dominant males and females. At the end of the experiment (right panel), females, dominant and subordinate males differed in their nectar consumption, but only during the clumped and not during the dispersed treatment. During the dispersed resource treatment at the beginning of the experiment subordinate males received less nectar than females, but this difference disappeared by the end of the experiment. Numbers above brackets are the p values from unequal variance T tests (Welch's tests), adjusted for multiple comparisons using the Holms method. Contrasts between treatments were from paired Welch's tests. For clarity, only p values smaller than 0.1 are shown. Each status group represents data from the same individuals. For clarity, only the lines connecting the same dominant males are shown.

289 4. Discussion

290 Similar to observations in free-living *Glossophaga* populations (Lemke 1984; Tschapka 2003), in this experiment
 291 *G. mutica* competed for nectar not only by exploitation but also by interference competition. However, the
 292 results show that the predisposition to defend resources and the influence of interference competition on
 293 individual nectar intake differed significantly between the sexes. Only a subset of individuals, most notably
 294 males in the mixed-sex groups, successfully defended flower patches. Dominant individuals were characterized
 295 by the highest frequency of chasing other individuals away from profitable flowers (chase scores), by the
 296 highest Glicko ratings, and by a substantial increase in nectar intake during the time periods of active defense
 297 by the end of the experimental run. Although the dominant males in the mixed groups chased females and
 298 other males about equally often, only the nectar intake of subordinate males but not of the females was
 299 affected by this behavior. Thus, male-initiated interference competition increased the difference in nectar
 300 intake between males but did not affect females. The frequency of aggressive interactions was higher, and
 301 males only defended resources successfully when the available nectar was concentrated at only one flower
 302 patch. This supports the hypothesis that clumped resources favor an increase in aggressive interactions
 303 (Grant 1993).

304 (a) Sex-dependent resource defense and its differential effect on nectar intake, 305 depending on social status

306 To our knowledge, this study is the first report of sex-dependent differences in resource defense behavior of
 307 neotropical nectar-feeding bats. In mixed sex groups, females seemed to be much less affected by the behavior
 308 of dominant males whereas subordinate males were excluded at least partially from the defended flower patch.

309 This finding is consistent with observations of free-flying *G. commissarisi*, in which males visited on average
310 a smaller number of artificial flowers than females did (Nachev and Winter 2019), presumably because of
311 interactions with other males. There are two possible explanations for this differential effect on subordinate
312 males and females. On the one hand, dominant males might just not be capable of excluding females. On
313 the other hand, dominant males could tolerate females in their defended patch because they might receive
314 additional benefits, for example tolerating females could lead to an increase in (future) mating opportunities.
315 Similar social dynamics have been described in the insectivorous bat species *Myotis daubentonii* (Senior,
316 Butlin, and Altringham 2005). Dominant males of this species temporarily exclude other males from profitable
317 habitats whereas females are tolerated and in addition to securing access to resources, the successful exclusion
318 of other males has been shown to increase the reproductive success of dominant males (Senior, Butlin, and
319 Altringham 2005). Similarly, it has been observed that male purple-throated carib hummingbirds (*Eulampis*
320 *jugularis*), which successfully defend highly profitable feeding-territories against other males while sharing the
321 available resources with females, experienced an increase in their mating success (Temeles and Kress 2010).
322 However, in our experiment dominant males chased females about as often or slightly more often as they
323 chased subordinate males (Table 1, Fig. S22). If females were able to feed in the defended patch because
324 dominant males tolerated them due to potential additional benefits, it could be that the detected chasing
325 events by dominant males differed in quality depending on the sex of the intruder. This was not further
326 quantified in the current study but could potentially be investigated using audio recordings (Knörnschild,
327 Glöckner, and Helversen 2010). We extracted the frequency of chasing events from data automatically
328 recorded at artificial flowers (successive detection of two different IDs while and after the first was feeding at
329 the flower). Therefore, it was not possible to determine if males showed behavioral differences when chasing
330 other males in comparison to chasing females. The recorded video revealed that individuals chased each
331 other not only directly at the artificial flowers but also in other areas of the flower patch. Since individuals
332 could only be identified by their ID tags directly at the ID reader attached to artificial flowers the sex of
333 individuals chasing each other in other areas of the experimental room remained unknown. However, after
334 the experiment some subordinate individuals showed marks from small injuries at their wings (see example
335 in Fig. S2) and such marks were only observed in males. This could be an indication that dominant males
336 directed more aggression (biting) towards subordinate males than towards females. Such sexual dimorphism
337 in aggressive resource defense is also known from other nectar-feeding vertebrates, like hummingbirds. The
338 beaks of the males of some territorial hummingbirds seem to be specifically adapted as intrasexually selected
339 weapons (Rico-Guevara et al. 2019).

340 (b) Some observations from the single-sex groups

341 Generally, females showed lower chasing frequencies, but, surprisingly, some females in the females-only
342 group showed an increased nectar consumption and chasing frequency, compared to the females in the mixed
343 groups (Figs. 4B, S25, S26). This observation prompted us to contrast the behavior of females in the two
344 different group types (single-sex versus mixed-sex). Females in the single-sex groups had higher chase scores
345 compared to females in mixed groups (Table S1). In single-sex groups, but not in mixed groups there was a
346 higher frequency of chases in the clumped than in the dispersed resource treatment (Table S1). The chased
347 score was only affected by treatment but not by group type and was higher in the clumped than in the
348 dispersed resource treatment (Table S1). Over the course of the experiment, the standard deviations in
349 nectar intake increased for females in the single-sex, but not in the mixed groups (Table S2). This increase
350 was only significant in the clumped, but not in the dispersed resource treatment (Table S2). The standard
351 deviations were higher in the single-sex groups than in the mixed groups, both in the clumped (group type
352 effect in Table S2) and in the dispersed resource treatments (estimate = -0.06, 95% CI = -0.12, -0.01). Thus,
353 it appears that in the absence of male individuals, some females exerted dominant behavior over the other
354 females, similar to males. These findings are similar to the social structure of resource defense found in some
355 nectar-feeding bird species. For example, in free-living ruby-throated hummingbirds females also have lower
356 levels of defense (Rousseau, Charette, and Bélisle 2014). Moreover, although both male and female *Eulampis*
357 *jugularis* hummingbirds defend feeding territories during the non-breeding season, males are always dominant
358 over females (Wolf and Hainsworth 1971; Temeles, Goldman, and Kudla 2005). It would be interesting to
359 better understand why females were less affected by the aggressive resource defense behavior of dominant
360 males compared to subordinate males and why females themselves did not consistently monopolize the

361 profitable patch against other females, not even in the females-only groups. One possibility is that females do
362 not need to defend flowers when a dominant male is already reducing the number of flower visitors and thus
363 increasing the amount of food available.

364 In all mixed sex groups, only one male per group became dominant and successfully defended flowers, whereas
365 in the males-only group two males exhibited dominant behavior (Fig. 4A). A closer look at the nectar
366 consumption at each flower revealed that on the last night of the experiment these two males had nearly
367 monopolized different flowers within the same patch rather than sharing access to the same flowers (Fig.
368 S28). Such flower or patch partitioning was also observed in the females-only groups (Figs. S33-S36), but
369 rarely seen in the mixed groups (Figs. S29-S32). The successful resource defense by two individuals in the
370 male-only group showed that resource defense can occur independent of the presence of females, but, this was
371 only based on a single observation.

372 (c) Social status and social hierarchy

373 Although the position of the rewarding patch during the clumped resource treatment changed between the
374 nights between the left and right, usually the same male continued to successfully defend the patch, especially
375 in the mixed-sex groups (Figs. S28-S32). This means that males defended the resources themselves and not a
376 particular location. Furthermore, this shows that even after changing the location of the defended patch
377 the same individuals were usually able to succeed in re-establishing their dominance against other males,
378 indicating a stable hierarchy at least for the duration of the experiment. The flower utilization pattern in
379 females-only groups was not as consistent (Figs. S33-S36).

380 The ability of an individual to successfully defend and monopolize resources is often correlated with distinct
381 physical characteristics such as body size (Searcy 1979). However, in our results weight as an approximation
382 of size did not correlate significantly with the chase score of individuals (Table 1) and therefore did not
383 predict which male succeeded in defending a flower patch. Another factor that could influence the success
384 in defending flowers is age and therefore experience (Arcese 1987; Yasukawa 1979). Since we could only
385 discriminate between young and adult animals, we cannot dismiss age and experience as a predictor of
386 successful flower defense.

387 In this study, subordinate males received considerably less nectar than dominant males and females (Fig. 5).
388 However, except in mixed group 1, subordinate males were rarely completely excluded from the flower patch
389 and their average nectar intake during the clumped resource treatment was still $0.3 \pm 0.18 \text{ mL h}^{-1}$ (mean \pm
390 SD). This result is in accordance with observations of free-living *G. soricina* in Colombia. There, subordinate
391 bats exploited the flowers defended by other individuals as soon as the dominant bat temporarily ceased
392 defending (Lemke 1984). Furthermore, in our study the frequency of chasing events decreased significantly
393 during the dispersed resource treatment in the second part of the night (Table 1). This supports the theoretical
394 prediction that aggressive defense behavior increases when resources are spatially concentrated (Grant and
395 Guha 1993). However, since the sequence of treatments was not controlled in this experiment, other factors
396 (e.g., time) cannot be ruled out. With the current data we cannot answer whether the dominant males would
397 successfully defend a patch if the treatment changed from dispersed to clumped, but we believe this is a
398 different question that should be addressed separately. Resource defense should only occur when the energy
399 gain outweighs the cost of aggressive interactions (Brown 1964). Thus, our results could be explained by the
400 decrease in quality of the defended patch once its nectar supply rate dropped to half. This is also supported
401 by the very low number of chases observed during training when the flowers gave unrestricted rewards and
402 were not separated in discrete patches. Together, these results suggest that along the different degrees of
403 territorial behavior, resource defense observed in *Glossophaga* seems to represent a transient monopolization
404 of resources instead of a longer-term permanent exclusion of intruders.

405 (d) Conclusion

406 Although flower defense behavior of *G. mutica* was investigated in a laboratory setting, we observed similar
407 behavior as described in free-living *Glossophaga* populations. Our results revealed a sexual dimorphism in
408 flower defense behavior in mixed-sex groups. Only males successfully defended flower patches and excluded
409 other males from their defended resource, whereas females remained unaffected by this male behavior and
410 continued to visit the flowers guarded by a male. In the absence of males females also defended flowers,

⁴¹¹ but not as consistently as males. This observed pattern is similar to resource defense behavior observed in
⁴¹² other nectar-feeding vertebrates. Furthermore, we could show that the frequency of aggressive interactions
⁴¹³ was, as predicted, higher when resources were clumped in one patch and transient. Future studies with
⁴¹⁴ free-living populations have to be conducted to assess how frequent and important resource defense in these
⁴¹⁵ nectar-feeding bats is and if males that are successful in defending resources have additional fitness advantages.

416 **Supplementary material**

417 **Video analysis**

418 There were 89 chase occurrences observed (f->f 4 times, f->m 2 times, m->f 59 times, m->m 24 times).
419 Every time the algorithm marked an event as a chase event, there were two individuals following each other.
420 Some chase sequences did not get detected. The individual that chased never drank immediately after the
421 chase at the same flower location where the chase occurred. There were 16 incidences that were difficult to
422 classify by observation or did not appear to be aggressive interactions.

