

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

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9 Abstract

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

27 Lay summary

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

32 Keywords:

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

34 1. Introduction

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

45 The establishment of feeding territories is well known for nectar-feeding birds (Gill and Wolf 1975; Carpenter
46 and Macmillen 1976; Boyden 1978; Ewald and Carpenter 1978). The cost of defense, however, a key parameter
47 in the economic defendability equation, is likely much higher for a nocturnal, echolocating bat than for a
48 diurnal, visually oriented bird. The successful resource defense is only possible after the competition is detected.
49 Visual detection in the daylight works well over long distances. In contrast, for a nocturnal, echolocating
50 bat, especially for phyllostomid bats that are able to echolocate with "whispering" or narrowly-focused calls
51 (Howell 1974; Gonzalez-Terrazas et al. 2016; Yoh et al. 2020), detecting intruders at a feeding territory's
52 boundary would require expensive patrolling flights.

53 Within bats, the flower visitors have an advantage in establishing territories compared to insect-hunting bats,

54 because bats feeding on insects must continually scan for elusive prey by active echolocation, whereas flower
55 visitors can approach a target with minimal echolocation when seeking specific flowers at known locations
56 (Thiele and Winter 2005; Winter and Stich 2005; Rose et al. 2016; Gonzalez-Terrazas et al. 2016; Simon et
57 al. 2021). Thus, it is not surprising that the longer-term defense of extensive feeding territories as commonly
58 observed in nectar-feeding birds is not known for glossophagine, nectar-feeding bats (but see Watzke 2006 for
59 nectar-feeding flying foxes). Nonetheless, several observations have documented aggressive food defense by
60 glossophagine bats. The inflorescences of *Agave desmettiana* with their copious nectar (Lemke 1985) may be
61 defended by males or females of *Glossophaga soricina* against conspecifics but only during some hours of
62 the night (Lemke 1984, 1985). When left unguarded, intruders quickly exploit the opportunity to feed from
63 the previously defended plants. The Costa Rican bat *Glossophaga commissarisi* occasionally defends and
64 temporarily monopolizes single inflorescences of the understory palm *Calyptrogyne ghiesbreghtiana* against
65 other hovering bats, perching bats and katydids (Tschapka 2003). A commonality in these reports is that
66 the defense does not cover the area of a typical feeding range but is restricted to a single or a few flowering
67 plants and is also limited to a small number of hours during the night. While these reports demonstrate that
68 glossophagine bats can show aggressive resource defense, the extent of territoriality and its relation to sex
69 remain unknown.

70 In this study, we investigated for a nocturnal, nectar-feeding mammal, the flower-visiting bat *Glossophaga*
71 (*mutica* (previously *G. soricina*, Calahorra-Oliart et al. (2021))), the role of aggressive interactions for gaining
72 access to nectar food. Economic defensibility predicts that clumped resources will be easier and less costly
73 to defend (Brown 1964; Gill and Wolf 1975; Carpenter and Macmillen 1976). We tested this predictions
74 using a naturalistic foraging paradigm in the laboratory. The occurrence of resource defense is predicted to
75 be highest at intermediate levels of food abundance (Gill and Wolf 1975; Carpenter and Macmillen 1976;
76 Carpenter 1978; Grant et al. 2002). In line with this prediction, the transient nature of nightly defense
77 behavior observed in the field suggests that changes in food-abundance or food-requirements that occur within
78 the night affected the strength of the observed behavior. To mimic the natural situation of chiropterophilous
79 flowers, which often replenish their nectar more or less continuously throughout a night (e.g. Tschapka and
80 von Helversen 2007), we programmed artificial flowers to provide nectar with a fixed interval reward schedule.
81 Once a nectar reward had been taken by any bat, the fixed interval had to pass before the next reward was
82 available at this flower. Theoretical models of interference competition predict that clumped resources lead
83 to more agonistic behavior and resource defense than evenly dispersed resources (Brown 1964; Carpenter and
84 Macmillen 1976; Grant 1993). To include a test of this prediction in our experimental design, we spatially
85 subdivided our flower field into two patches and programmed them to automatically change the spatial
86 distribution of available nectar resources during the night. We performed our study with 36 individuals of
87 male and female *G. mutica*. By using artificial flowers in a closed environment, we could track all flower visits
88 and total nectar consumption of every individual in the group. Each individual carried an electronic ID tag
89 and flowers were equipped with ID sensors. This also enabled us to detect and quantify a typical class of
90 aggressive interactions between pairs of individuals directly at the artificial flowers fully automatically.
91 Our novel experimental set-up thus allowed us to perform a mostly automated experimental test of models
92 of interference competition and resource defense with a mammal under the controlled conditions of the
93 laboratory. This new approach may pave the way for further such studies with other groups of organisms.

94 2. Materials and methods

95 (a) Subjects and housing

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

105 rings (A C Hughes Ltd., Middlesex, UK) around the forearm for visual identification. Temperature in the
 106 experimental and colony room was kept at 20-25°C, air humidity at 65-75%, and light conditions were 12:12
 107 LD (light off at 16h).

108 **(b) Experimental set-up**

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

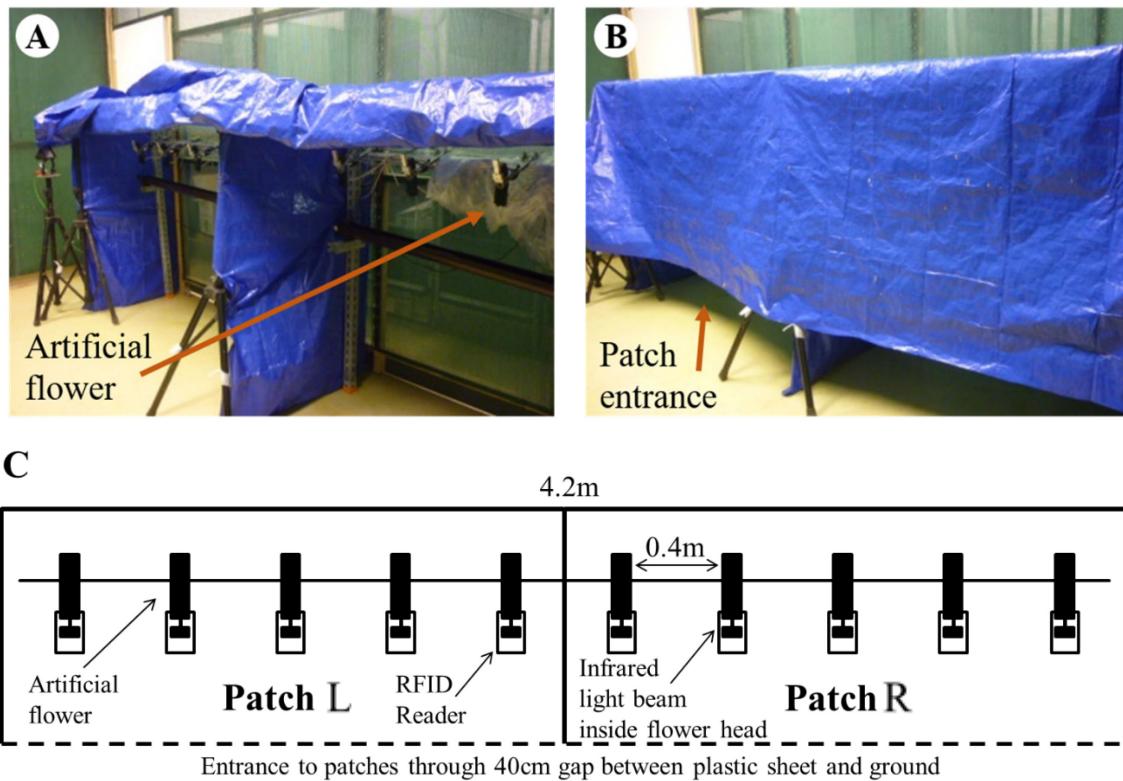


Figure 1: Experimental set-up consisting of two spatially separated patches of five flowers each. (A) The ten flowers were mounted 1.2m above ground. They were divided into two patches, L and R. (B) During experiments the patches were separated by plastic sheets. To make it more demanding for bats to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

122 **(c) Experimental procedure**

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

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

136 During the experiment, the two flower patches were covered and spatially separated (Fig. 1). Experimental
137 nights were divided into two phases. During the first phase of the night only one of the two flower patches was
138 rewarding, and therefore the resources were spatially clumped at a single location. The fixed time interval
139 between rewards at each flower was 60s. During the second phase of the night both patches gave rewards,
140 resources were evenly dispersed across the two patches, and the fixed time interval between two rewards at a
141 flower was increased to 120s. Therefore, the amount of food available per unit time did not change during
142 the whole night; only the spatial distribution of food changed from the clumped resource treatment with one
143 patch rewarding (five flowers) during the first phase of the night to the dispersed resource treatment with two
144 patches rewarding (ten flowers) during the second phase of the night. With this experimental schedule,
145 the maximal amount of nectar the bats could collect was 108mL, which corresponds to 18mL nectar per
146 individual per night, roughly 150% of their daily requirement (Winter and von Helversen 2001). The side of
147 the rewarding patch during the first phase of the night was chosen pseudo-randomly and the same patch
148 was never chosen in more than two consecutive nights. For the mixed groups, the duration of the clumped
149 resource treatment was six hours and the experiment lasted nine nights (seven nights for the first mixed
150 group). For the same-sex groups, the duration of the first part of the night was variable (range = 4-8h, mean
151 = 6h) and the experiment lasted eight nights for the male group and seven nights for the female groups.

152 **(d) Chasing behavior**

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

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

180

181 (e) Statistical analysis

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

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

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

215 3. Results

216 (a) Behavioral observations

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

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

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

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

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

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

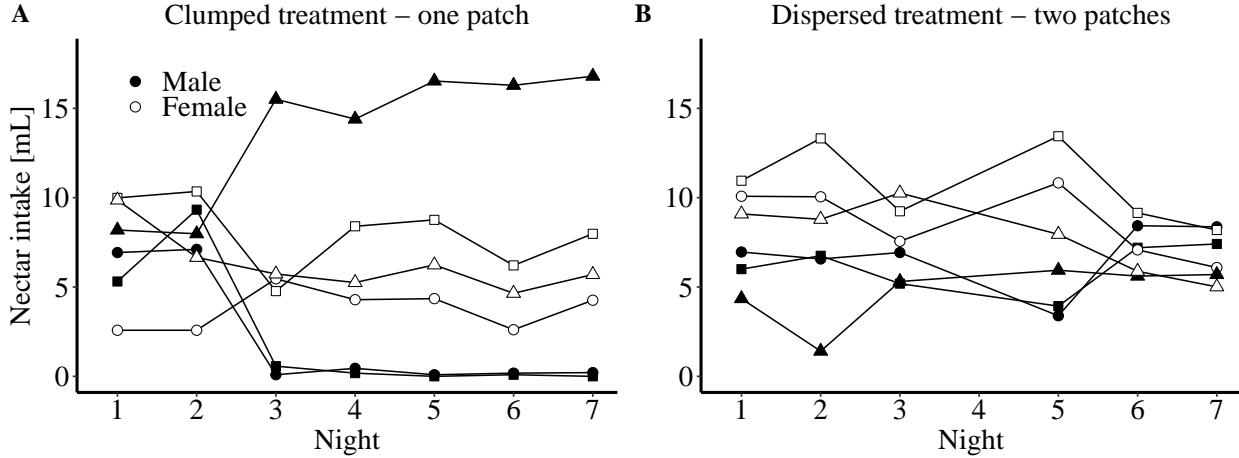


Figure 2: Example of the change of individual nectar consumption from the clumped treatment (A) to the dispersed treatment (B) during an experiment of one mixed group (3 males, 3 females, symbols show different individuals). (A) During the clumped resource treatment (first part of the experimental night) 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.