423

424 f->f appear to be less aggressive

425 f->m appear aggressive

426 m->f appear aggressive

427 m->m appear aggressive

428

429 **Supplementary figures**

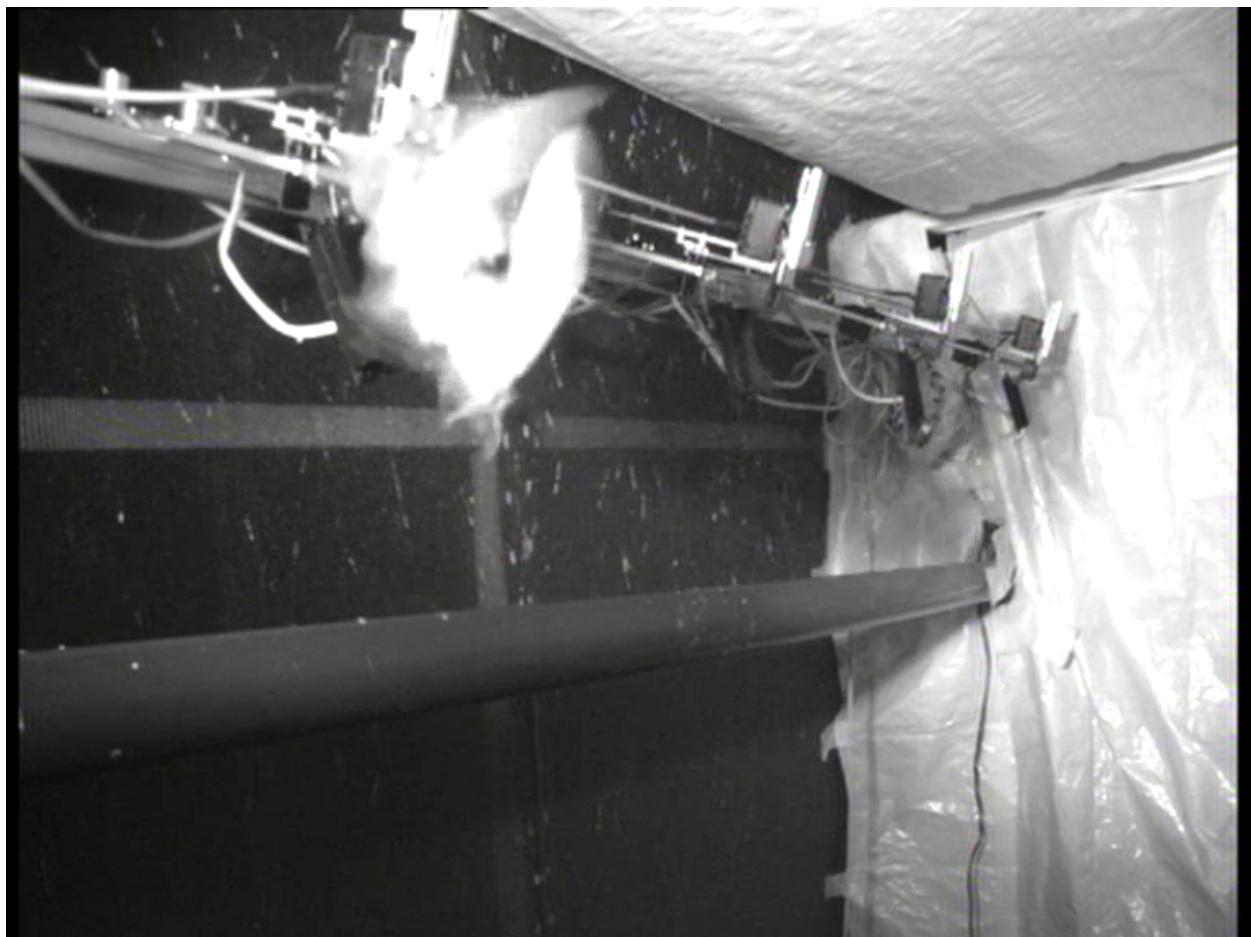


Figure S1: Video of the dominant male in mixed group 3 chasing all bats approaching the rewarding flowers in the rewarding patch during the clumped resource treatment.

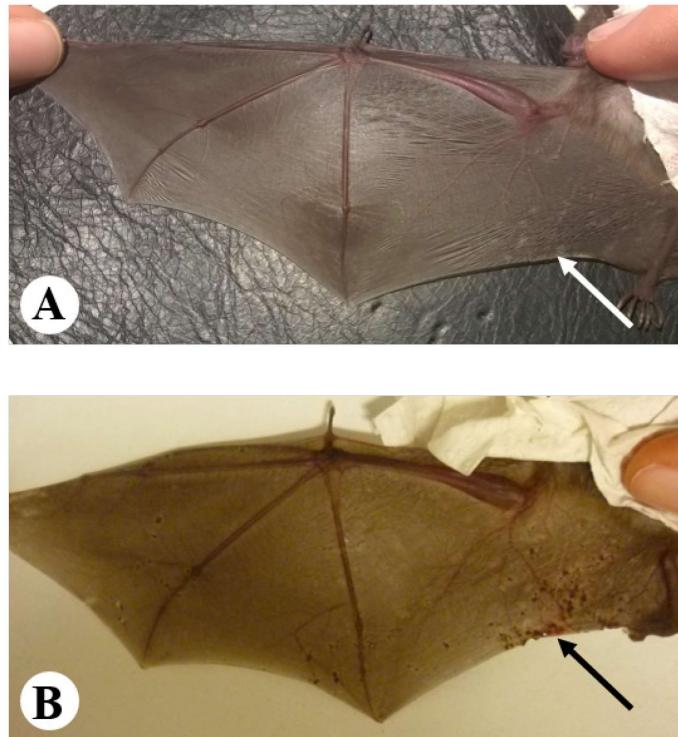


Figure S2: Wing images of a subordinate male from mixed group 4. The same individual was photographed before (**A**) and after the experiment (**B**). The black arrow points to the scarred location due to wing injuries, purportedly caused by the dominant male.

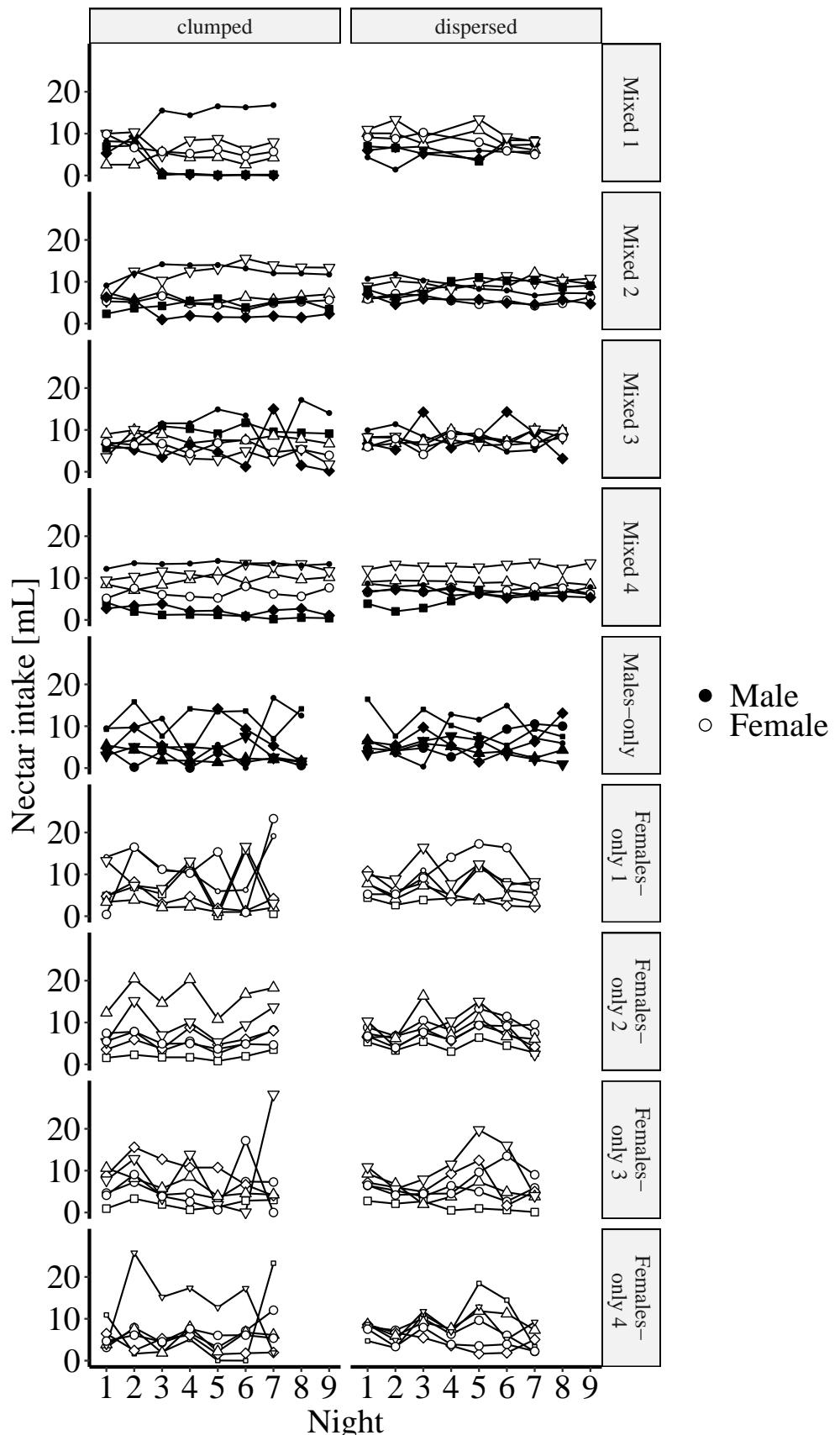


Figure S3: Change of individual nectar consumption from the clumped treatment (left) to the dispersed treatment (right) for all experimental groups (rows). $^{18}\text{Males}$ are shown with filled symbols and females with open symbols. Small symbols indicate dominant individuals, according to proportion of chasing and nectar intake during the last two nights of the experiment.

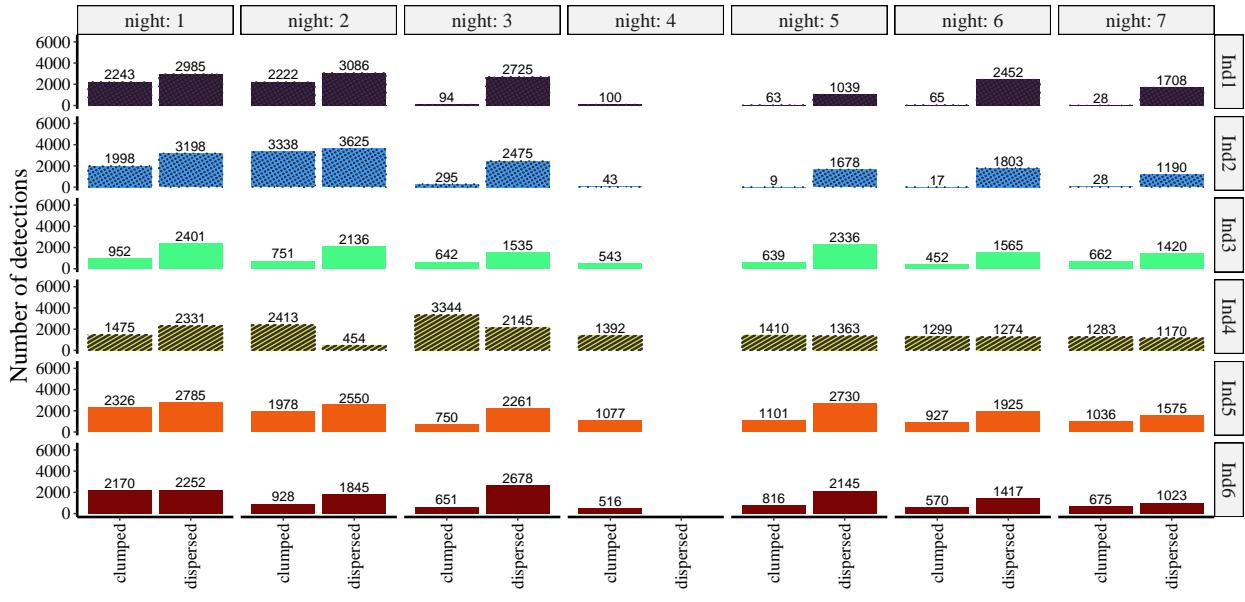


Figure S4: Raw number of detections for all bats in mixed group 1. Dotted bars represent subordinate males, striped bars represent dominant males and unhatched bars - females.

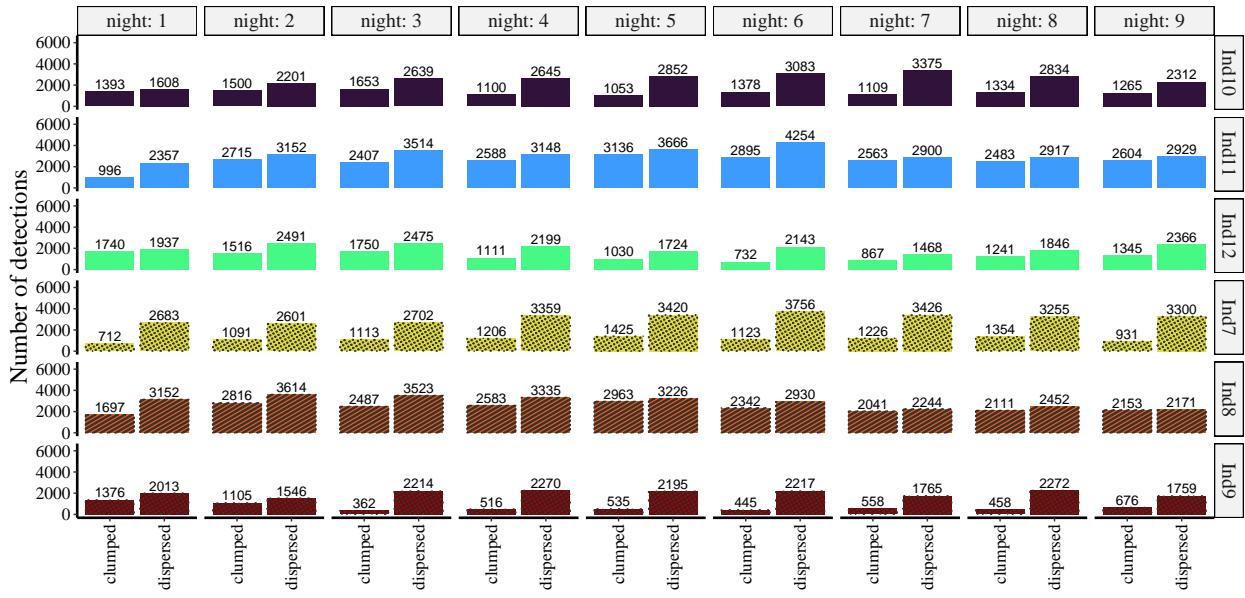


Figure S5: Raw number of detections for all bats in mixed group 2. Same notation as in Fig. S4, but the colors correspond to different individuals.

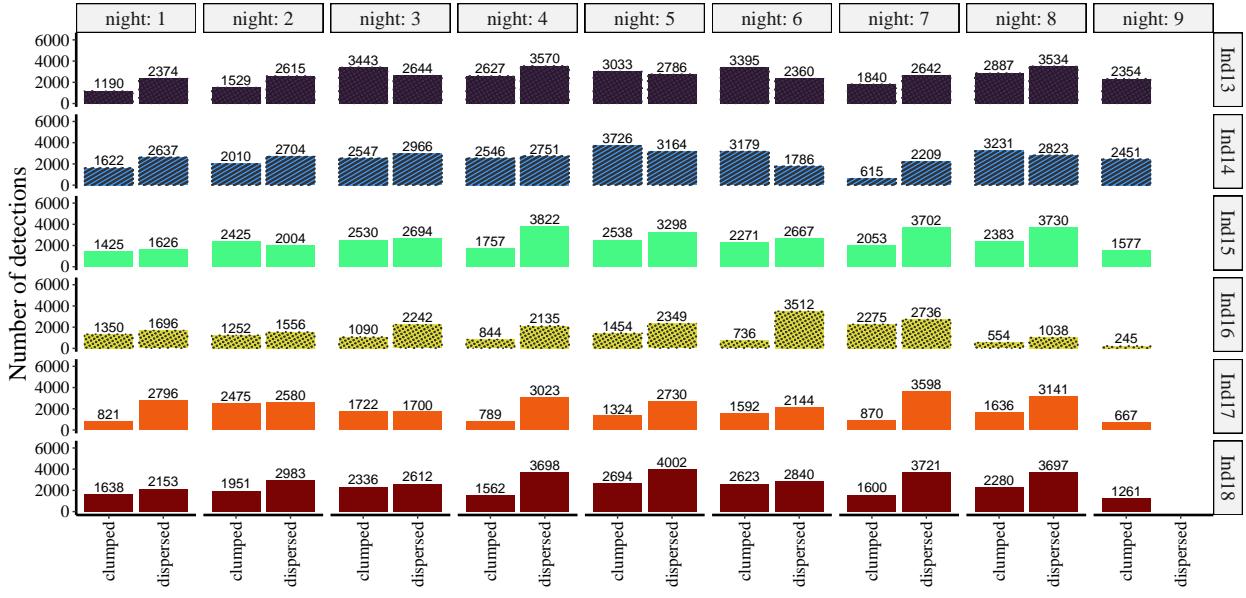


Figure S6: Raw number of detections for all bats in mixed group 3. Same notation as in Fig. S4, but the colors correspond to different individuals.

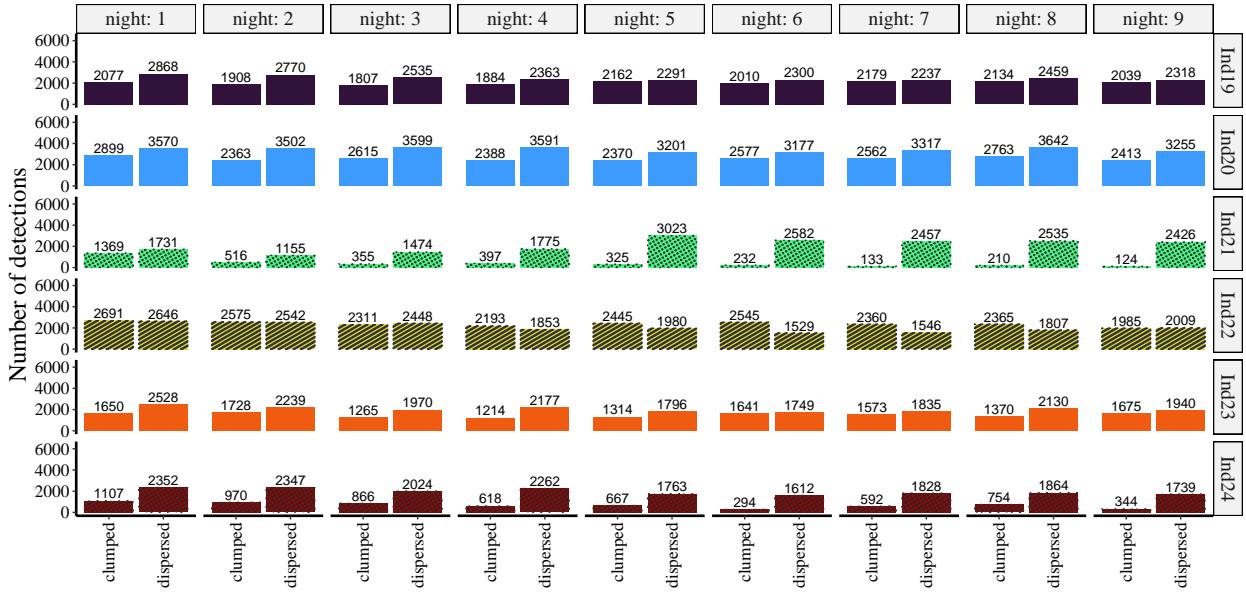


Figure S7: Raw number of detections for all bats in mixed group 4. Same notation as in Fig. S4, but the colors correspond to different individuals.

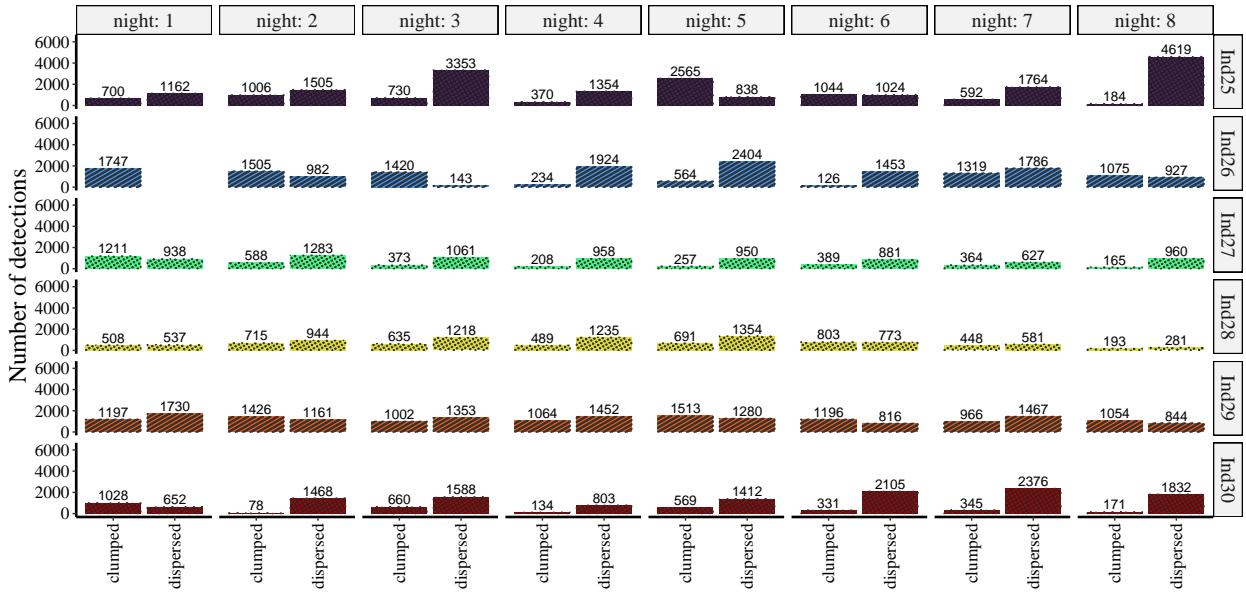


Figure S8: Raw number of detections for all bats in males-only group. Same notation as in Fig. S4, but the colors correspond to different individuals.

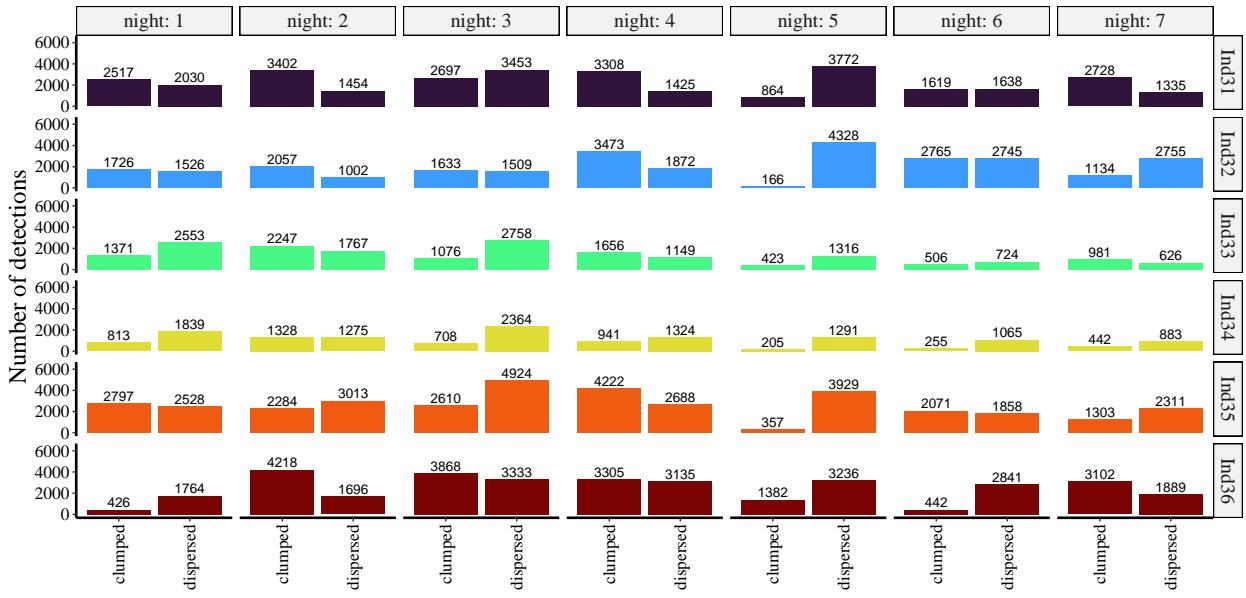


Figure S9: Raw number of detections for all bats in females-only group 1.

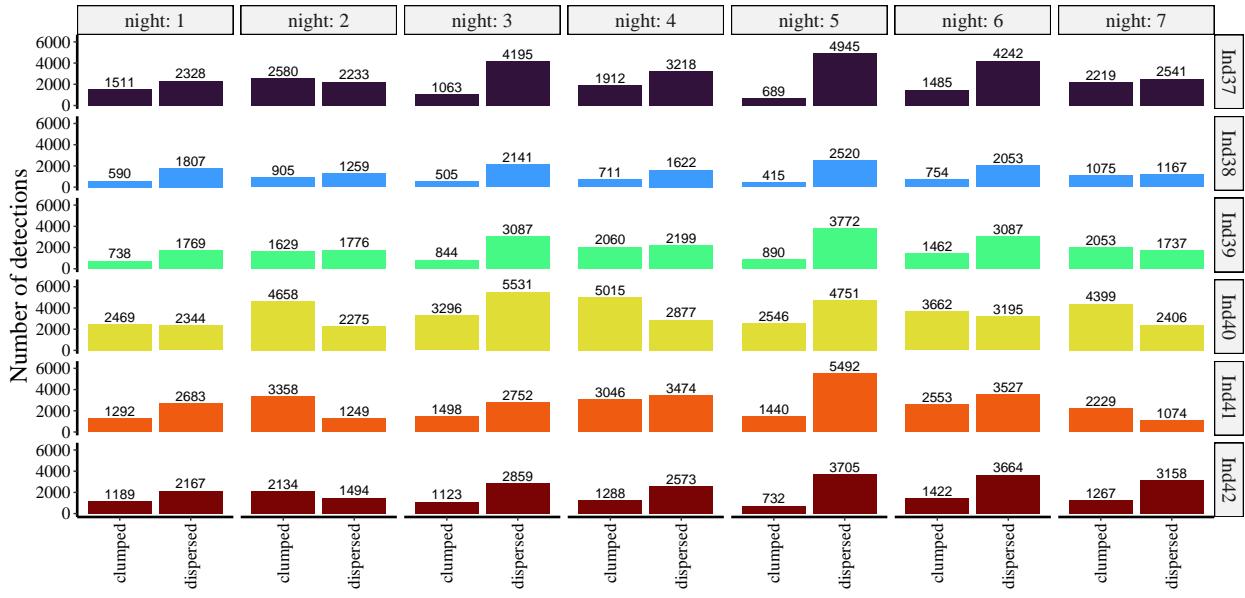


Figure S10: Raw number of detections for all bats in females-only group 2.