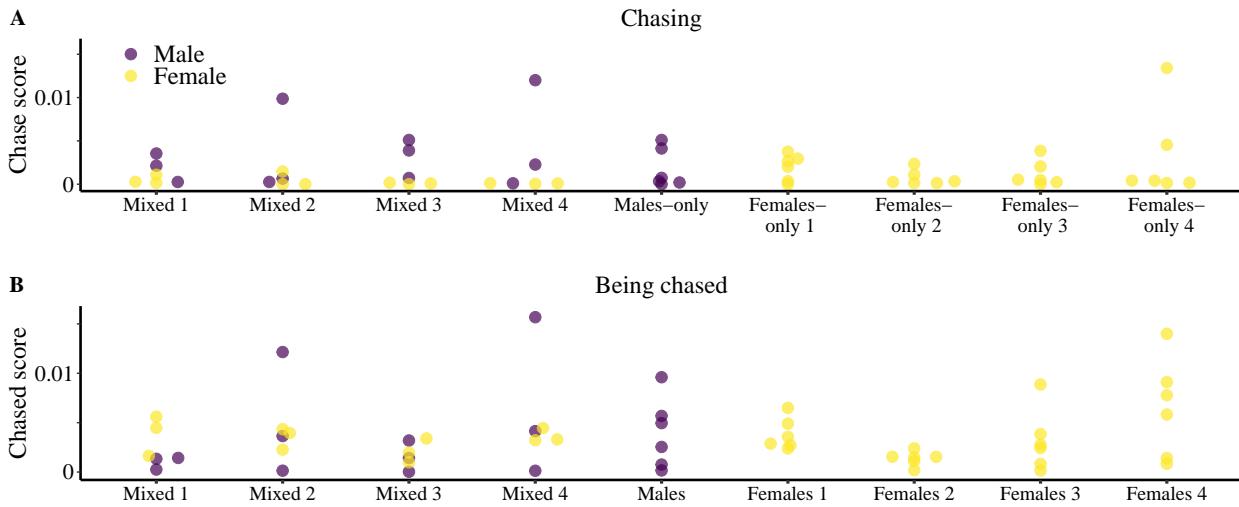


Figure 3: Sexes differed in the frequency of chasing or being chased during the clumped resource treatment. (A) Males (dark symbols) chased others significantly more than females did (light symbols, Table 1). Shown are the individual proportions of chasing events (chase scores) over the whole experiment. 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

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

252 Resource defense should lead to a larger between-individual difference in nectar consumption (Brown 1964).
 253 Differences in nectar consumption were quantified as the standard deviation of nectar intake in each group,
 254 separately for males and females. During the clumped resource treatment, the standard deviation was higher
 255 for males than for females (Table 2, Fig. S24) and increased significantly over time for males but not for
 256 females (Table 2, Fig. S24). For females in the clumped resource treatment the increase in standard deviation
 257 was significantly smaller than in males (significant interaction between sex and night, Table 2), and was not
 258 itself significant (estimate = 0.02, 95% CI = 0, 0.06). Compared to the clumped resource treatment, in the
 259 dispersed resource treatment the effect of experimental night was significantly lower for males (interaction
 260 between treatment and night, Table 2), but not for females (estimate = 0, 95% CI = -0.02, 0.02). Moreover,
 261 in the dispersed resource treatment there was no significant increase in standard deviation over the course of
 262 the experiment in males (estimate = 0.02, 95% CI = -0.01, 0.05) nor in females (estimate = 0.03, 95% CI =
 263 0, 0.06). Overall, for both males (significant effect of treatment) and females (estimate = -0.11, 95% CI =
 264 -0.16, -0.06) the standard deviations were generally higher in the clumped than in the dispersed resource
 265 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

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

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

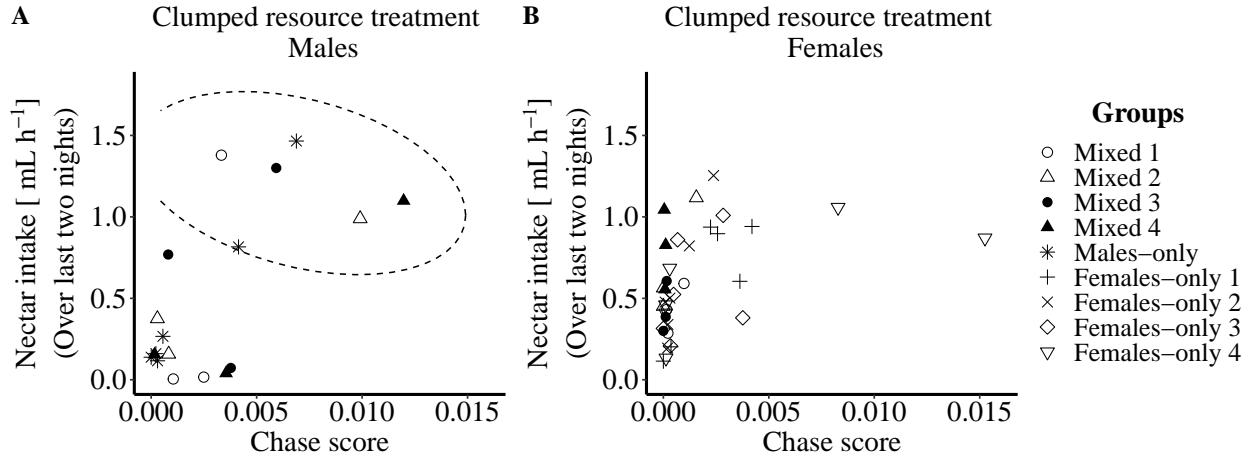


Figure 4: Influence of chasing frequency (chase score) on nectar intake in the clumped resource treatment during the last two nights of the experiment. (A) Males that more often chased other males also consumed more nectar. Males were divided into two non-overlapping groups by considering the chasing 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.

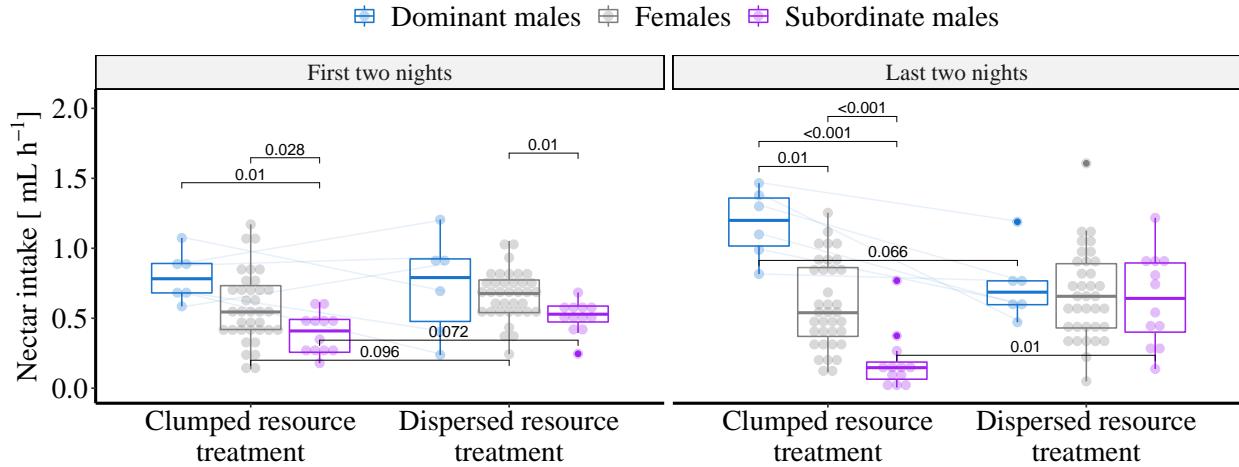


Figure 5: Comparison of nectar intake during the first and last two nights of the experiment depending on sex and social status. During the clumped resource distribution (left in each panel), already at the beginning of the experiment (left panel) subordinate males collected significantly less nectar 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.

291 4. Discussion

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

306 (a) Sex-dependent resource defense and its differential effect on nectar intake, 307 depending on social status

308 To our knowledge, this study is the first report of sex-dependent differences in resource defense behavior of
 309 neotropical nectar-feeding bats. In mixed sex groups, females seemed to be much less affected by the behavior
 310 of dominant males whereas subordinate males were excluded at least partially from the defended flower patch.
 311 This finding is consistent with observations of free-flying *G. commissarisi*, in which males visited on average

312 a smaller number of artificial flowers than females did (Nachev and Winter 2019), presumably because of
313 interactions with other males. There are two possible explanations for this differential effect on subordinate
314 males and females. On the one hand, dominant males might just not be capable of excluding females. On
315 the other hand, dominant males could tolerate females in their defended patch because they might receive
316 additional benefits, for example tolerating females could lead to an increase in (future) mating opportunities.
317 Similar social dynamics have been described in the insectivorous bat species *Myotis daubentonii* (Senior et
318 al. 2005). Dominant males of this species temporarily exclude other males from profitable habitats whereas
319 females are tolerated and in addition to securing access to resources, the successful exclusion of other males
320 has been shown to increase the reproductive success of dominant males (Senior et al. 2005). Similarly, it has
321 been observed that male purple-throated carib hummingbirds (*Eulampis jugularis*), which successfully defend
322 highly profitable feeding-territories against other males while sharing the available resources with females,
323 experienced an increase in their mating success (Temeles and Kress 2010).
324 However, in our experiment dominant males chased females about as often or slightly more often as they
325 chased subordinate males (Table 1, Fig. S22). If females were able to feed in the defended patch because
326 dominant males tolerated them due to potential additional benefits, it could be that the detected chasing
327 events by dominant males differed in quality depending on the sex of the intruder. This was not further
328 quantified in the current study but could potentially be investigated using audio recordings (Knörnschild
329 et al. 2010; Hörmann et al. 2020). We extracted the frequency of chasing events from data automatically
330 recorded at artificial flowers (successive detection of two different IDs while and after the first was feeding at
331 the flower). Therefore, it was not possible to determine if males showed behavioral differences when chasing
332 other males in comparison to chasing females. The recorded video revealed that individuals chased each
333 other not only directly at the artificial flowers but also in other areas of the flower patch. Since individuals
334 could only be identified by their ID tags directly at the ID reader attached to artificial flowers the sex of
335 individuals chasing each other in other areas of the experimental room remained unknown. However, after
336 the experiment some subordinate individuals showed marks from small injuries at their wings (see example
337 in Fig. S2) and such marks were only observed in males. This could be an indication that dominant males
338 directed more aggression (biting) towards subordinate males than towards females. Such sexual dimorphism
339 in aggressive resource defense is also known from other nectar-feeding vertebrates, like hummingbirds. The
340 beaks of the males of some territorial hummingbirds seem to be specifically adapted as intrasexually selected
341 weapons (Rico-Guevara et al. 2019).

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

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

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

374 (c) Social status and social hierarchy

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

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

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

407 (d) Conclusion

408 Although flower defense behavior of *G. mutica* was investigated in a laboratory setting, we observed similar
409 behavior as described in free-living *Glossophaga* populations. Our results revealed a sexual dimorphism in
410 flower defense behavior in mixed-sex groups. Only males successfully defended flower patches and excluded
411 other males from their defended resource, whereas females remained unaffected by this male behavior and
412 continued to visit the flowers guarded by a male. In the absence of males females also defended flowers against
413 other females, but not as consistently as males. This observed pattern is similar to resource defense behavior

⁴¹⁴ observed in other nectar-feeding vertebrates. Furthermore, we could show that the frequency of aggressive
⁴¹⁵ interactions was, as predicted, higher when resources were clumped in one patch and transient. Future studies
⁴¹⁶ with free-living populations have to be conducted to assess how frequent and important resource defense in
⁴¹⁷ these nectar-feeding bats is and if males that are successful in defending resources have additional fitness
⁴¹⁸ advantages.

419 **Supplementary material**

420 **Video analysis**

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

426

427 f->f appear to be less aggressive

428 f->m appear aggressive

429 m->f appear aggressive

430 m->m appear aggressive

431

432 **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.

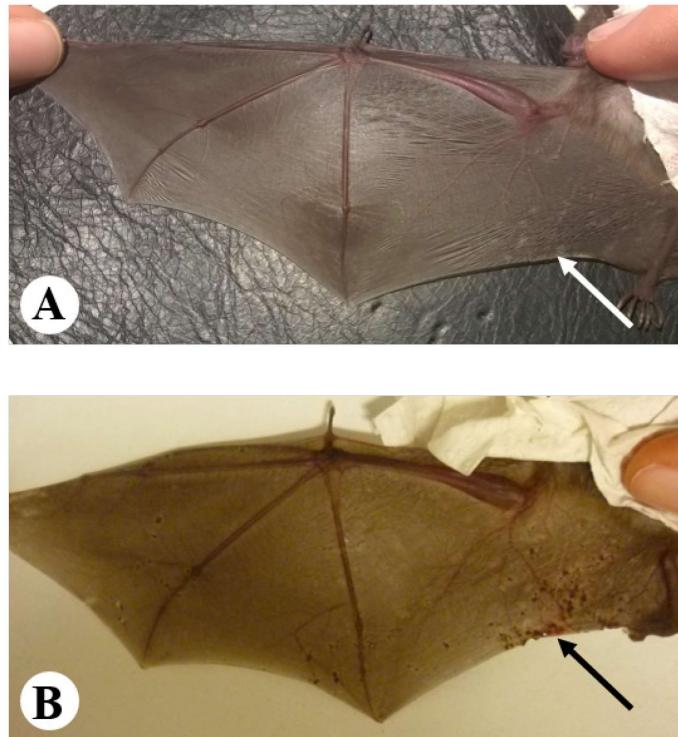


Figure S2: Wing images of a subordinate male from mixed group 4. The same individual was photographed before (**A**) and after the experiment (**B**). The black arrow points to the scarred location due to wing injuries, purportedly caused by the dominant male.