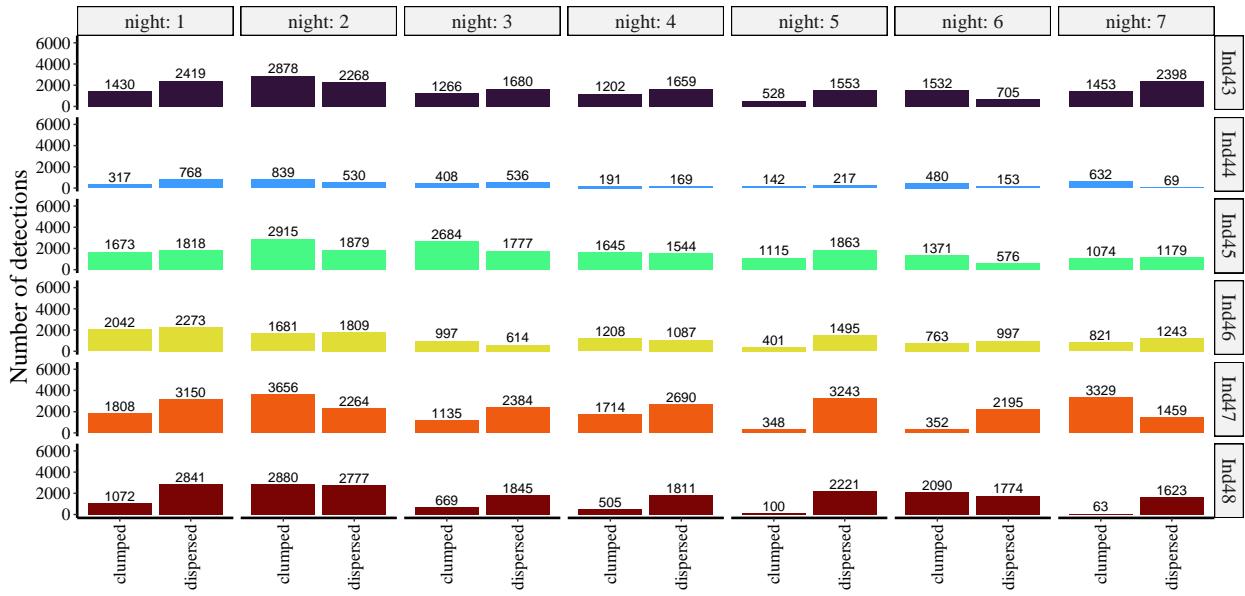


Figure S11: Raw number of detections for all bats in females-only group 3.

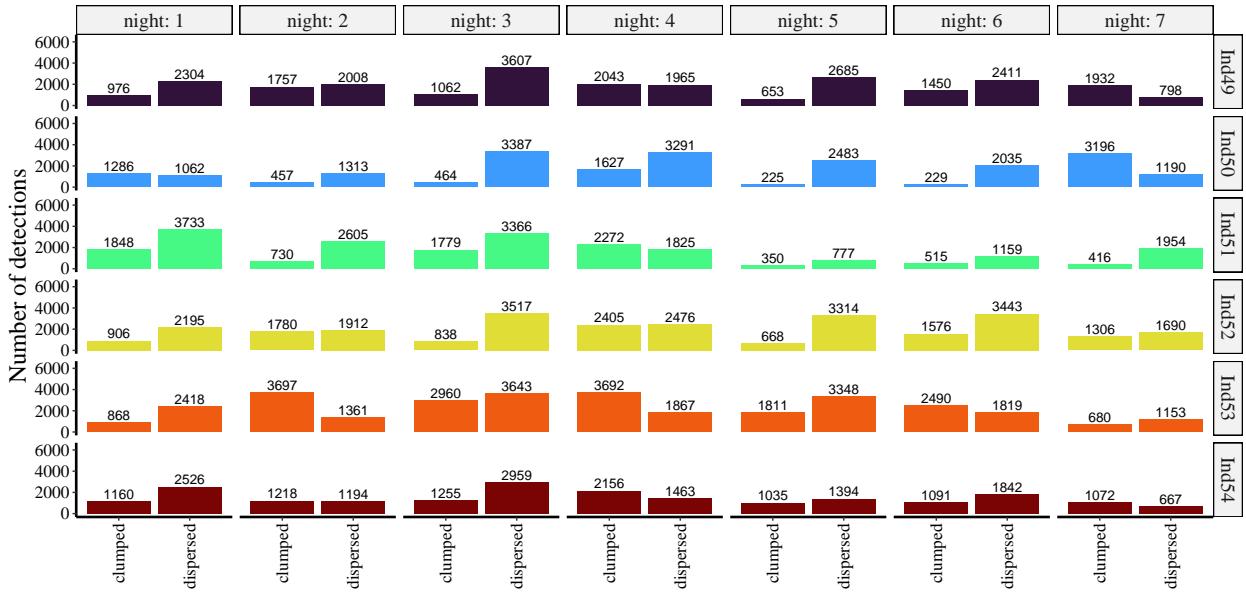


Figure S12: Raw number of detections for all bats in females-only group 4.

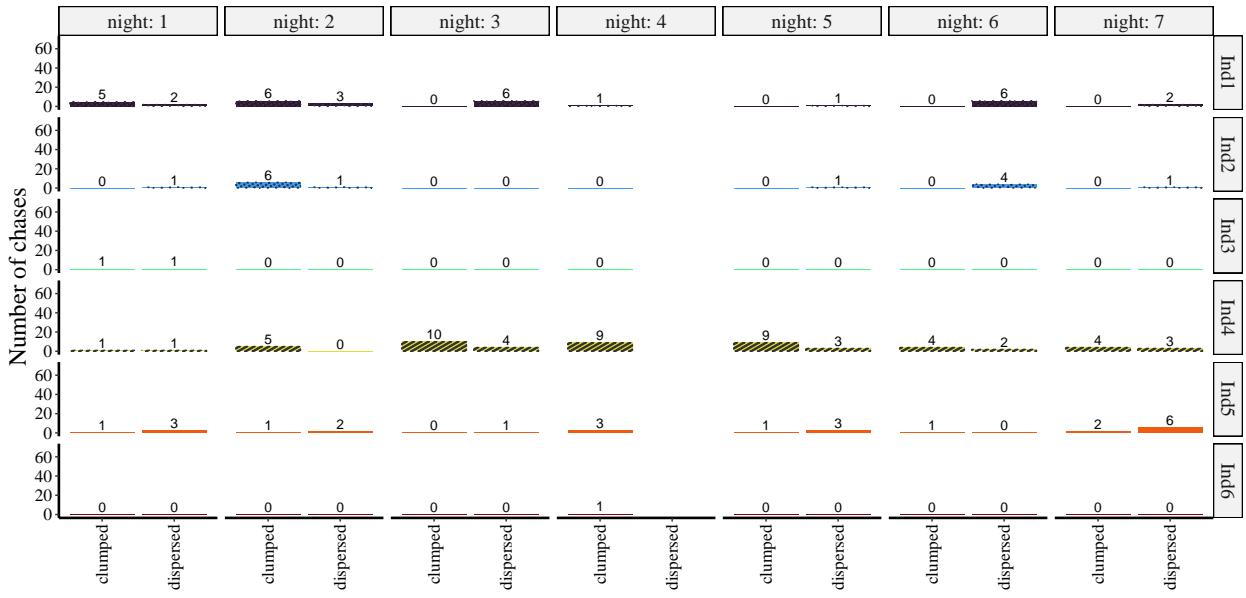


Figure S13: Raw number of chase events for all bats in mixed group 1. Same notation as in Fig. S4, but the colors correspond to different individuals.

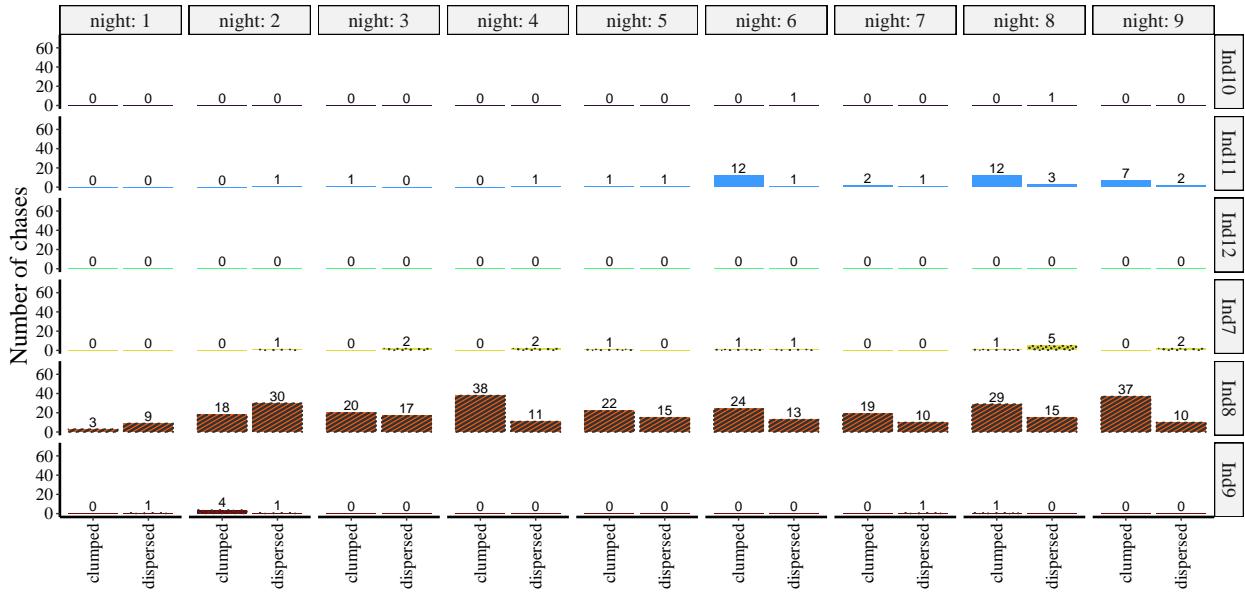


Figure S14: Raw number of chase events for all bats in mixed group 2. Same notation as in Fig. S4, but the colors correspond to different individuals.

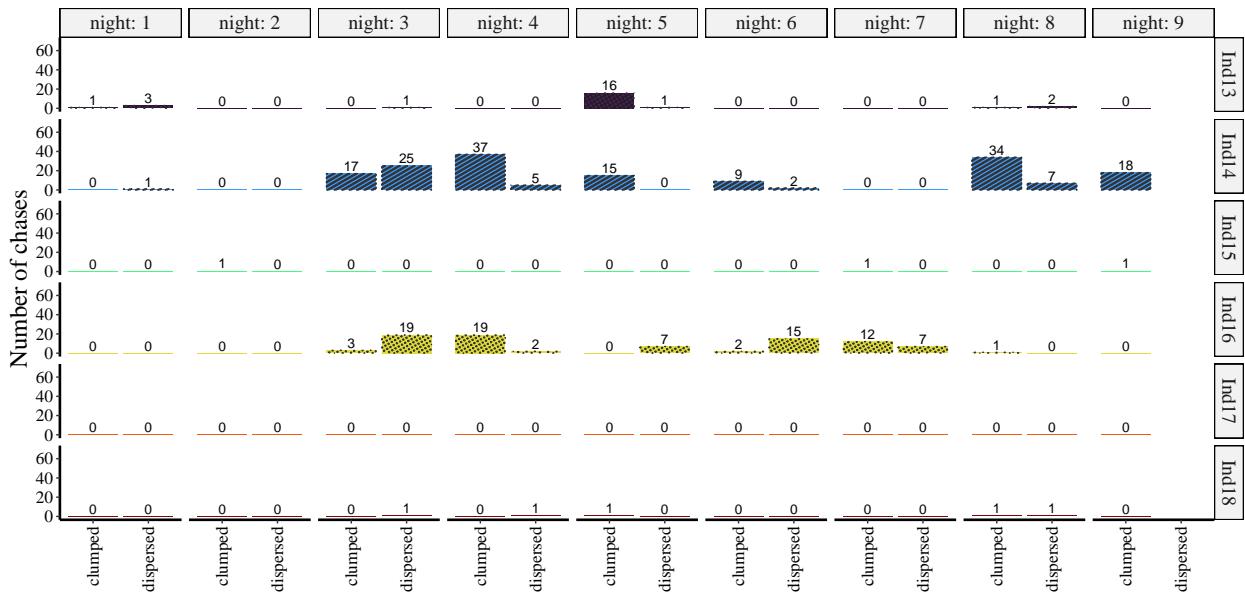


Figure S15: Raw number of chase events for all bats in mixed group 3. Same notation as in Fig. S4, but the colors correspond to different individuals.

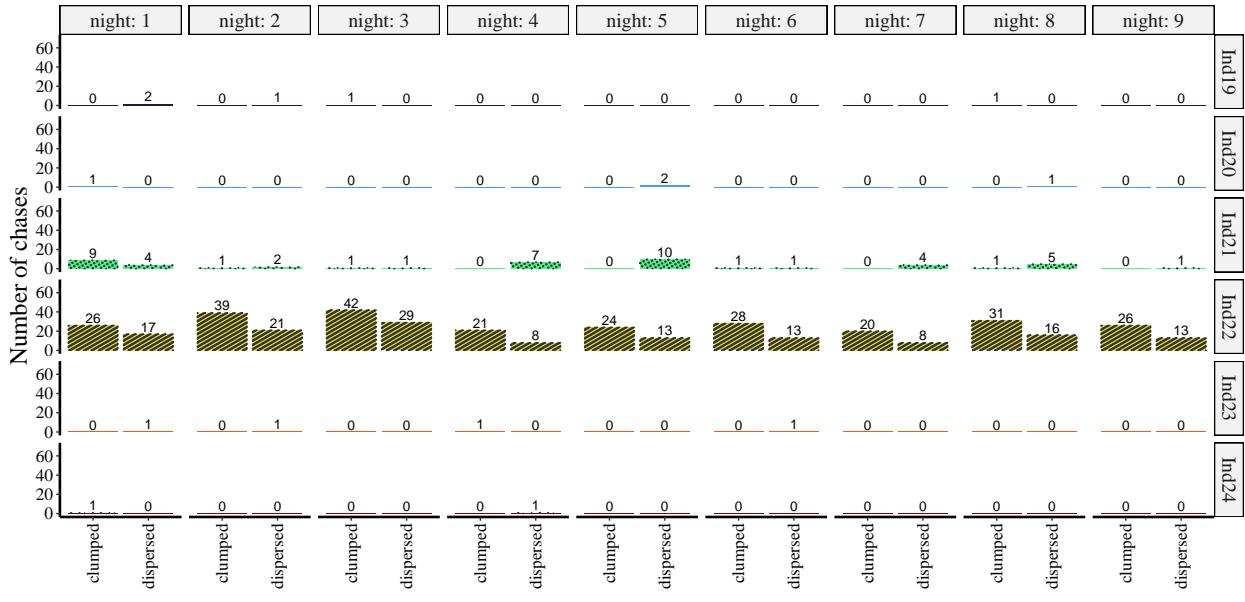


Figure S16: Raw number of chase events for all bats in mixed group 4. Same notation as in Fig. S4, but the colors correspond to different individuals.

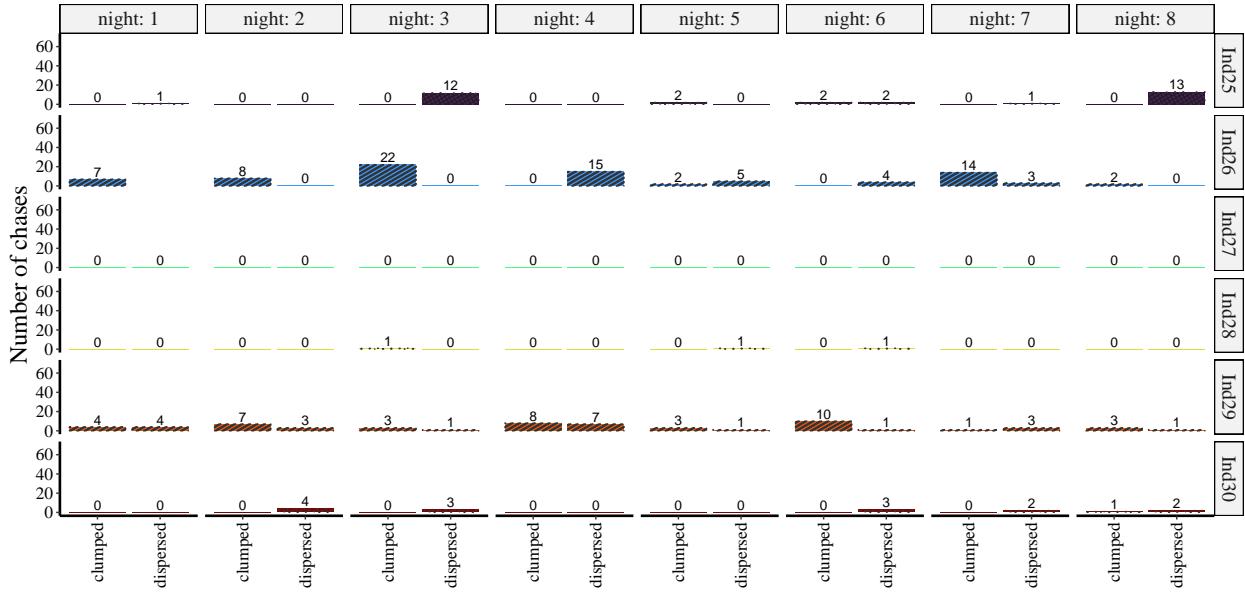


Figure S17: Raw number of chase events for all bats in males-only group. Same notation as in Fig. S4, but the colors correspond to different individuals.

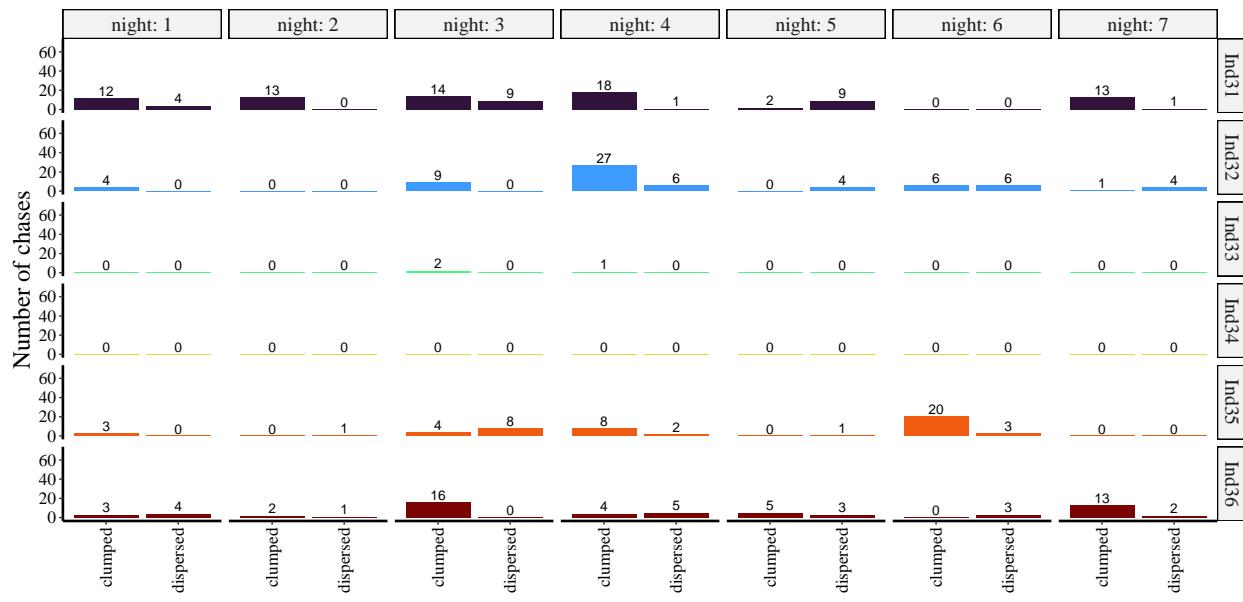


Figure S18: Raw number of chase events for all bats in females-only group 1.

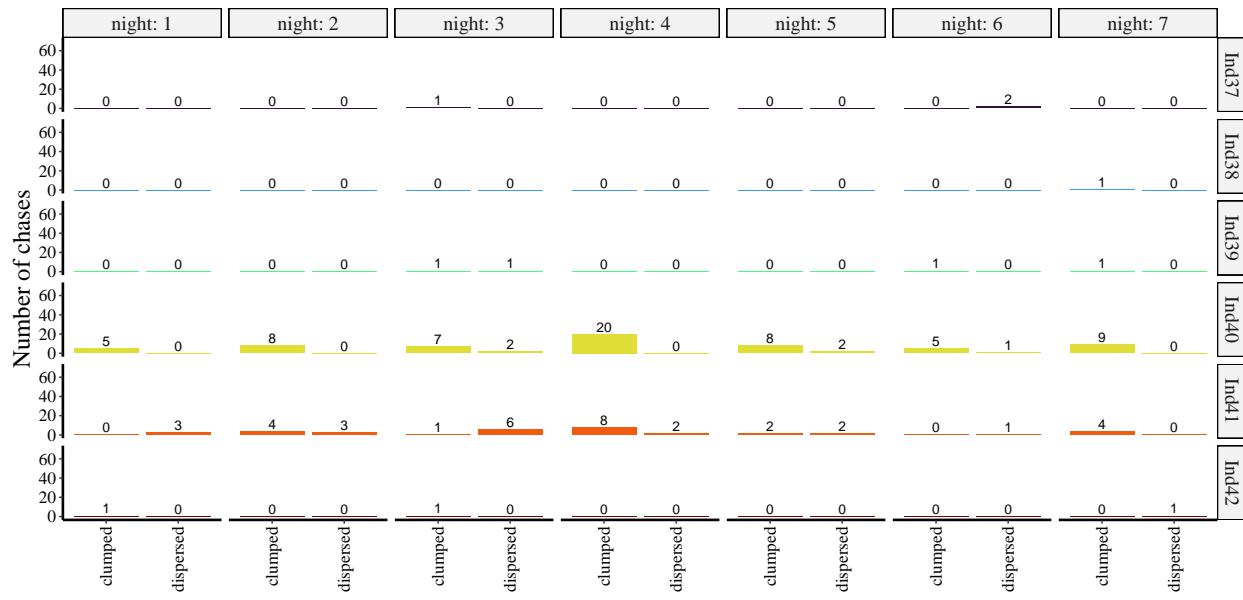


Figure S19: Raw number of chase events for all bats in females-only group 2.

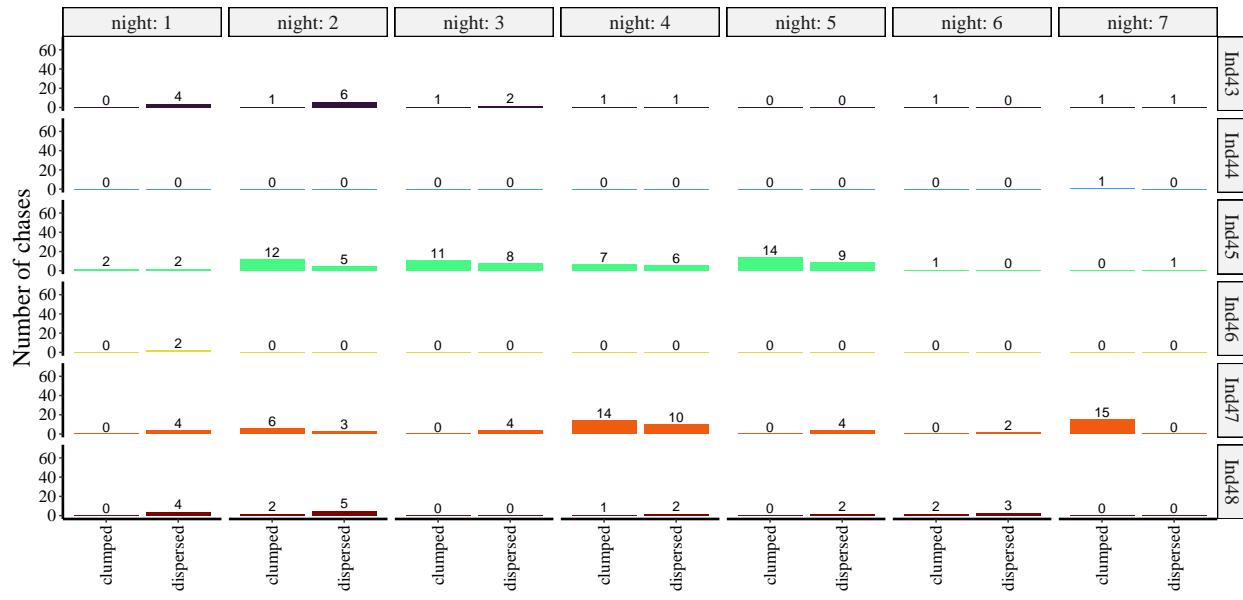


Figure S20: Raw number of chase events for all bats in females-only group 3.