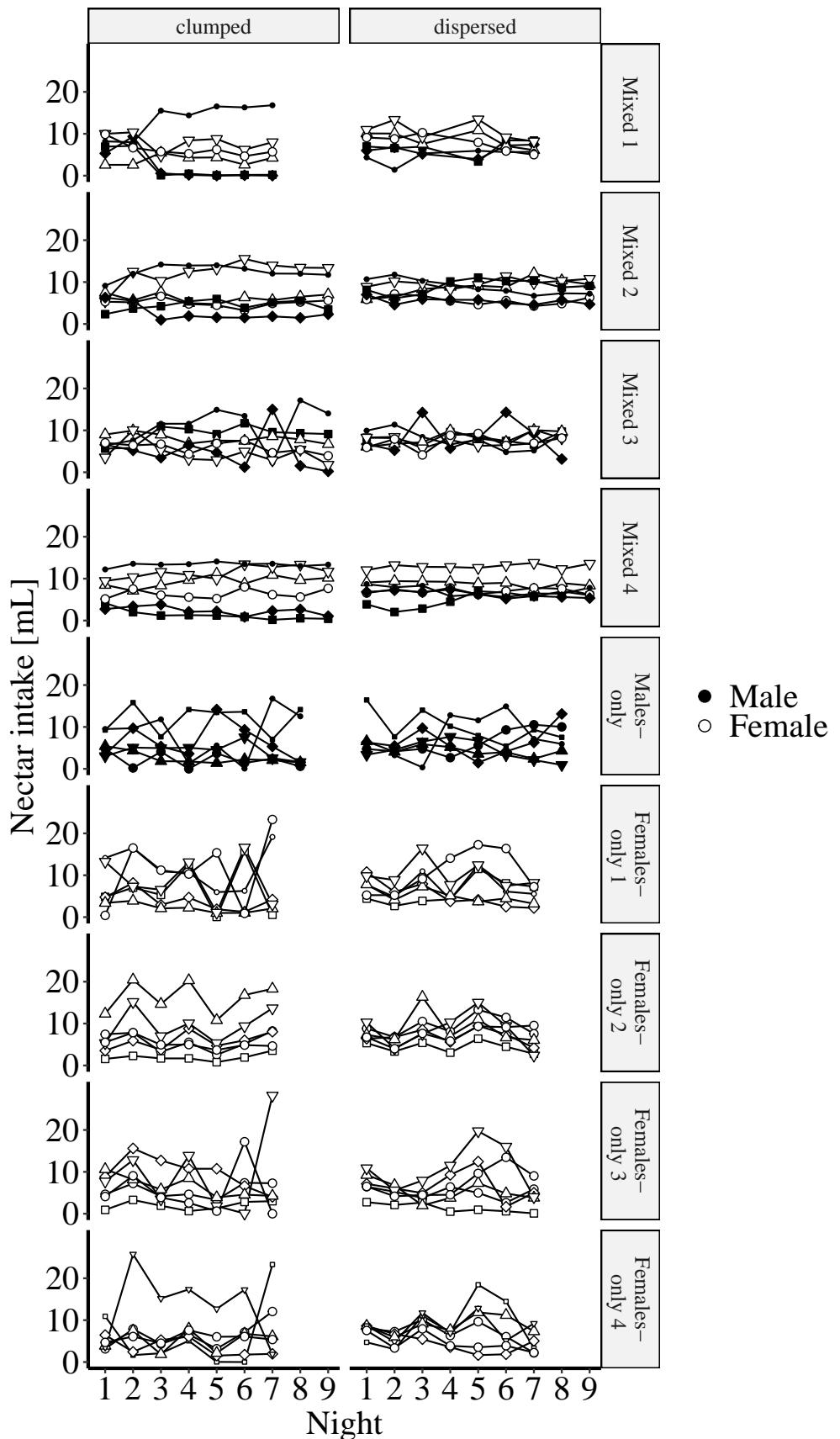


Figure S3: Change of individual nectar consumption from the clumped treatment (left) to the dispersed treatment (right) for all experimental groups (rows). $^{18}\text{Males}$ are shown with filled symbols and females with open symbols. Small symbols indicate dominant individuals, according to proportion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

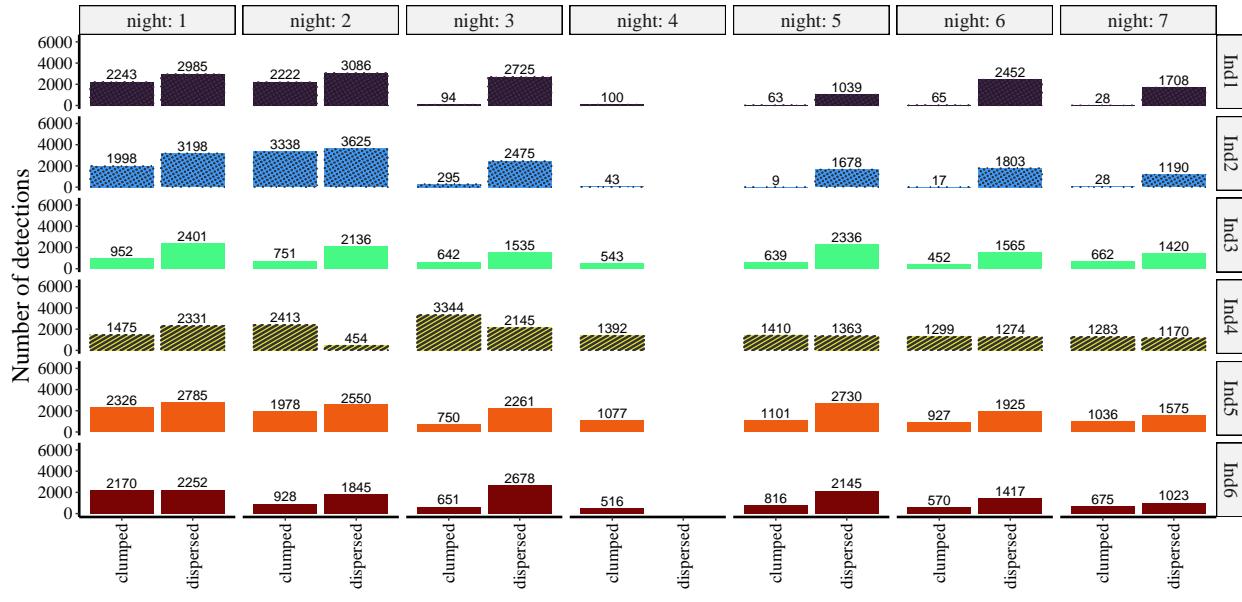


Figure S4: Raw number of detections for all bats in mixed group 1. Dotted bars represent subordinate males, striped bars represent dominant males and unhatched bars - females.

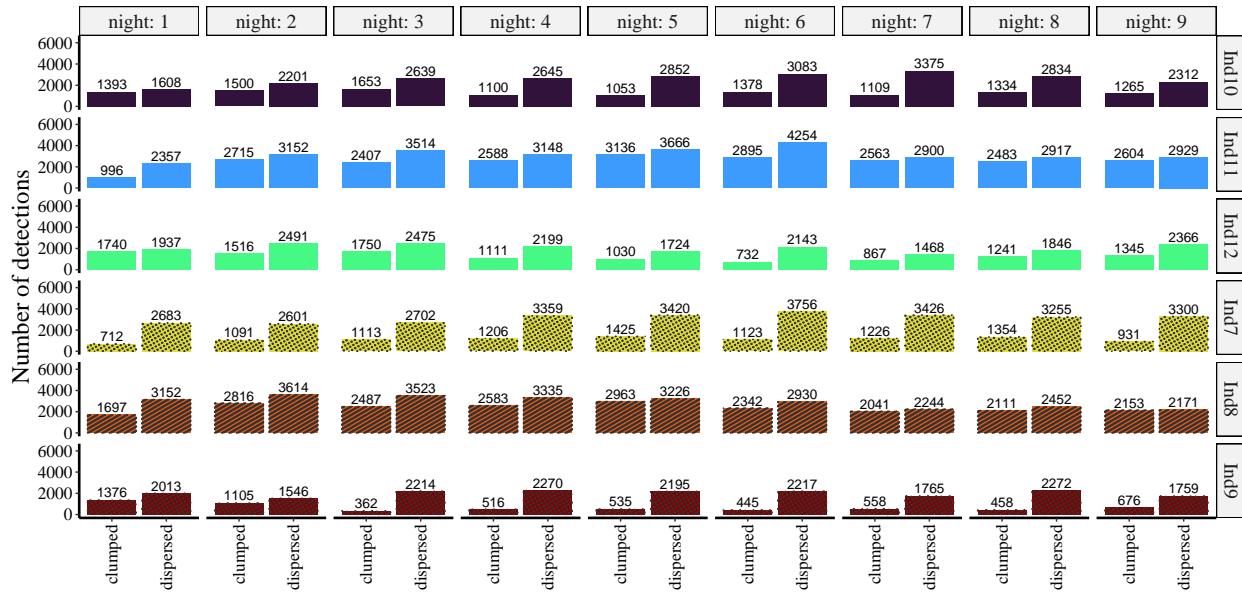


Figure S5: Raw number of detections for all bats in mixed group 2. Same notation as in Fig. S4, but the colors correspond to different individuals.

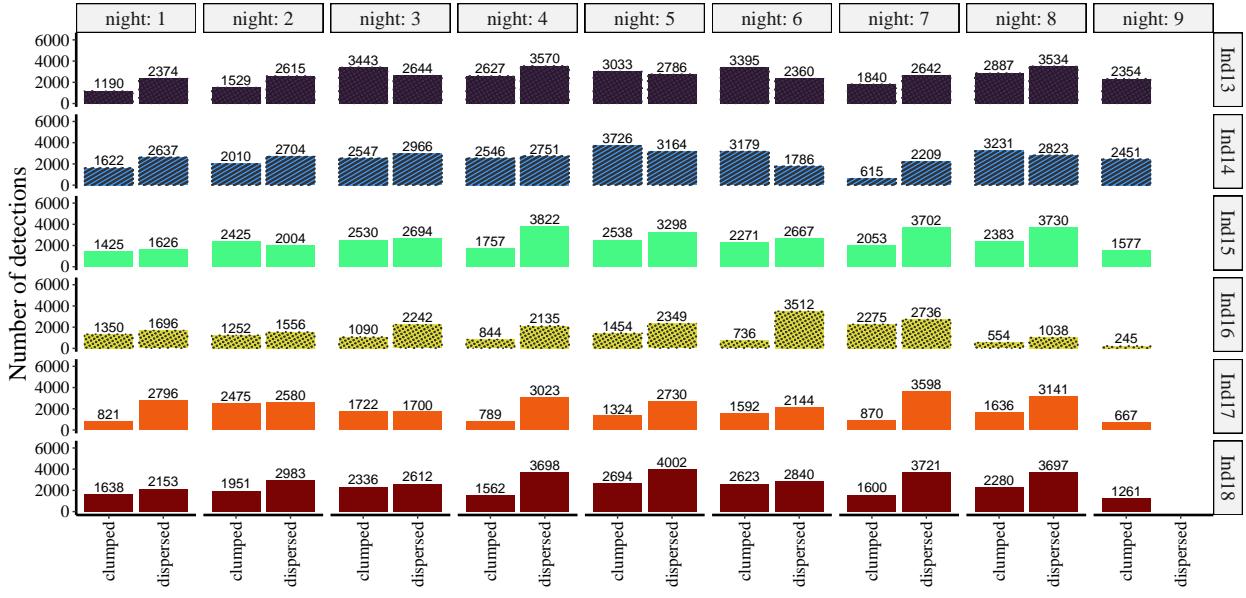


Figure S6: Raw number of detections for all bats in mixed group 3. Same notation as in Fig. S4, but the colors correspond to different individuals.

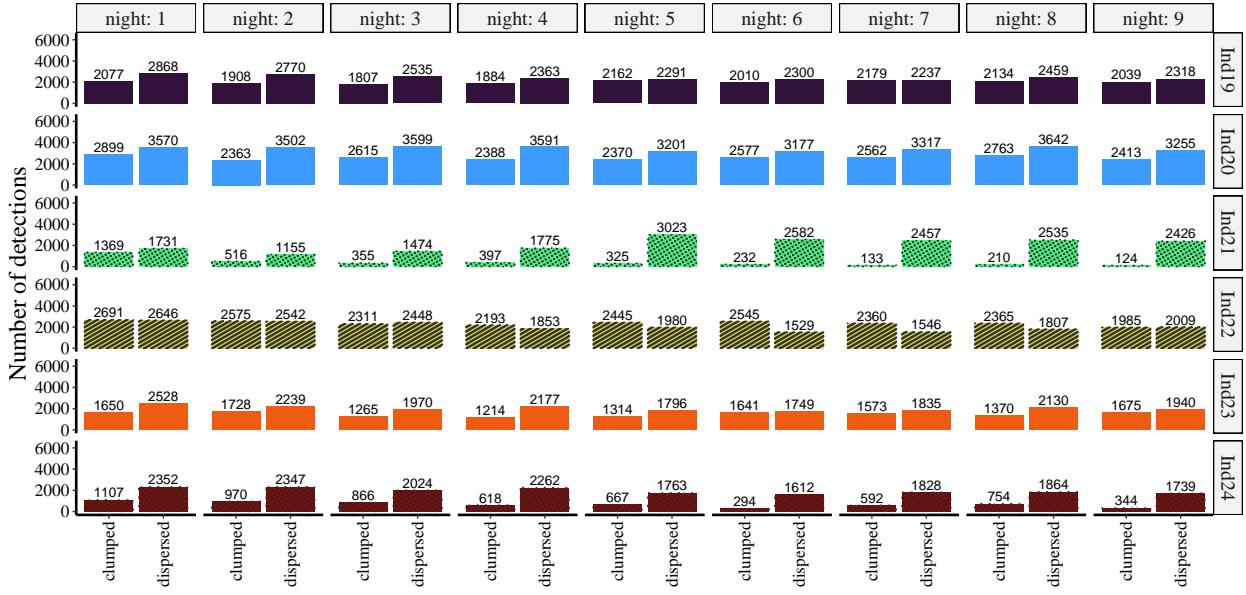


Figure S7: Raw number of detections for all bats in mixed group 4. Same notation as in Fig. S4, but the colors correspond to different individuals.

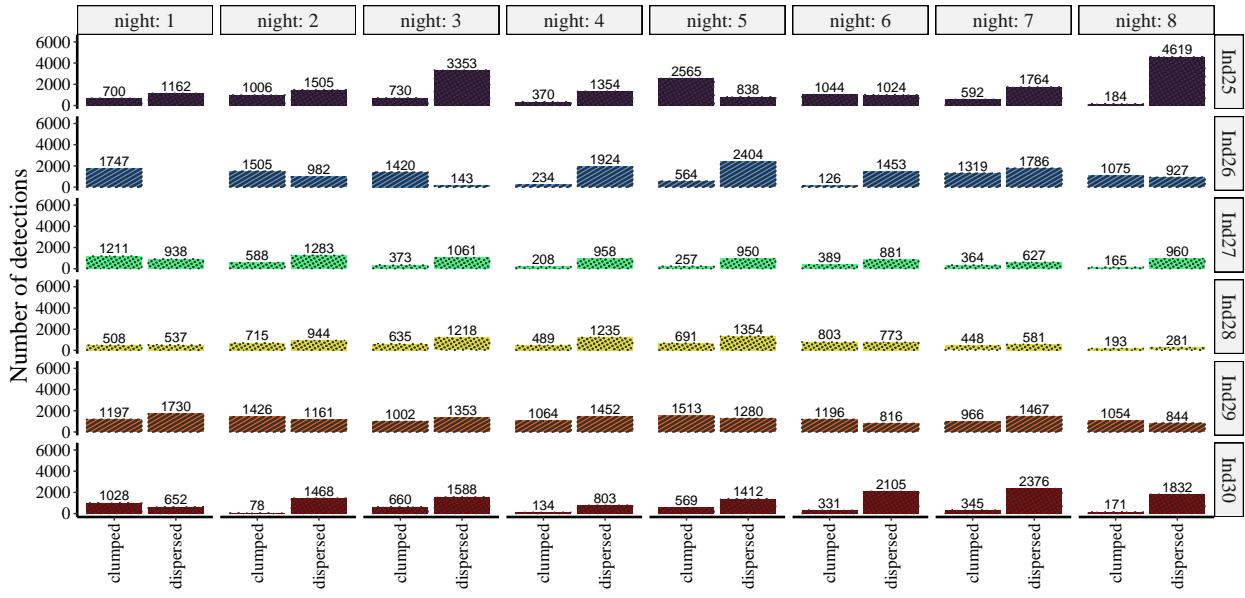


Figure S8: Raw number of detections for all bats in males-only group. Same notation as in Fig. S4, but the colors correspond to different individuals.

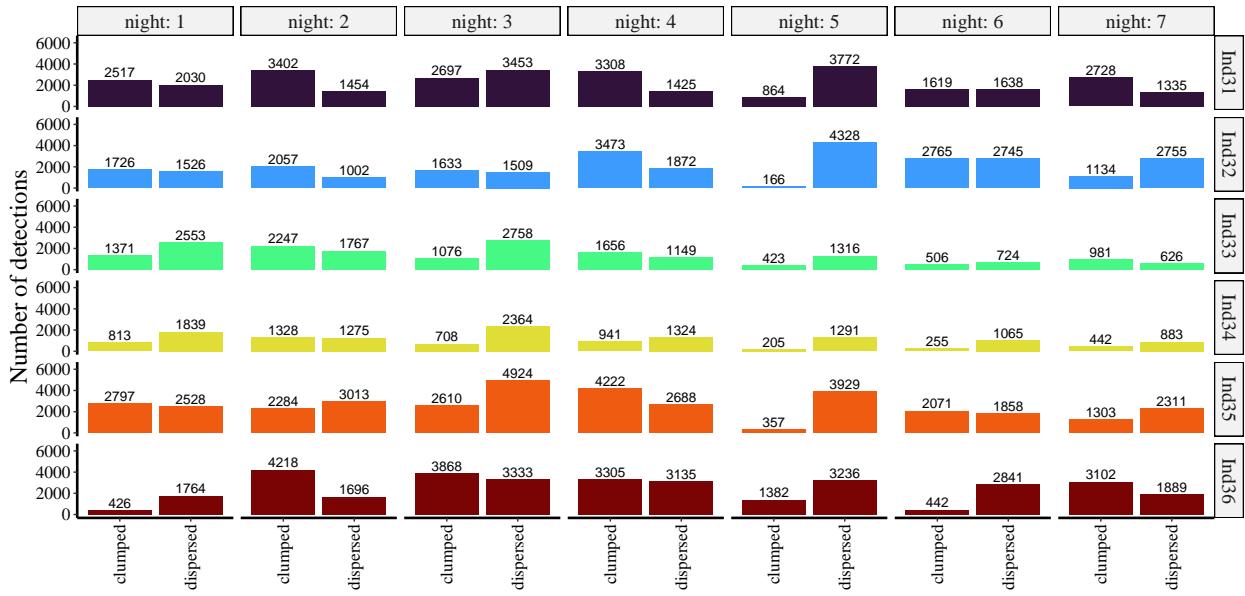


Figure S9: Raw number of detections for all bats in females-only group 1.

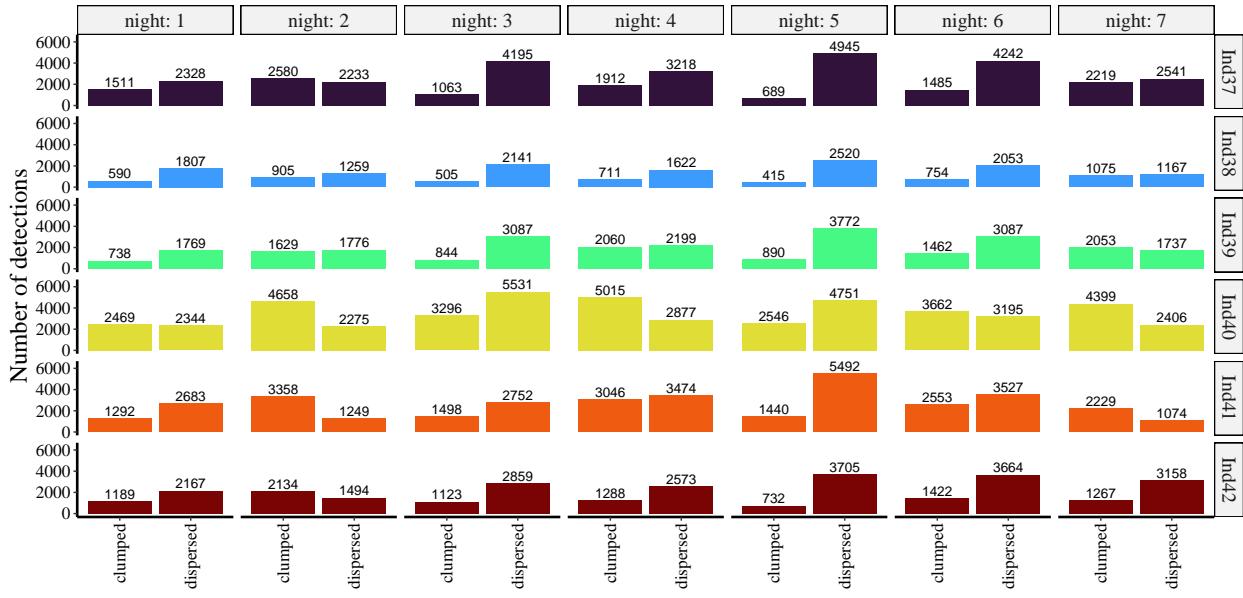


Figure S10: Raw number of detections for all bats in females-only group 2.

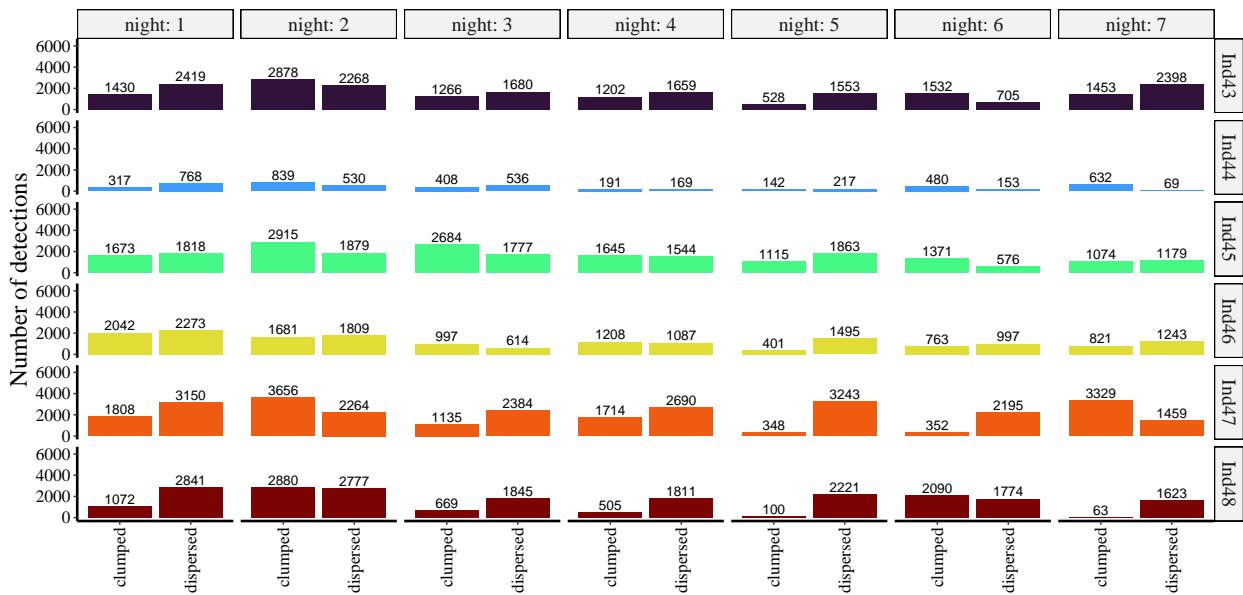


Figure S11: Raw number of detections for all bats in females-only group 3.

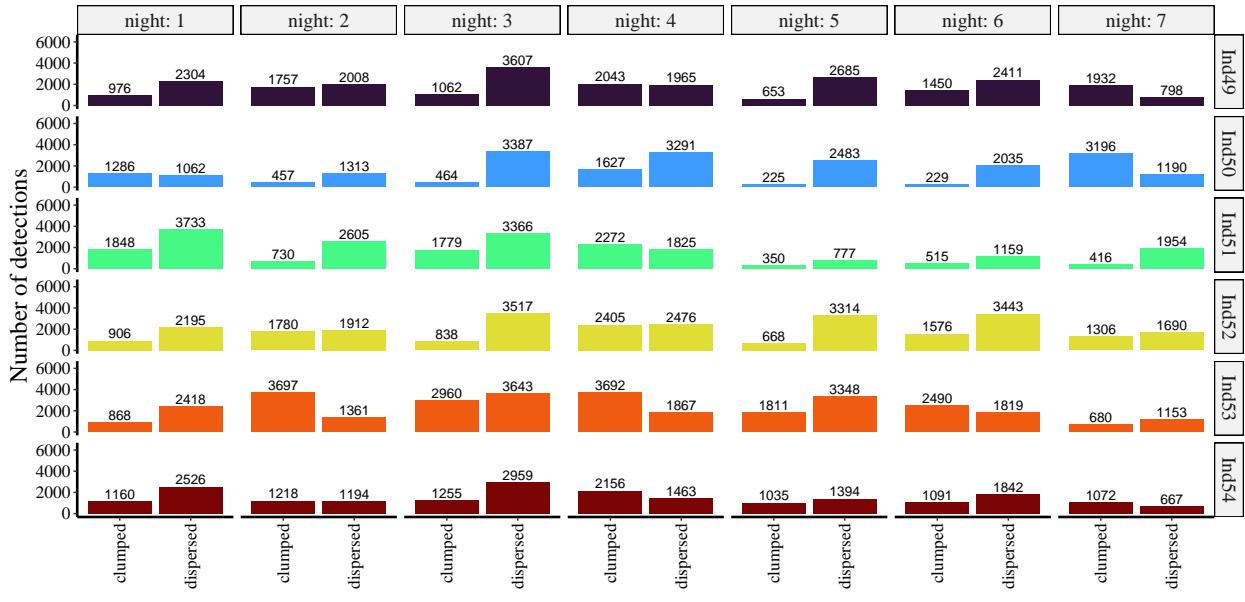


Figure S12: Raw number of detections for all bats in females-only group 4.

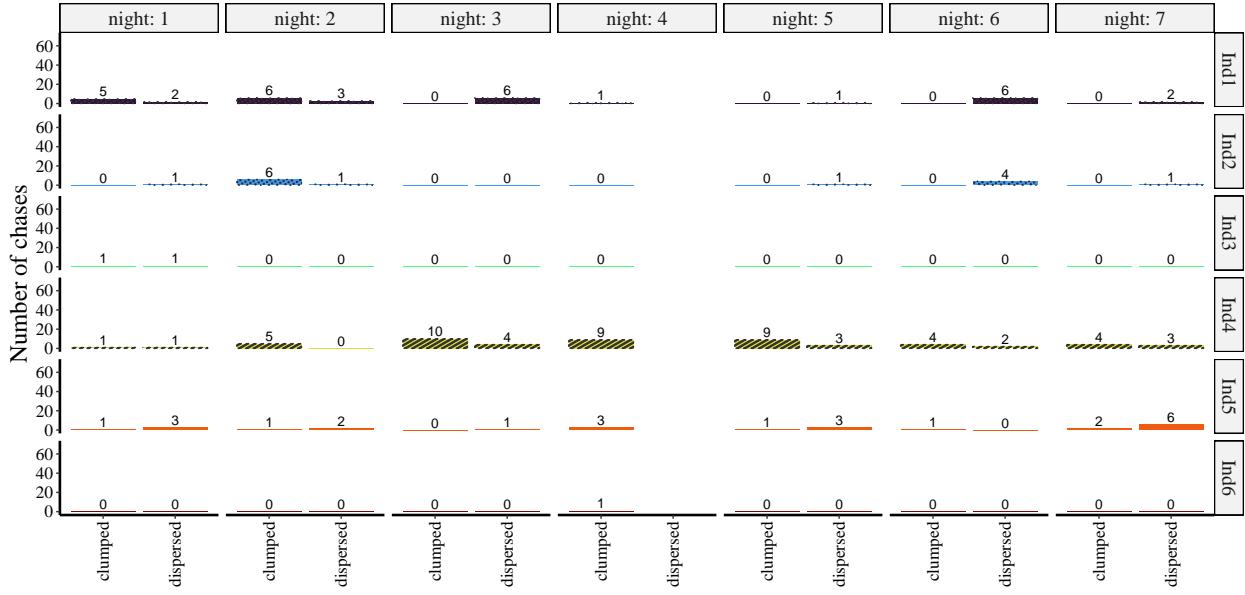


Figure S13: Raw number of chase events for all bats in mixed group 1. Same notation as in Fig. S4, but the colors correspond to different individuals.