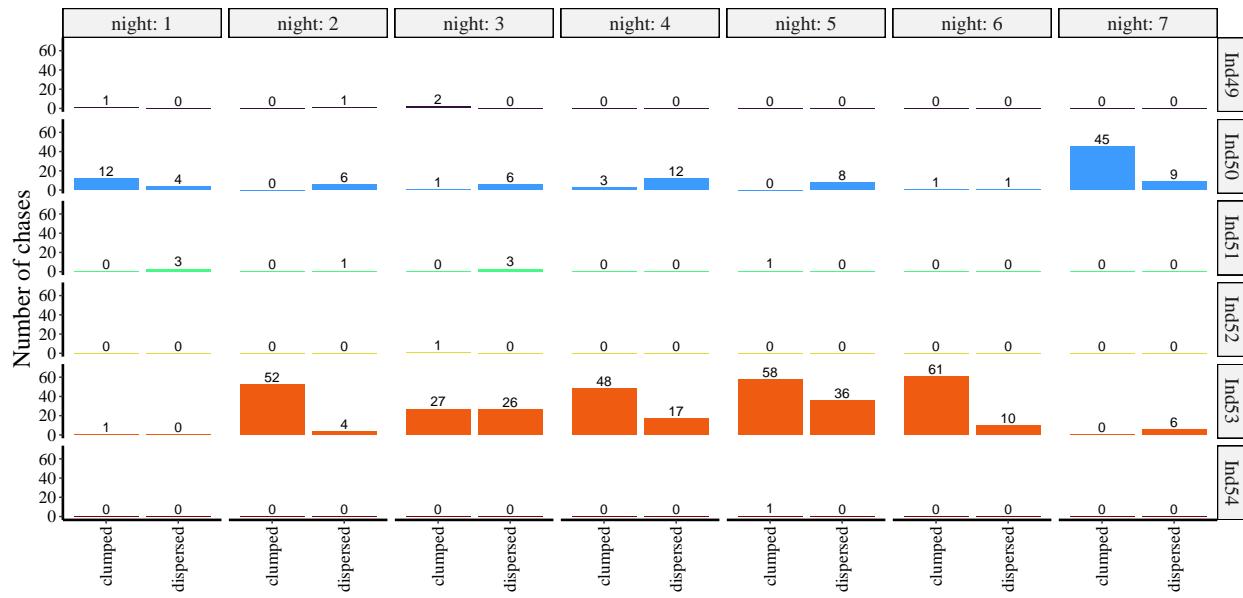


Figure S21: Raw number of chase events for all bats in females-only group 4.

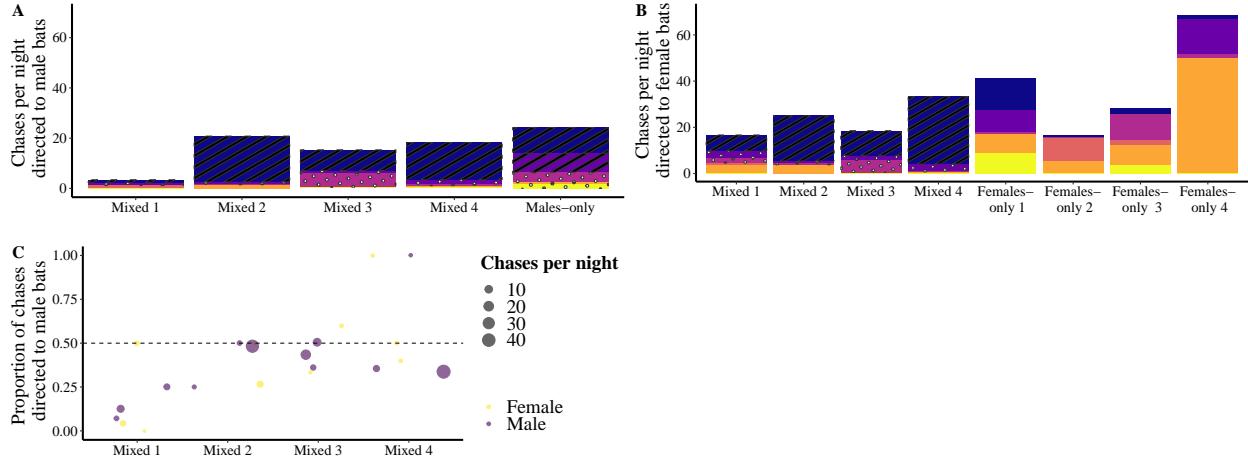


Figure S22: Frequency of chase events directed to bats of either sex. **(A, B)** Colored bars give the frequency of chase events per night (total chases divided by number of nights) over the main experiment by each individual from each group (abscissa) towards male (**A**) and female (**B**) bats. The dominant males are shown with stripes and the subordinate males are shown with dots. **(C)** Relative frequency of chase events directed towards male bats for male (purple) and female (yellow) bats from all mixed experimental groups (abscissa). The size of the dots represents the mean frequency of chase events per night.

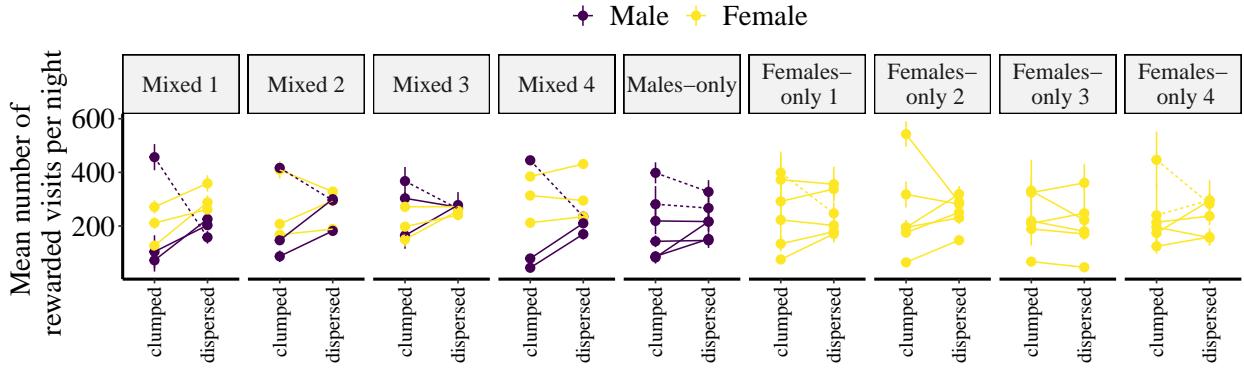


Figure S23: Number of rewarded visits per night (mean \pm SE) during the clumped and dispersed reward treatments for male (purple) and female (yellow) bats in each experimental group (panels). Data from the same individuals are connected with lines. Individuals with highest intake rates (most “dominant” individuals) are connected with dashed lines.

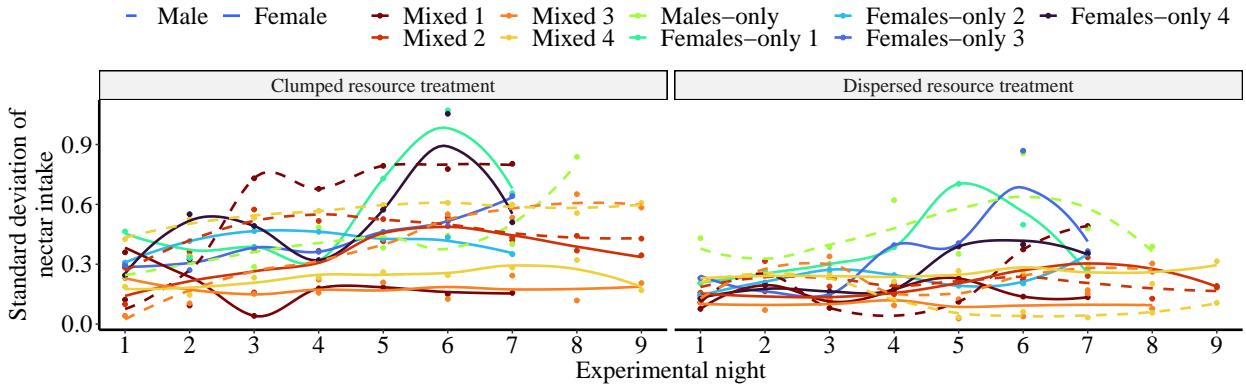


Figure S24: The standard deviation of group nectar consumption was used to measure the between-individual differences in nectar intake. It was calculated for the clumped (left panel) and the dispersed (right panel) resource treatments, separately for males (dashed lines) and females (continuous lines) from each experimental group (different colors). For visualization only, lines give the corresponding fits based on locally weighted scatterplot smoothing (loess). The statistical analysis was based on linear regression (see Methods).

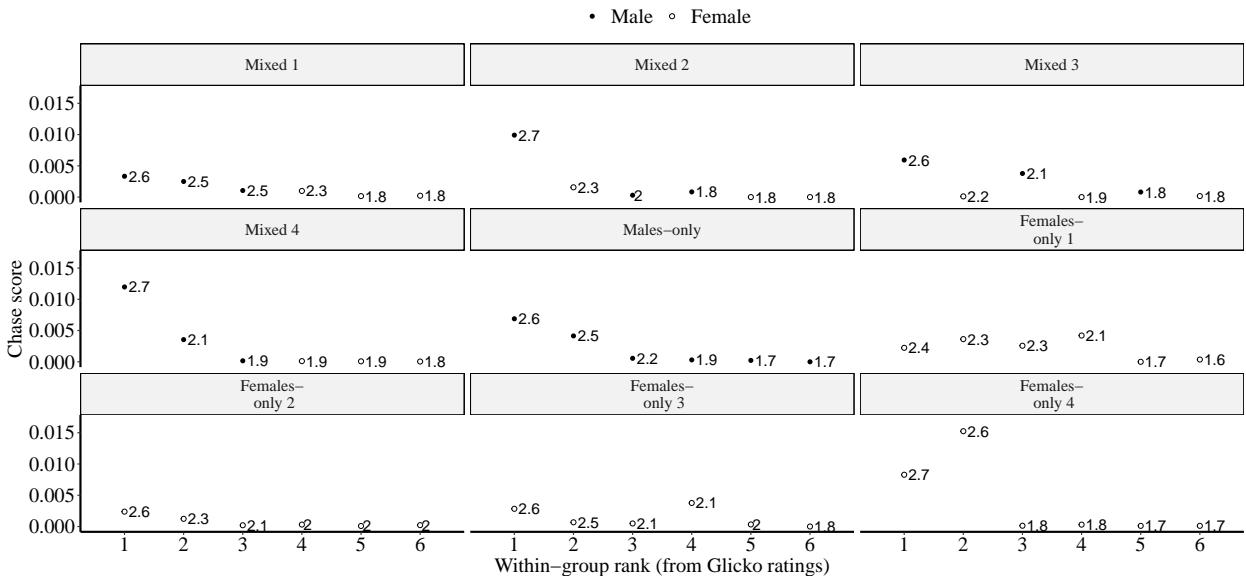


Figure S25: Glicko ratings within the six experimental groups. Over the last two experimental nights, the males (closed symbols) with the highest chase scores were also the individuals with the highest Glicko rating in each group (panels) during the clumped resource treatment. In female-only groups this correspondence was found only in group 2. Numbers at symbols give the Glicko rating in thousands.