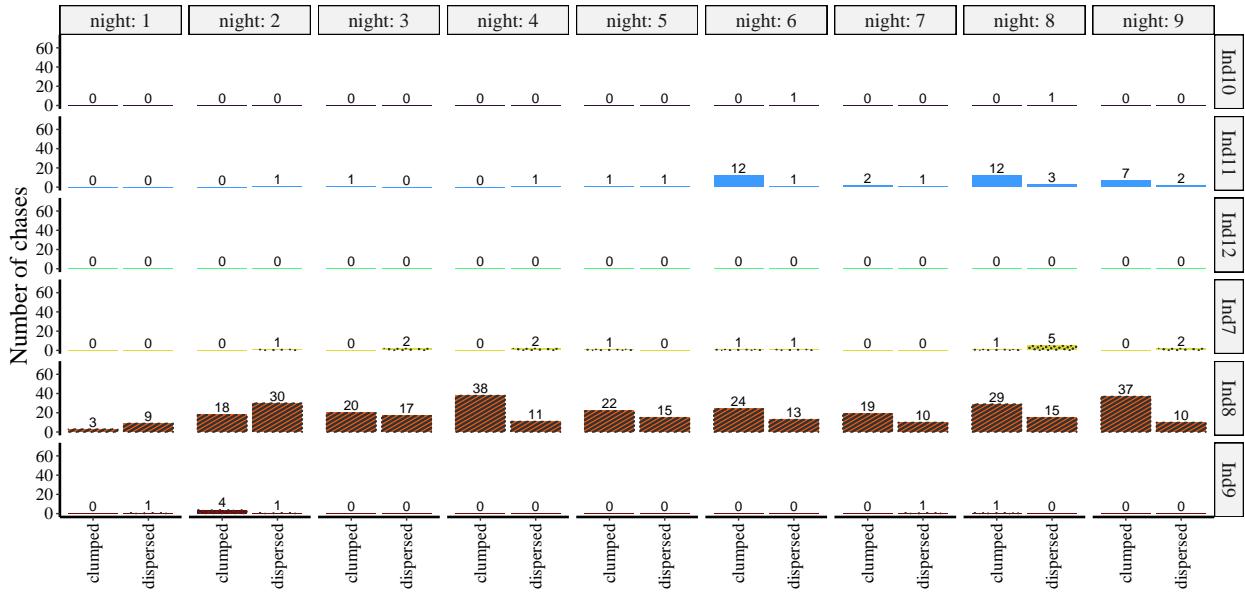


Figure S14: Raw number of chase events for all bats in mixed group 2. Same notation as in Fig. S4, but the colors correspond to different individuals.

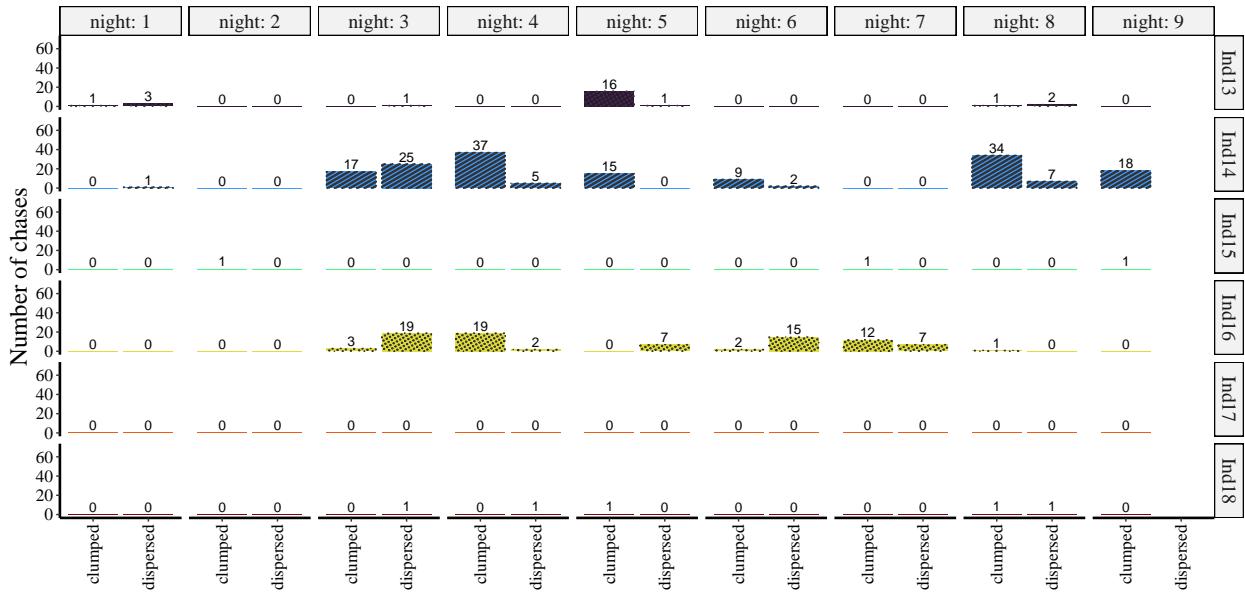


Figure S15: Raw number of chase events for all bats in mixed group 3. Same notation as in Fig. S4, but the colors correspond to different individuals.

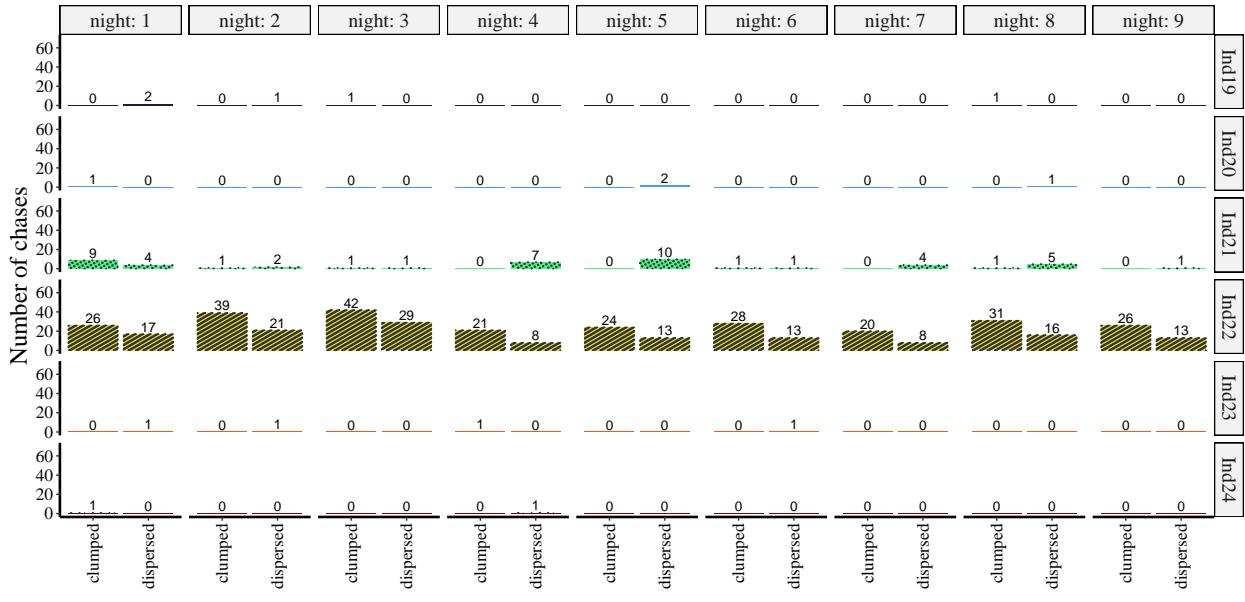


Figure S16: Raw number of chase events for all bats in mixed group 4. Same notation as in Fig. S4, but the colors correspond to different individuals.

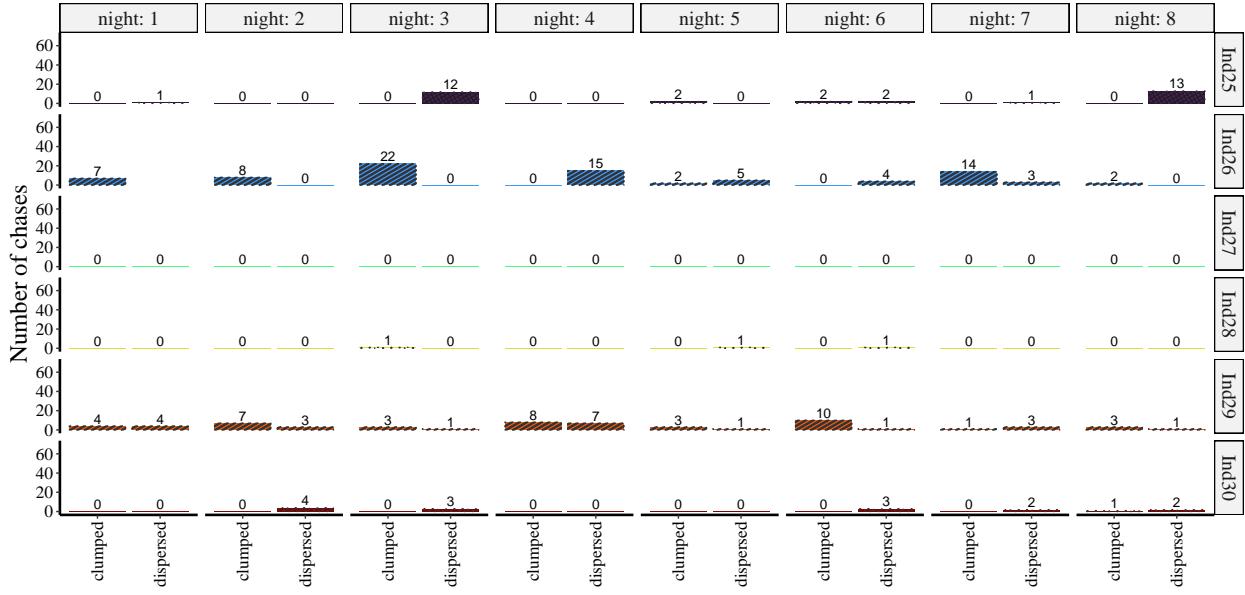


Figure S17: Raw number of chase events for all bats in males-only group. Same notation as in Fig. S4, but the colors correspond to different individuals.

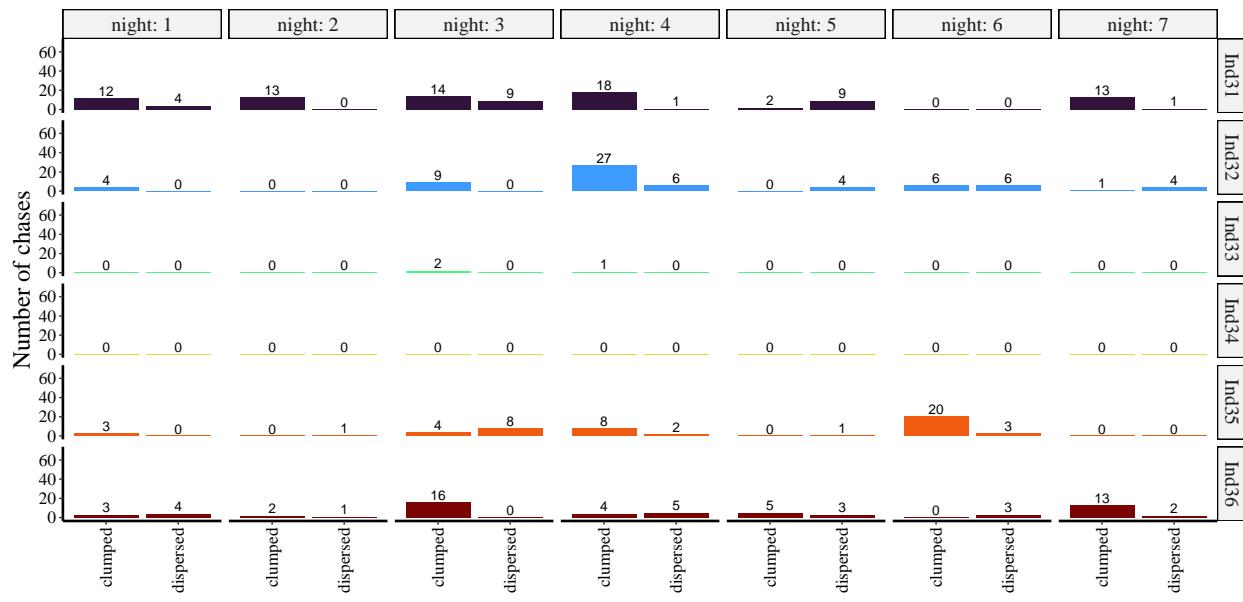


Figure S18: Raw number of chase events for all bats in females-only group 1.

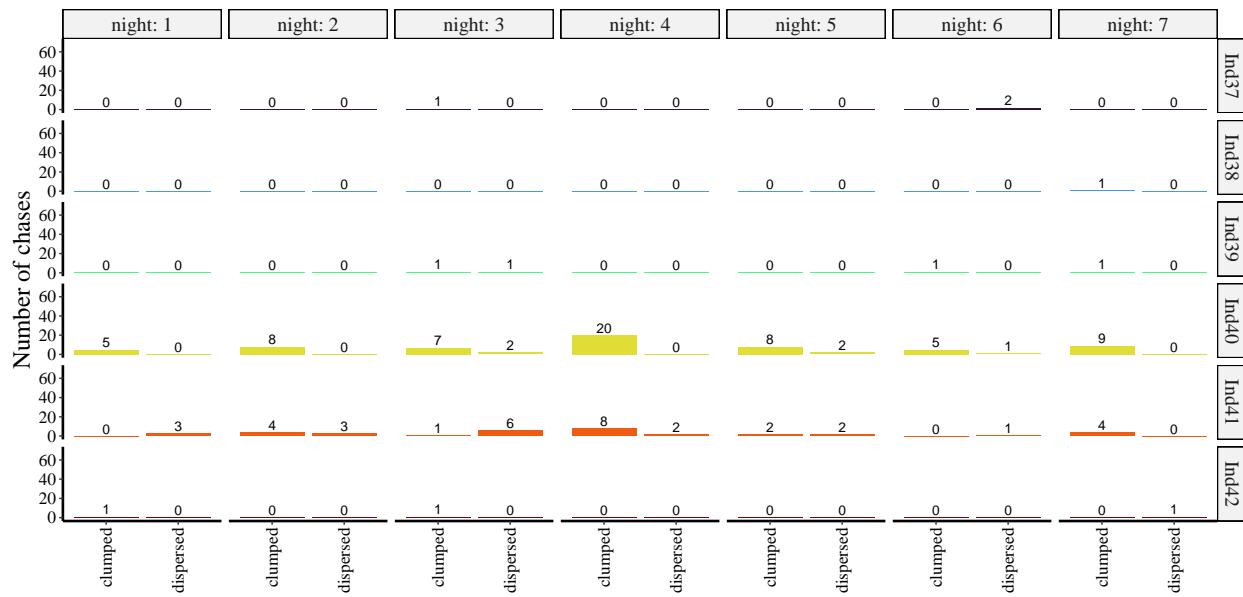


Figure S19: Raw number of chase events for all bats in females-only group 2.

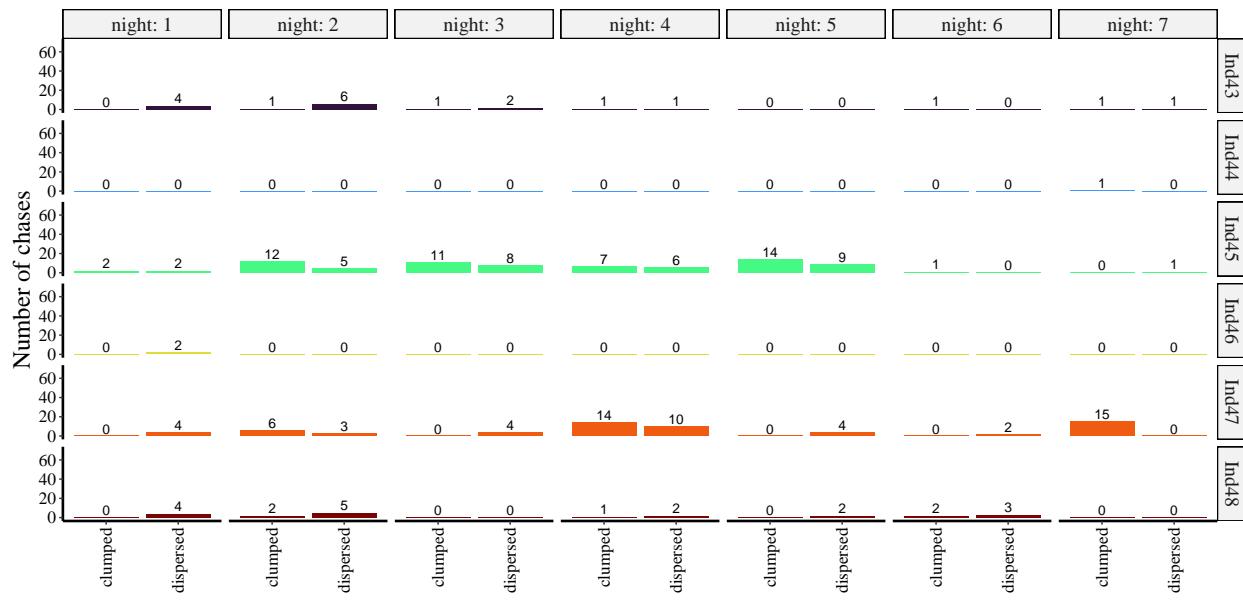


Figure S20: Raw number of chase events for all bats in females-only group 3.

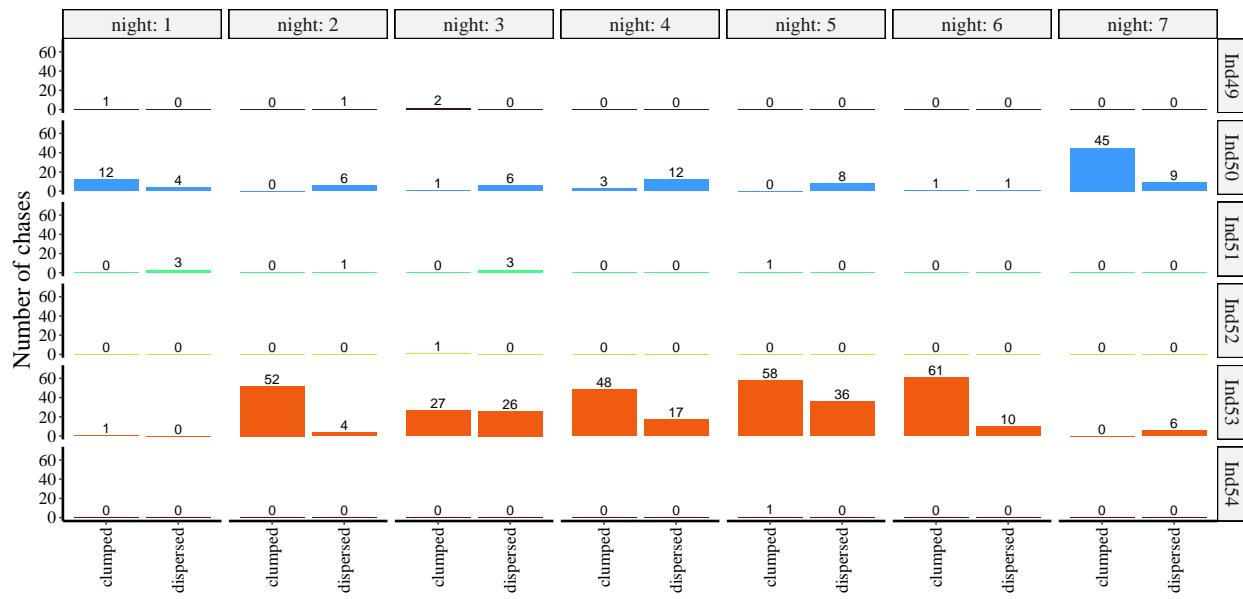


Figure S21: Raw number of chase events for all bats in females-only group 4.

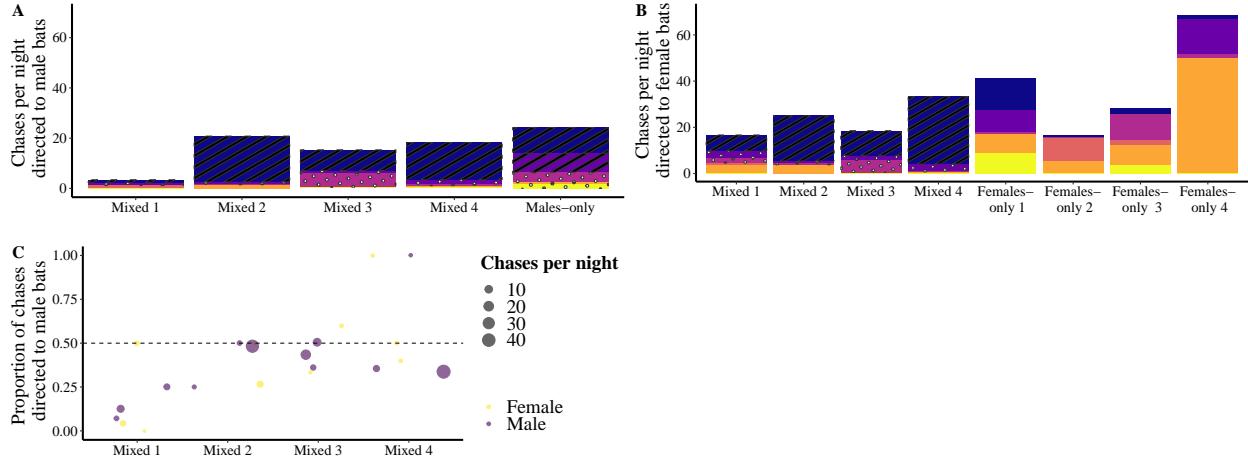


Figure S22: Frequency of chase events directed to bats of either sex. (**A, B**) Colored bars give the frequency of chase events per night (total chases divided by number of nights) over the main experiment by each individual from each group (abscissa) towards male (**A**) and female (**B**) bats. The 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.

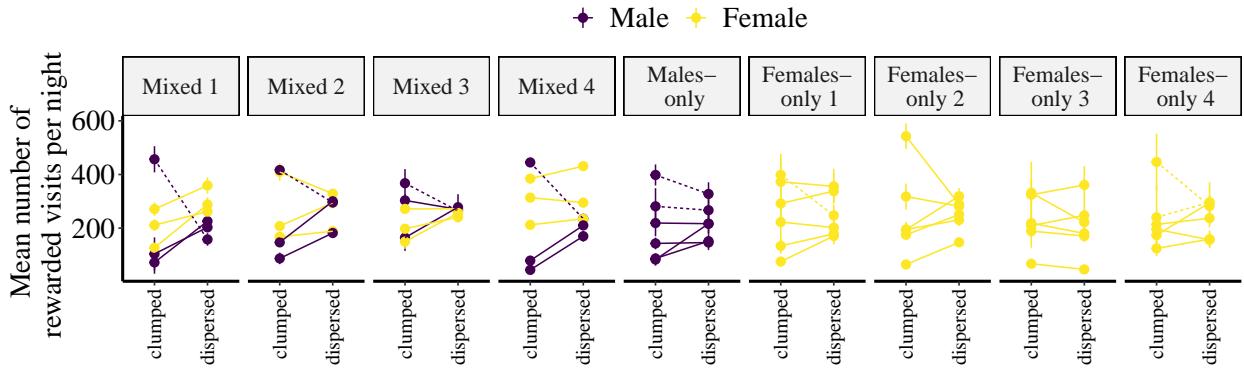


Figure S23: Number of rewarded visits per night (mean \pm SE) during the clumped and dispersed reward treatments for male (purple) and female (yellow) bats in each experimental group (panels). Data from the same individuals are connected with lines. Data from individuals classified as “dominant” are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

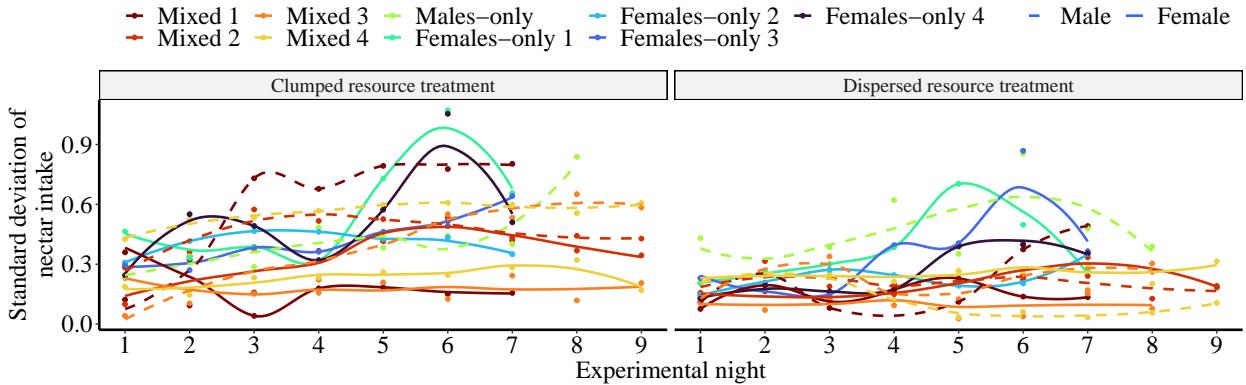


Figure S24: The standard deviation of group nectar consumption was used to measure the between-individual differences in nectar intake. It was calculated for the clumped (left panel) and the dispersed (right panel) resource treatments, separately for males (dashed lines) and females (continuous lines) 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).