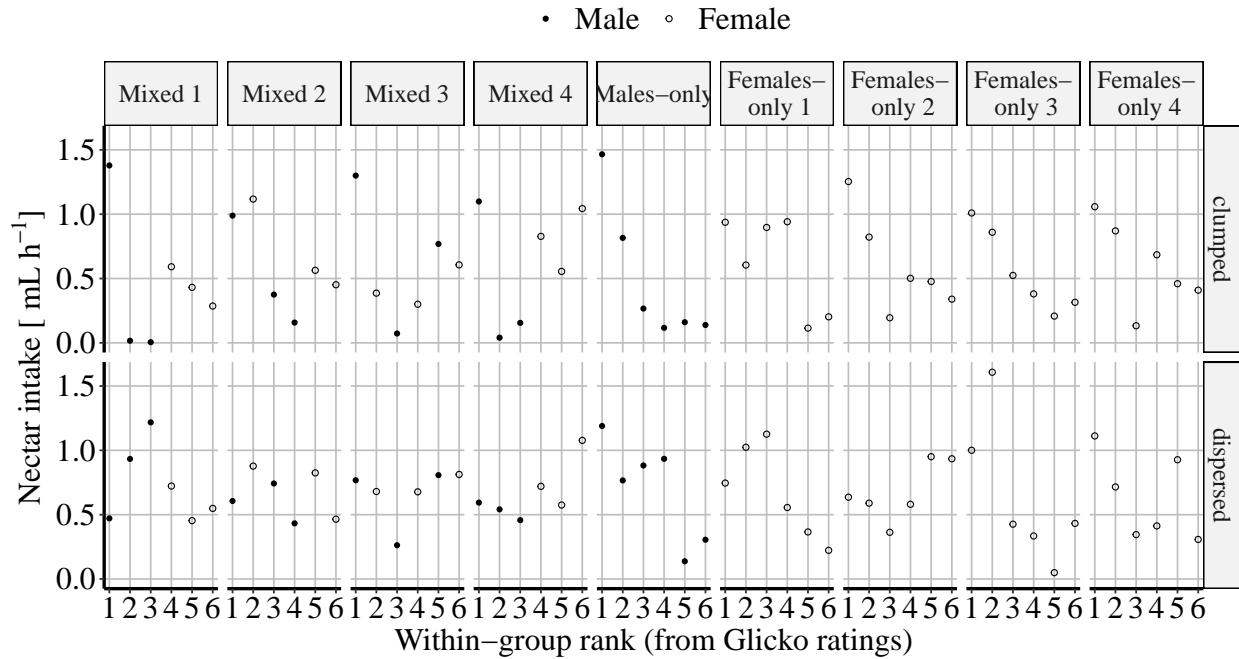


Figure S26: Male bats or female bats in the single-sex groups with the highest Glicko ratings had the highest nectar intake rates during the clumped, but generally not during the dispersed resource treatment.

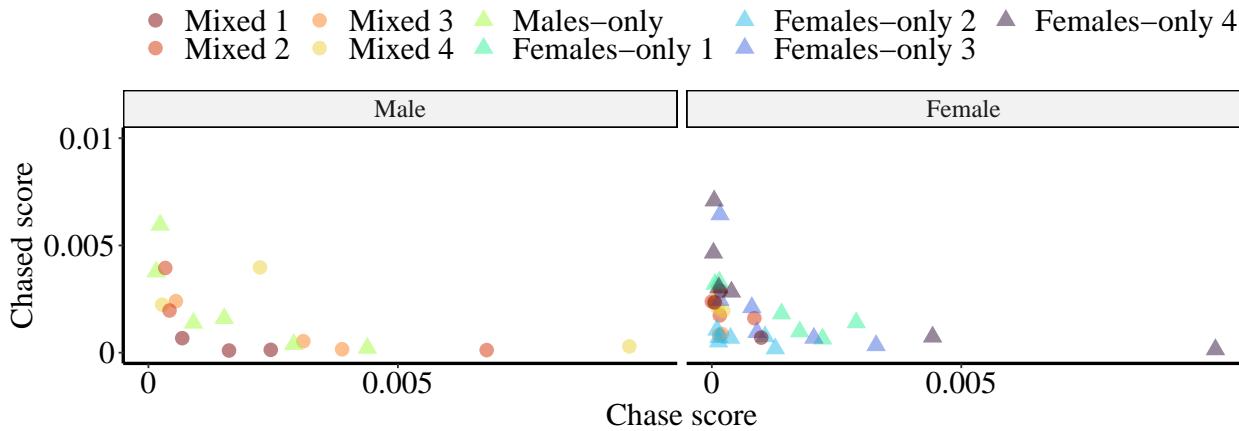


Figure S27: The relationship between chase score and chase score (proportion of chases versus the proportion of being chased out of all detections) for female (right) and male (left) individuals in all experimental groups (different colors). Mixed groups are shown with circles and single-sex groups, with triangles.

Table S1: Summary of fixed effects from generalized linear mixed-effects models of chasing frequency and the frequency of being chased for female bats only.

Model	term	estimate	95% credible interval	pMCMC
Chase score	(Intercept)	-5.74	(-13.88, 1.93)	0.1540
	group type (mixed)	-1.59	(-2.9, -0.21)	0.0340
	treatment (dispersed)	-0.66	(-0.99, -0.34)	0.0005
	weight	-0.19	(-0.99, 0.59)	0.6310
	group type (mixed):treatment (dispersed)	0.58	(-0.08, 1.24)	0.0880
Chased score	(Intercept)	-8.34	(-13.02, -3.16)	0.0010
	group type (mixed)	0.27	(-0.6, 1.26)	0.5250
	treatment (dispersed)	-1.14	(-1.39, -0.92)	0.0005
	weight	0.19	(-0.31, 0.65)	0.3990
	group type (mixed):treatment (dispersed)	0.21	(-0.15, 0.55)	0.2470

Note: Fixed estimates whose credible intervals do not span zero are shown in bold. pMCMC = posterior probability

Table S2: Summary of fixed effects from a generalized linear mixed-effects model of the standard deviation of nectar intake over time for female bats only.

term	estimate	95% credible interval	pMCMC
(Intercept)	0.50	(0.41, 0.6)	0.000
group type (mixed)	-0.27	(-0.4, -0.14)	0.003
treatment (dispersed)	-0.18	(-0.24, -0.11)	0.000
night	0.05	(0.01, 0.1)	0.030
group type (mixed):treatment (dispersed)	0.12	(0.04, 0.2)	0.007
group type (mixed):night	-0.05	(-0.11, 0.01)	0.116
treatment (dispersed):night	-0.01	(-0.04, 0.02)	0.573
group type (mixed):treatment (dispersed):night	0.01	(-0.03, 0.05)	0.648

Note: Fixed estimates whose credible intervals do not span zero are shown in bold. pMCMC = posterior probability

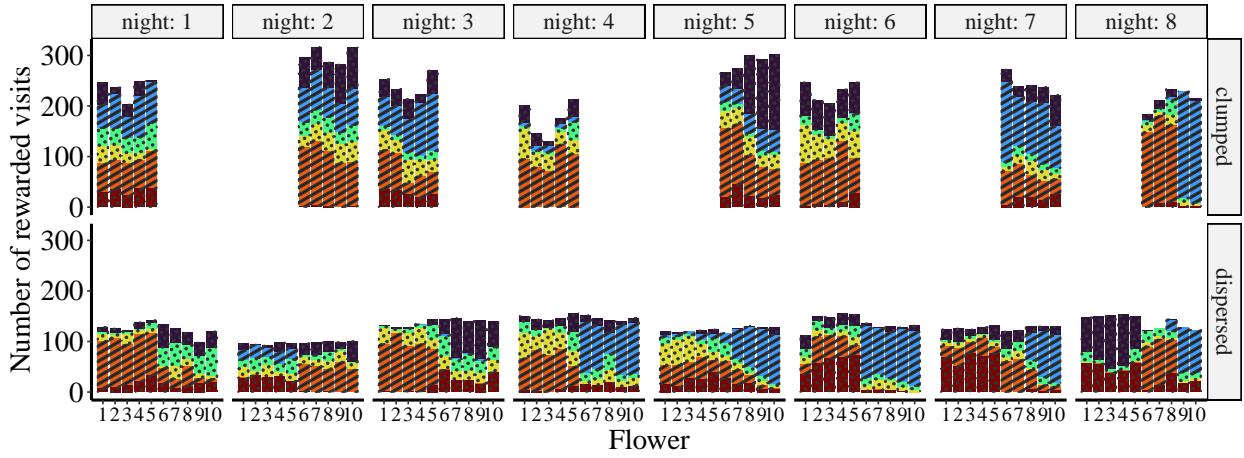


Figure S28: Distribution of rewarded visits across flowers for the six bats in the males-only group. The colored bars give the number of rewarded visits of each individual at the ten flowers during the clumped (top) and dispersed (bottom) resource treatments for each experimental night (columns). The dominant males are shown with stripes and the subordinate males are shown with dots. This was the only group with two males behaving as dominant. On the last night, rather than sharing all flowers within the defended patch, the dominant males partitioned the patch into two subpatches, with each bat defending its own partition.

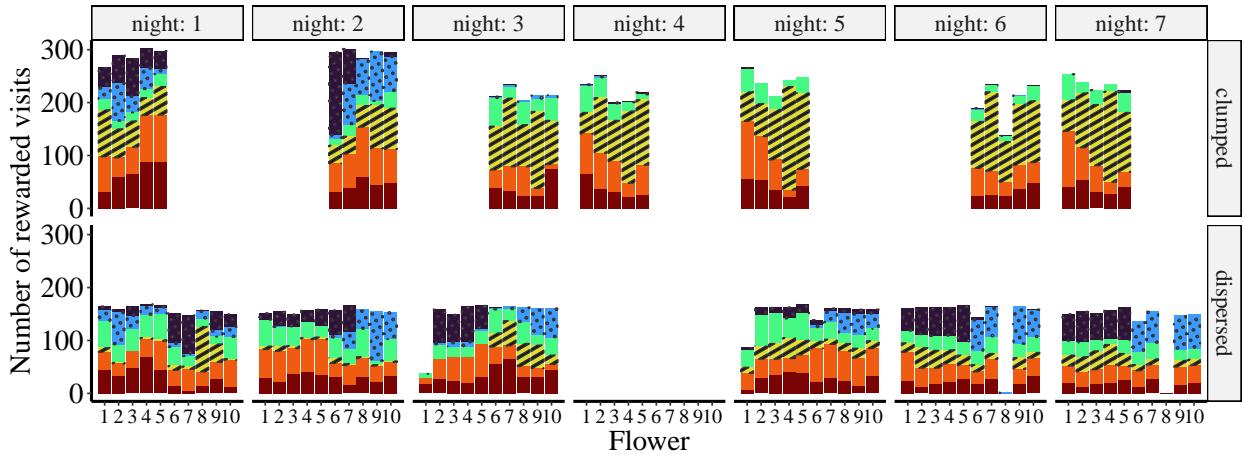


Figure S29: Distribution of rewarded visits across flowers for the six bats in mixed group 1. The colored bars give the number of rewarded visits of each individual at the ten flowers during the clumped (top) and dispersed (bottom) resource treatments for each experimental night (columns). The dominant male is shown with stripes, the subordinate males are shown with dots, and the females are shown with solid bars. Due to a technical malfunction on night 4, there were no rewards delivered in the dispersed resource treatment and the data were excluded from analysis.

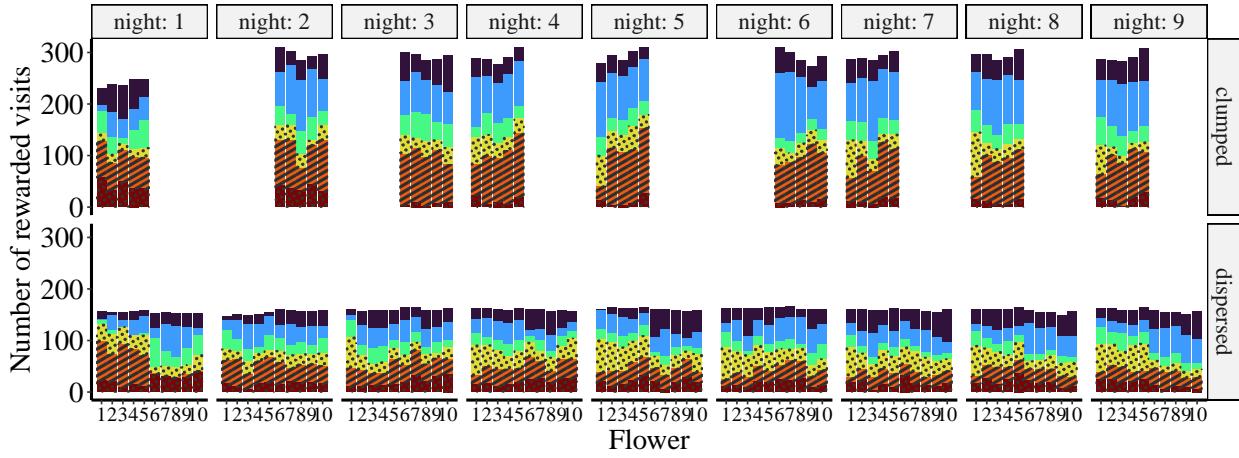


Figure S30: Distribution of rewarded visits across flowers for the six bats in mixed group 2. Same notation as in Fig. S29, but the colors correspond to different individuals.