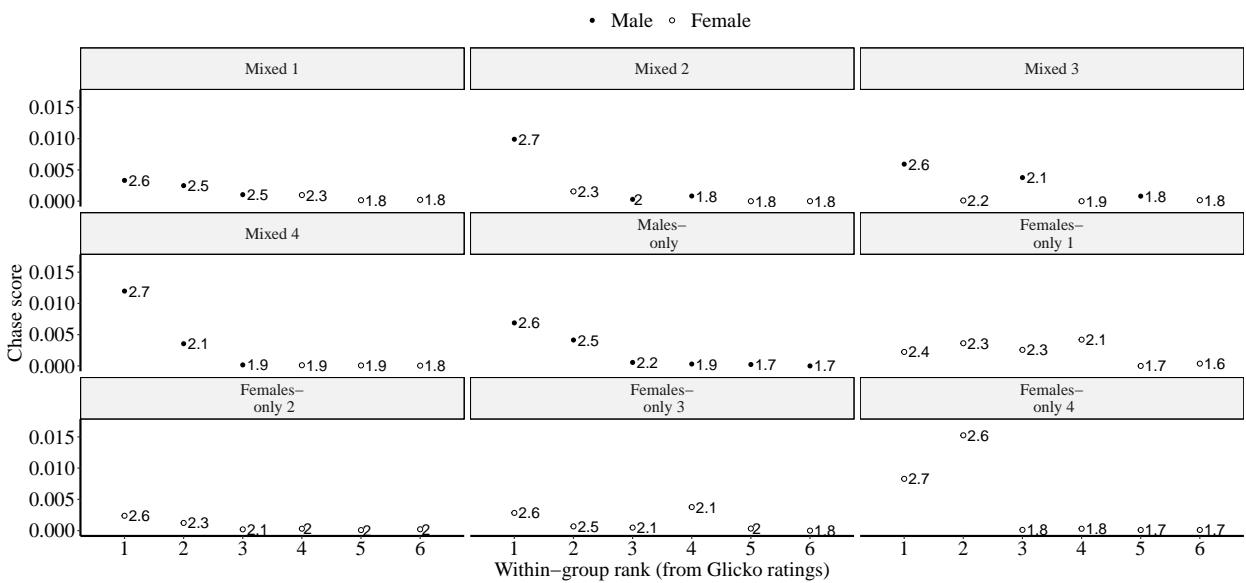


Figure S25: Glicko ratings within the six experimental groups. Over the last two experimental nights, the males (closed symbols) with the highest chase scores were also the individuals with the highest Glicko rating in each group (panels) during the clumped resource treatment. In female-only groups this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

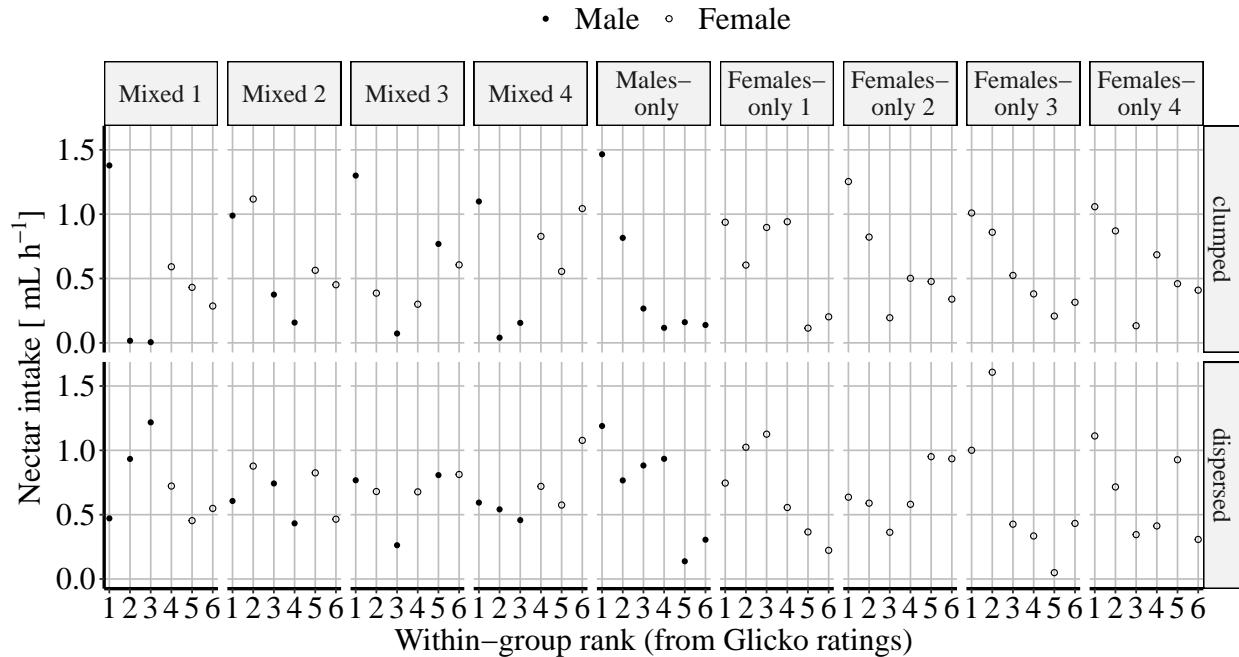


Figure S26: Male bats or female bats in the single-sex groups with the highest Glicko ratings had the highest nectar intake rates during the clumped, but generally not during the dispersed resource treatment.

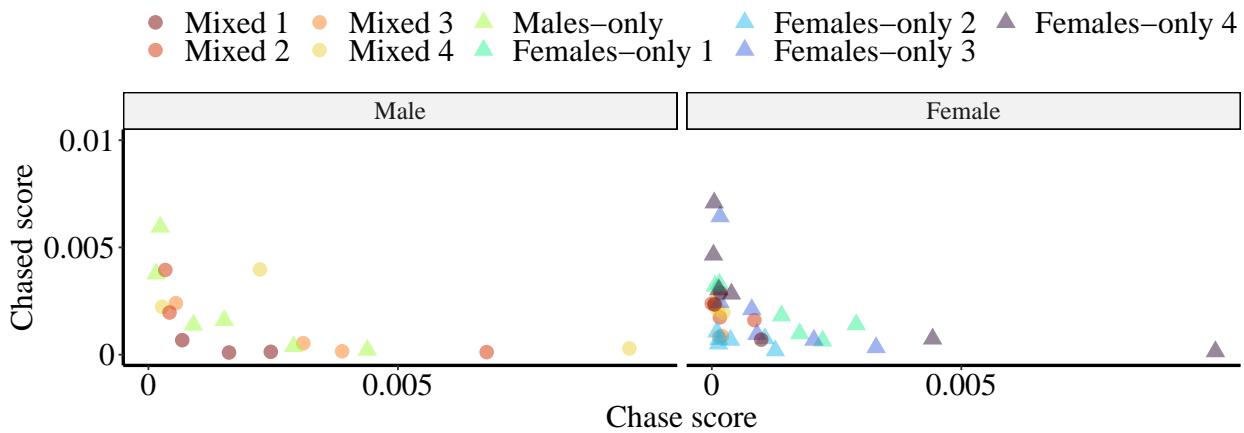


Figure S27: The relationship between chase score and chased score (proportion of chases versus the proportion of being chased out of all detections) for female (right) and male (left) individuals in all experimental groups (different colors). Mixed groups are shown with circles and single-sex groups,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

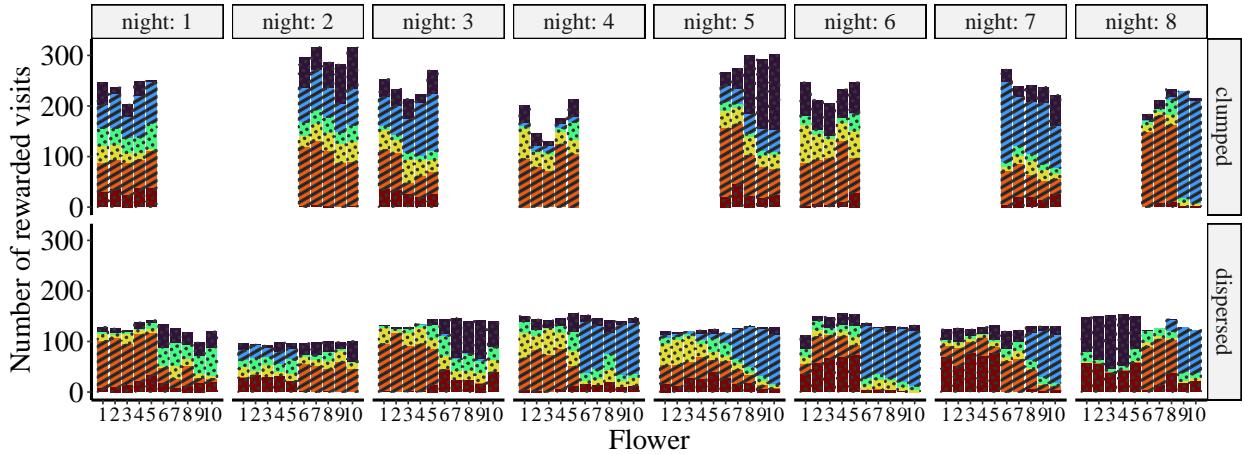


Figure S28: Distribution of rewarded visits across flowers for the six bats in the males-only group. The colored bars give the number of rewarded visits of each individual at the ten flowers during the clumped (top) and dispersed (bottom) resource treatments for each experimental night (columns). The 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.

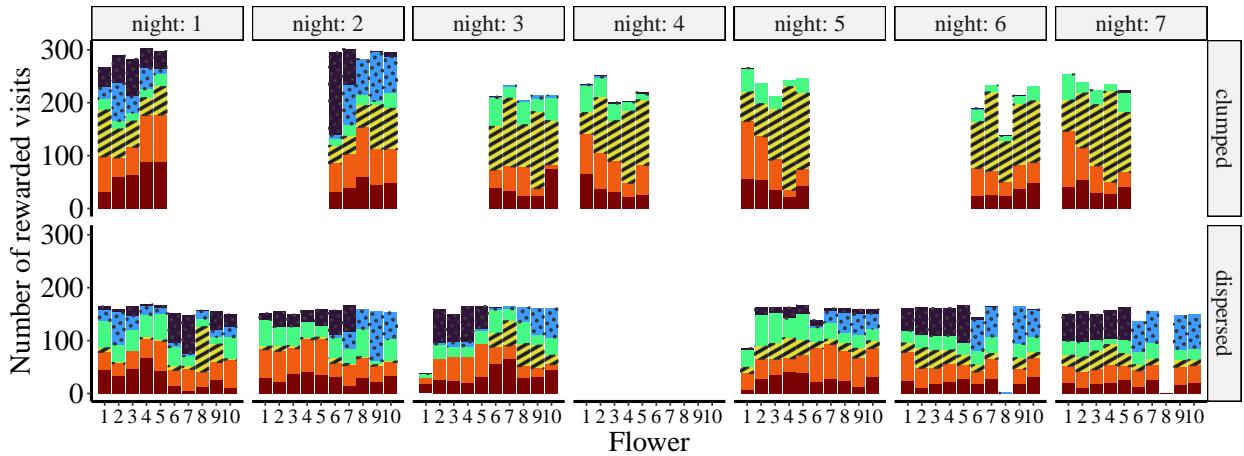


Figure S29: Distribution of rewarded visits across flowers for the six bats in mixed group 1. The colored bars give the number of rewarded visits of each individual at the ten flowers during the clumped (top) and dispersed (bottom) resource treatments for each experimental night (columns). The dominant 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.

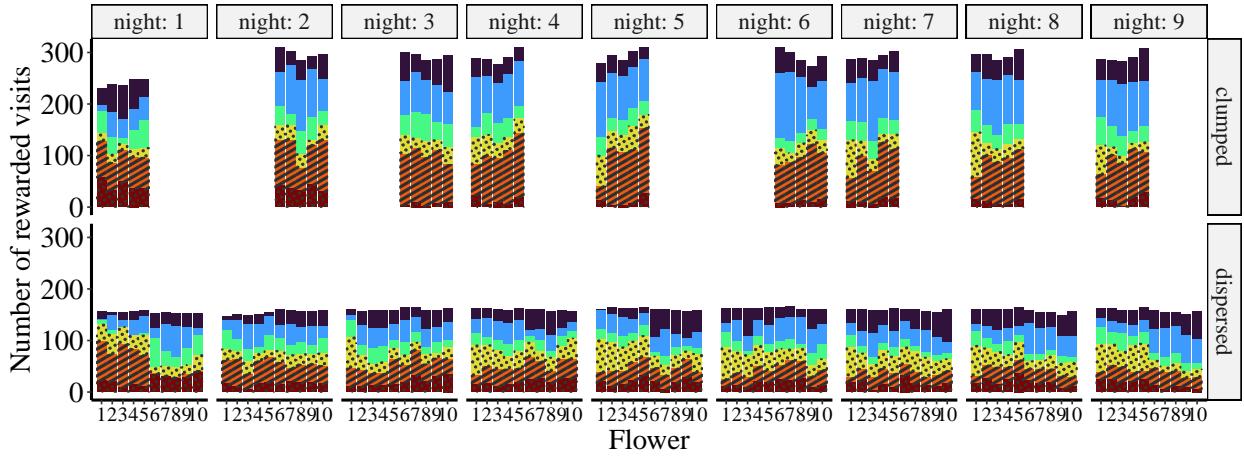


Figure S30: Distribution of rewarded visits across flowers for the six bats in mixed group 2. Same notation as in Fig. S29, but the colors correspond to different individuals.

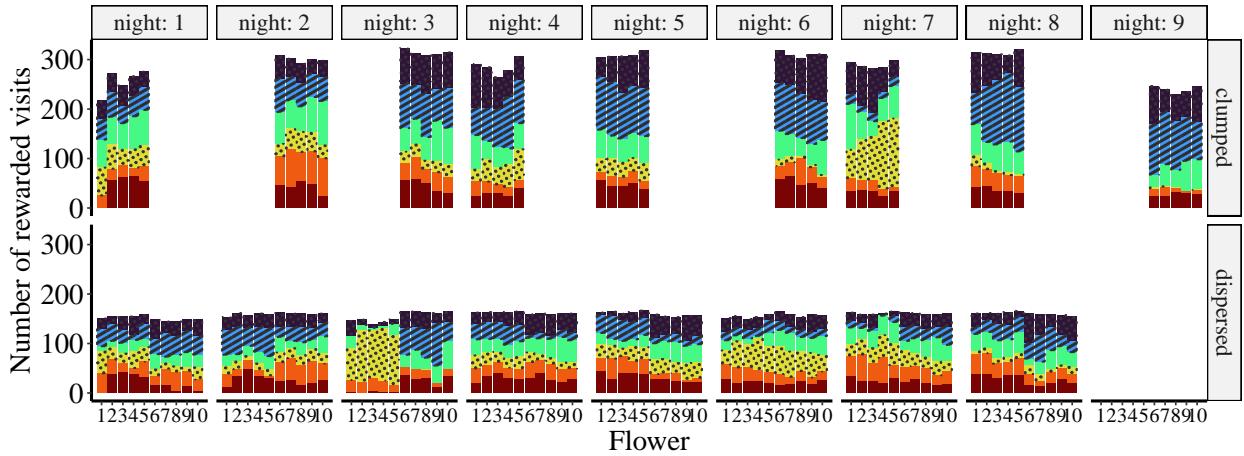


Figure S31: Distribution of rewarded visits across flowers for the six bats in mixed group 3. Same notation as in Fig. S29, but the colors correspond to different individuals. Due to a technical malfunction on night 9, there were no rewards delivered in the dispersed resource treatment and the data were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

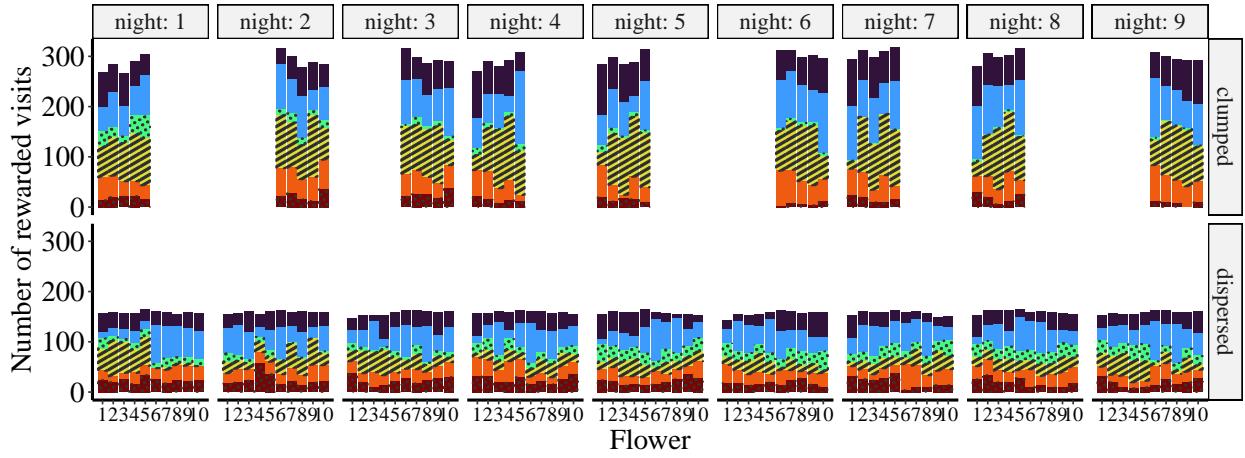


Figure S32: Distribution of rewarded visits across flowers for the six bats in mixed group 4. Same notation as in Fig. S29, but the colors correspond to different individuals.

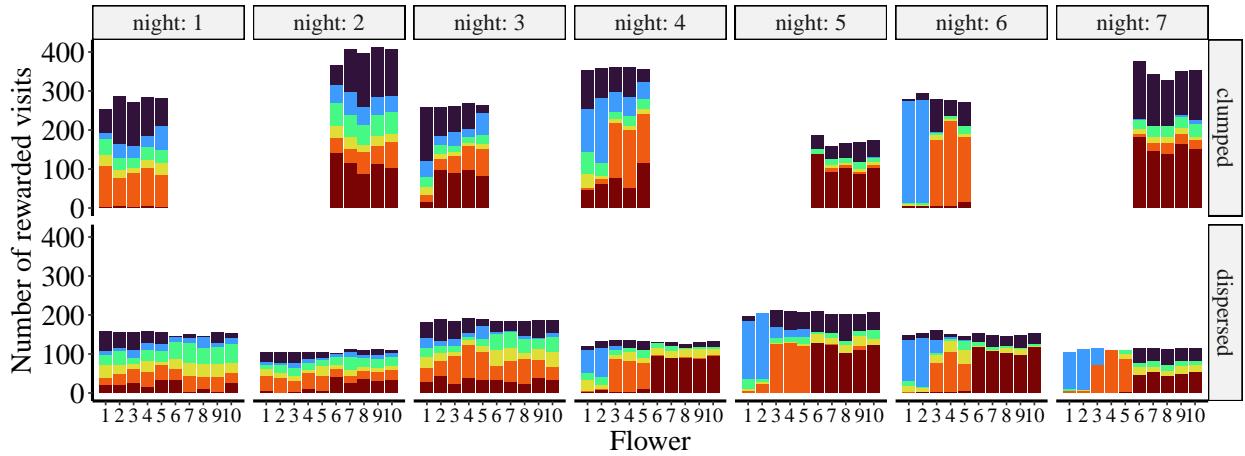


Figure S33: Distribution of rewarded visits across flowers for the six bats in the females-only group 1. Same notation as in Fig. S29, but the colors correspond to different individuals.

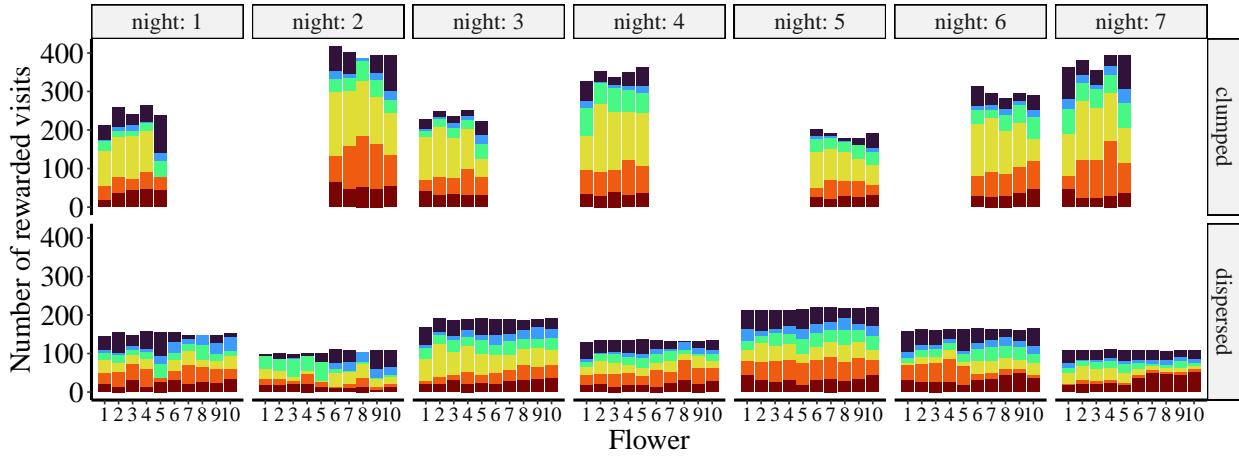


Figure S34: Distribution of rewarded visits across flowers for the six bats in the females-only group 2. Same notation as in Fig. S29, but the colors correspond to different individuals.

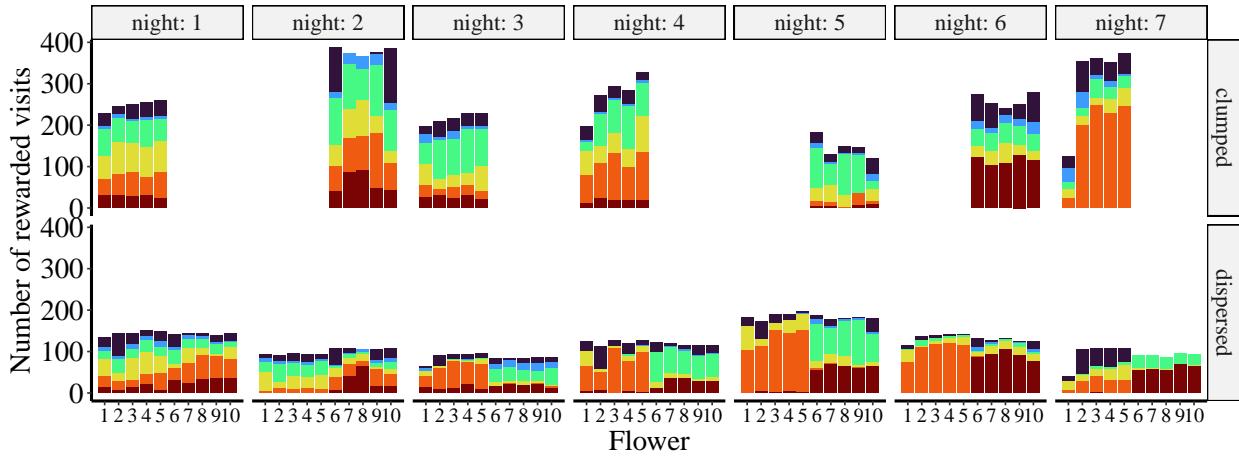


Figure S35: Distribution of rewarded visits across flowers for the six bats in the females-only group 3. Same notation as in Fig. S29, but the colors correspond to different individuals.

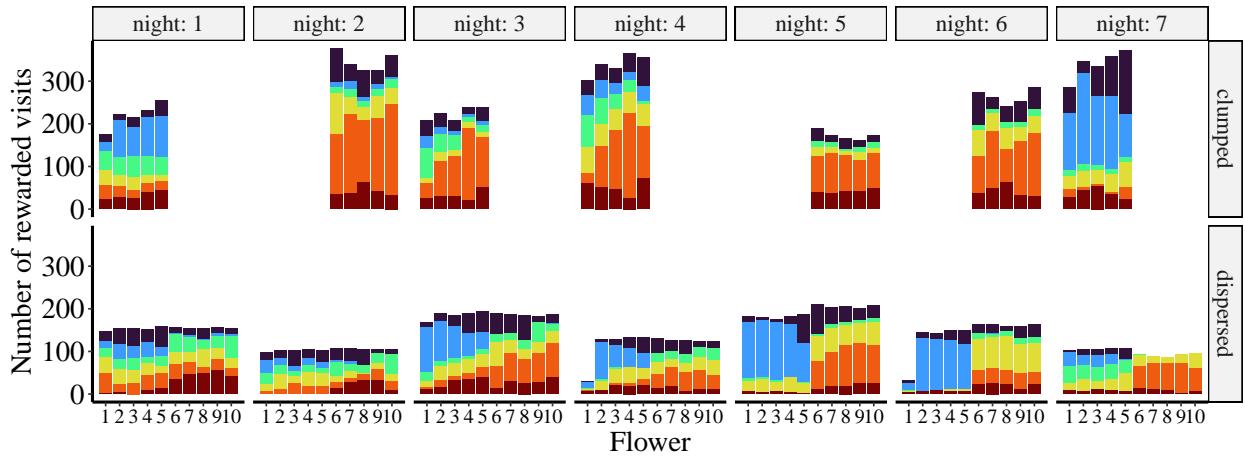


Figure S36: Distribution of rewarded visits across flowers for the six bats in the females-only group 4. Same notation as in Fig. S29, but the colors correspond to different individuals.

⁴³³ **Authors' contributions**

⁴³⁴ S.W. Conceptualization, Methodology, Software, Data collection, Formal Analysis, Video Analysis, Writing—
⁴³⁵ original draft. V.N. Conceptualization, Methodology, Software, Formal Analysis, Data curation, Writing—
⁴³⁶ review and editing, Visualization, Supervision, Project Administration.
⁴³⁷ Y.W. Conceptualization, Resources, Methodology, Software (data acquisition), Writing—review and editing,
⁴³⁸ Supervision, Funding.

⁴³⁹ **Competing interests**

⁴⁴⁰ We declare we have no competing interests.

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⁴⁴⁹ **Data Availability**

⁴⁵⁰ All data and code are available in the Zenodo repository: <https://doi.org/10.5281/zenodo.5205511>.

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