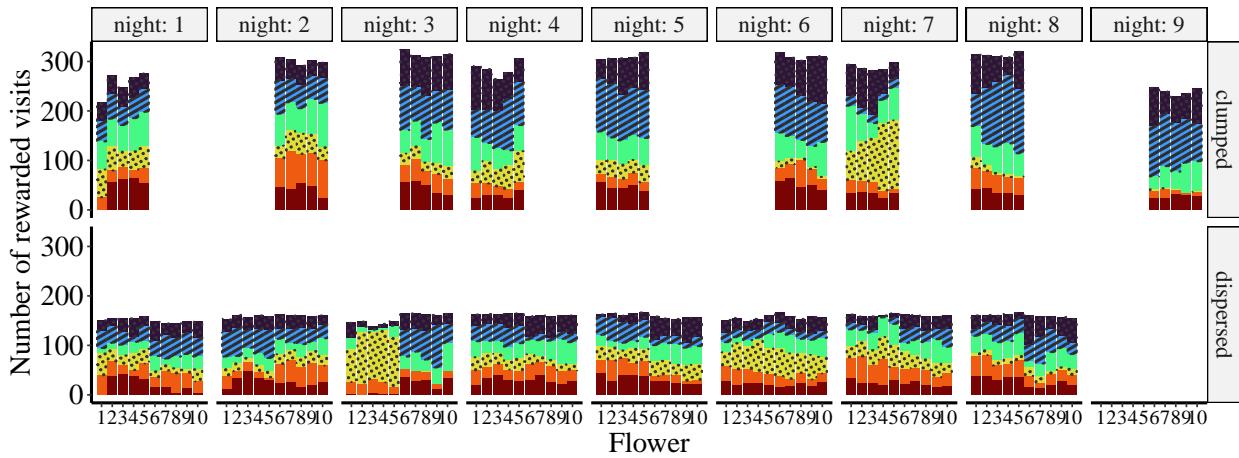


Figure S31: Distribution of rewarded visits across flowers for the six bats in mixed group 3. Same notation as in Fig. S29, but the colors correspond to different individuals. Due to a technical malfunction on night 9, there were no rewards delivered in the dispersed resource treatment and the data were excluded from analysis.

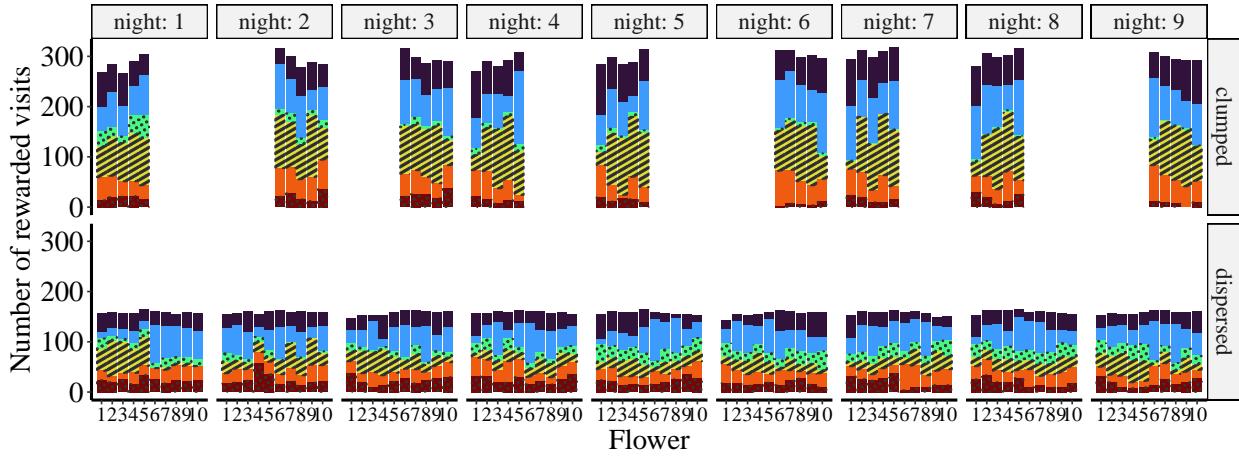


Figure S32: Distribution of rewarded visits across flowers for the six bats in mixed group 4. Same notation as in Fig. S29, but the colors correspond to different individuals.

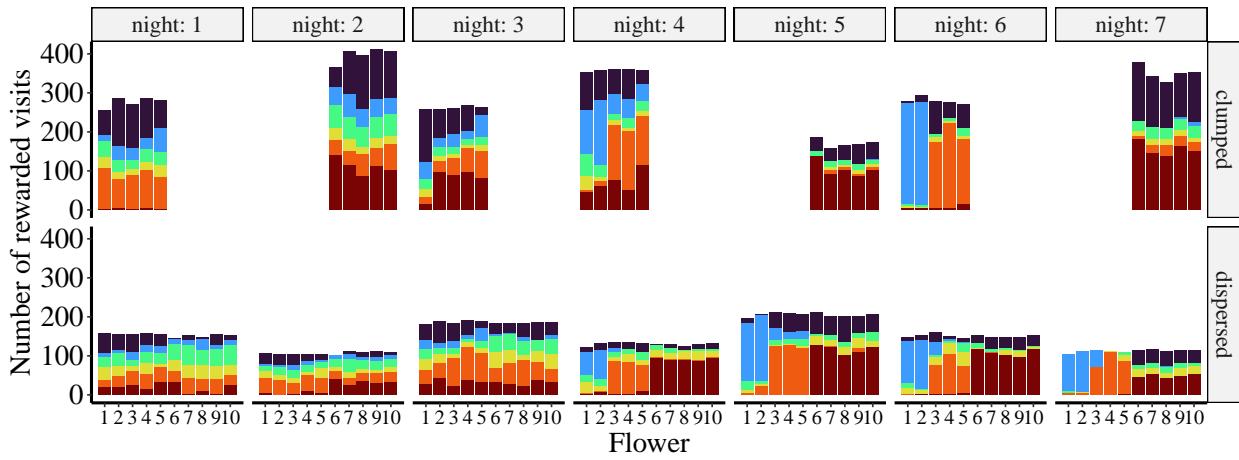


Figure S33: Distribution of rewarded visits across flowers for the six bats in the females-only group 1. Same notation as in Fig. S29, but the colors correspond to different individuals.

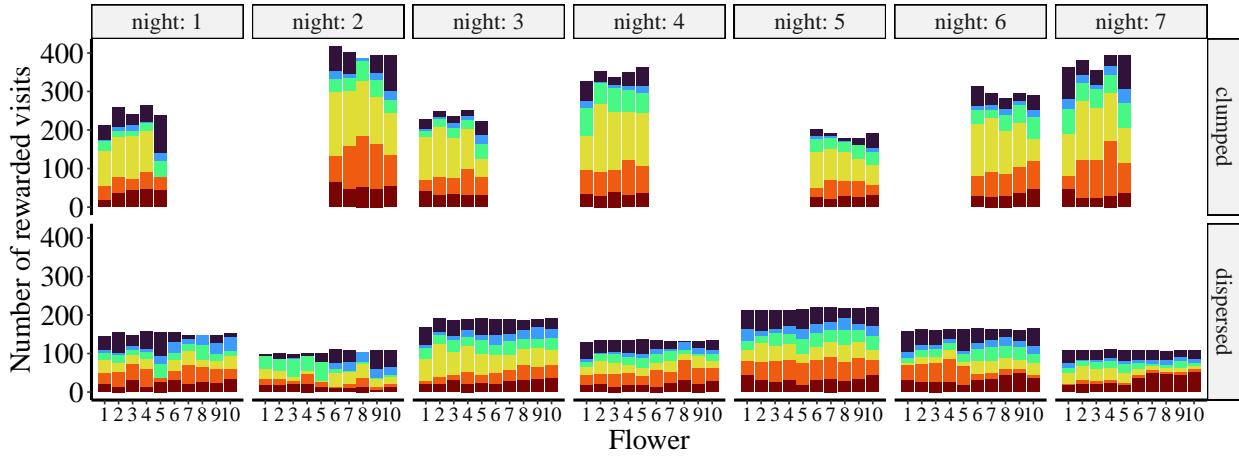


Figure S34: Distribution of rewarded visits across flowers for the six bats in the females-only group 2. Same notation as in Fig. S29, but the colors correspond to different individuals.

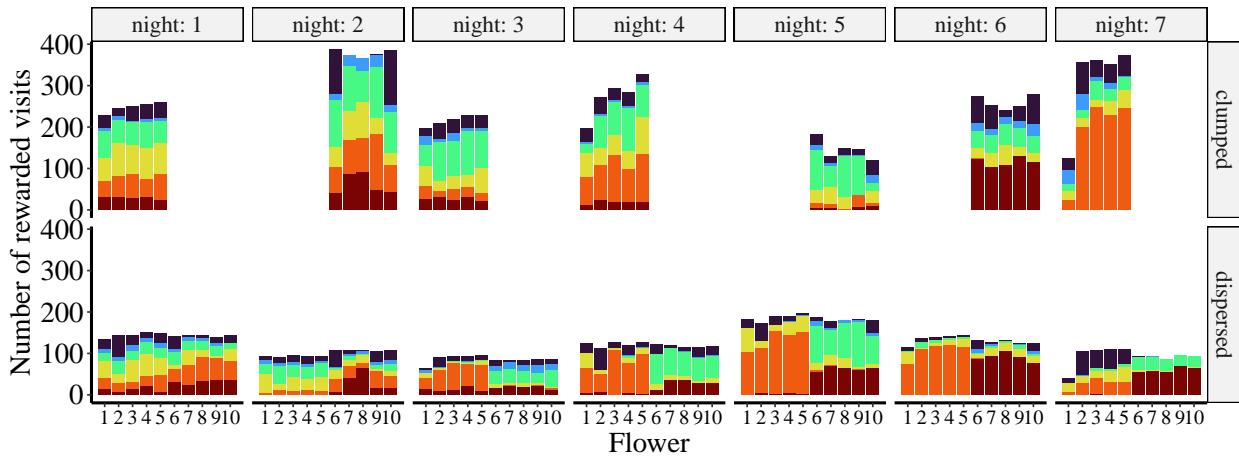


Figure S35: Distribution of rewarded visits across flowers for the six bats in the females-only group 3. Same notation as in Fig. S29, but the colors correspond to different individuals.

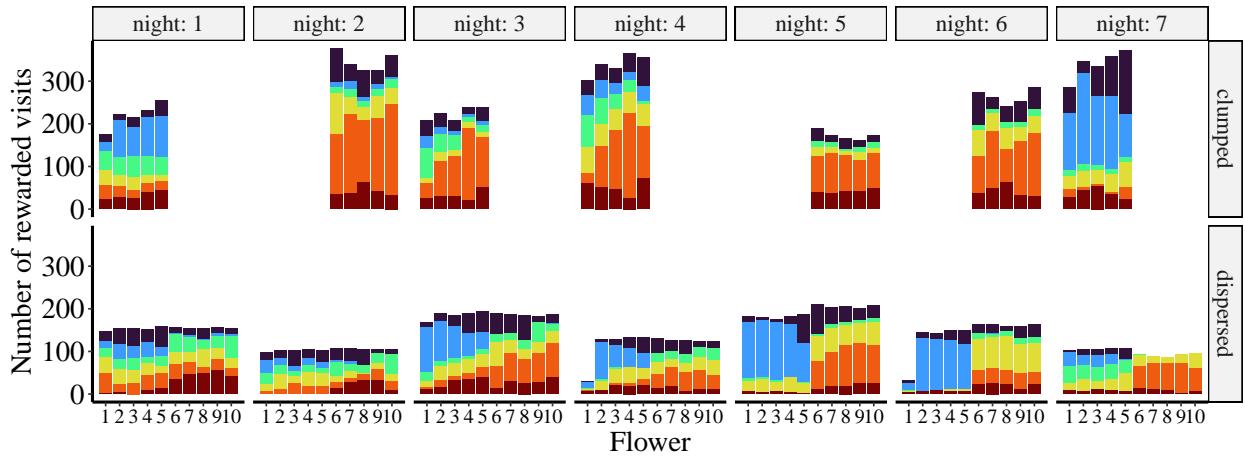


Figure S36: Distribution of rewarded visits across flowers for the six bats in the females-only group 4. Same notation as in Fig. S29, but the colors correspond to different individuals.

⁴³⁰ **Authors' contributions**

⁴³¹ S.W. Conceptualization, Methodology, Software, Data collection, Formal Analysis, Video Analysis, Writing—
⁴³² original draft. V.N. Conceptualization, Methodology, Software, Formal Analysis, Data curation, Writing—
⁴³³ review and editing, Visualization, Supervision, Project Administration.
⁴³⁴ Y.W. Conceptualization, Resources, Methodology, Software (data acquisition), Writing—review and editing,
⁴³⁵ Supervision, Funding.

⁴³⁶ **Competing interests**

⁴³⁷ We declare we have no competing interests.

⁴³⁸ **Funding**

⁴³⁹ S.W. was supported by an Elsa-Neumann-Stipendium des Landes Berlin.

⁴⁴⁰ **Acknowledgements**

⁴⁴¹ We thank Katja Frei and Peggy Hoffmann for assistance with the main experiments and animal keeping,
⁴⁴² Alexej Schatz for programming of the control software, and Peter Spende, Francesco Bagorda, and Waldemar
⁴⁴³ Krzok for help with the experimental hardware. We also thank Marion Rivalan and Lucille Alonso for a
⁴⁴⁴ fruitful discussion on the analysis of social behavior.

⁴⁴⁵ **Data Availability**

⁴⁴⁶ All data and code are available in the Zenodo repository: <https://doi.org/10.5281/zenodo.5205511>.

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