

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

²
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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 distributed 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 additional advantage if they are intimately familiar with their
54 feeding area. Compared to an insect-hunting bat that must continually scan for elusive prey by active
55 echolocation, a flower visitor can approach a target with minimal echolocation when seeking specific flowers
56 at known locations (Thiele and Winter 2005; Winter and Stich 2005; Gonzalez-Terrazas et al. 2016; Rose et
57 al. 2016). 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 the
62 night (Lemke 1984, 1985). When left unguarded, intruders quickly exploited 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 was that
66 the defense did not cover the area of a typical feeding range but was restricted to a single or a few flowering
67 plants and was also limited to a small number of hours during the night. Still, glossophagine bats can show
68 aggressive resource defense.

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

91 2. Materials and methods

92 (a) Subjects and housing

93 Experiments were conducted with 36 individuals of the small, (9-10g) neotropical nectarivorous bat species
94 formerly identified as *Glossophaga soricina* (Pallas's long-tongued bat). In view of the recent taxonomic
95 revision of the *G. soricina* species complex (Calahorra-Oliart, Ospina-Garcés, and León-Paniagua 2021), it is
96 relevant to note that the founders of our colony used in this and all our previous studies were caught at the
97 Cueva de las Vegas, Municipio de Tenampulco, Mexico and transported to Germany in 1988 by Otto von
98 Helversen. Thus they belong to the species *G. mutica*. Bats came from our captive colony and were older
99 than one year as judged by finger joint ossification (Brunet-Rossini and Wilkinson 2009). They carried radio
100 frequency identification (RFID) tags attached to cable tie collars (total weight of collar with tag = 0.2g, max.
101 2.4% of the body weight) that were removed after the experiment. Additionally, bats had numbered plastic
102 split rings (A C Hughes Ltd., Middlesex, UK) around the forearm for visual identification. Temperature in
103 the experimental and colony room was kept at 20-25°C, air humidity at 65-75%, and light conditions were

104 12:12 LD (light off at 16h).

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

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

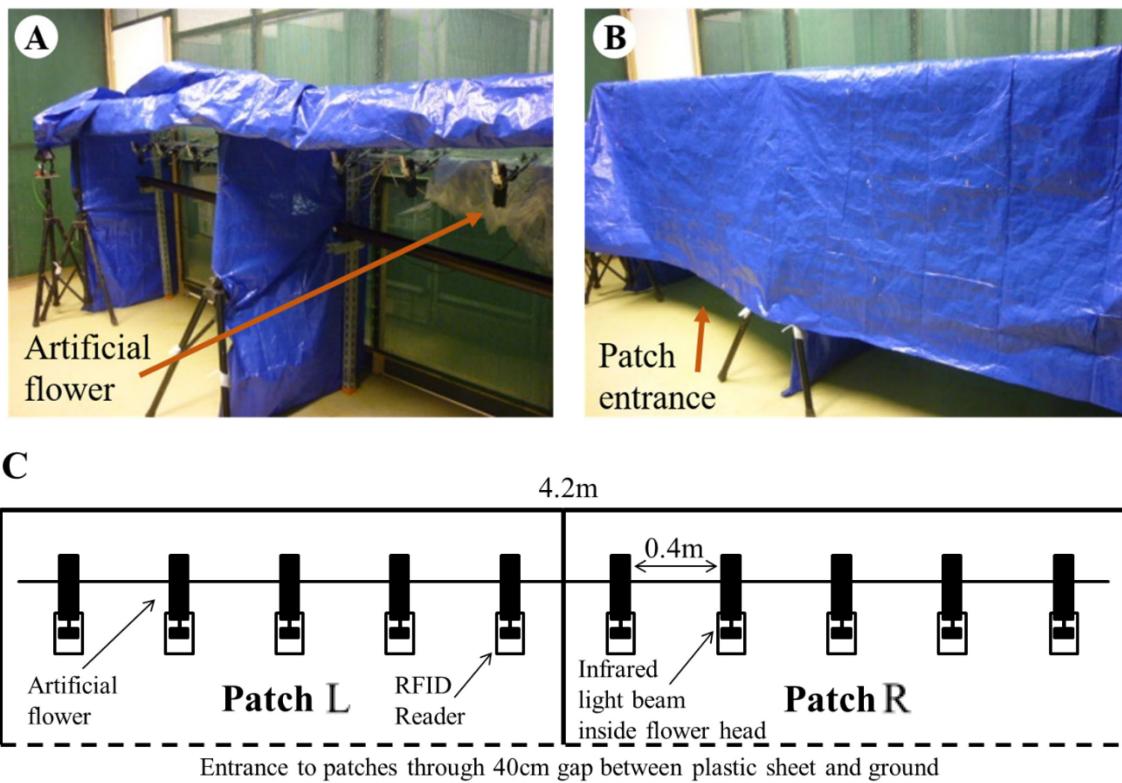


Figure 1: Experimental set-up consisting of two spatially separated patches of five flowers each. (A) The ten flowers were mounted 1.2m above ground. They were divided into two patches, L and R. (B) During experiments the patches were separated by plastic sheets. To make it more demanding for bats to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

119 **(c) Experimental procedure**

120 Six bats were randomly caught from the colony and were tested simultaneously as a group. Four experimental
121 groups consisted of three males together with three females (mixed groups), whereas one group consisted of

122 six males, and another of six females. All bats were weighed before the experiment.
123 During the nightly experiments, in addition to the nectar provided by artificial flowers, bats had access to
124 pollen and water and to 6mL of additional food containing 1.2g NektarPlus (Nekton, Keltern, Germany)
125 and 1.8g milk powder (Milasan Folgemilch 2, Sunval Baby Food GmbH, Mannheim, Germany) dissolved in
126 water. Rewards at flowers consisted always of 30 μ L nectar (15% w/w sugar concentration, sucrose: fructose
127 1:2). Before the experimental schedule started, individuals were allowed to familiarize themselves with the
128 set-up and the artificial flowers. Since during this training phase the plastic cover was removed, the two
129 flower patches were not spatially separated and every flower visit was rewarded. This phase lasted for one to
130 four nights until each bat visited the flowers regularly. One female of the first mixed group did not visit any
131 artificial flower during the first night and was replaced by another female.
132 During the experiment, the two flower patches were covered and spatially separated (Fig. 1. Experimental
133 nights were divided into two phases. During the first phase of the night only one of the two flower patches was
134 rewarding, and therefore the resources were spatially clumped at a single location. The fixed time interval
135 between rewards at each flower was 60s. During the second phase of the night both patches gave rewards,
136 resources were evenly distributed across the two patches, and the fixed time interval between two rewards at
137 a flower was increased to 120s. Therefore, the amount of food available per unit time did not change during
138 the whole night; only the spatial distribution of food changed from the clumped resource condition with one
139 patch rewarding (five flowers) during the first phase of the night to the distributed resource condition with two
140 patches rewarding (ten flowers) during the second phase of the night. With this experimental schedule,
141 the maximal amount of nectar the bats could collect was 108mL, which corresponds to 18mL nectar per
142 individual per night, roughly 150% of their daily requirement (Winter and Helversen 2001). The side of
143 the rewarding patch during the first phase of the night was chosen pseudo-randomly and the same patch
144 was never chosen in more than two consecutive nights. For the mixed groups, the duration of the clumped
145 resource condition was six hours and the experiment lasted nine nights (seven nights for the first mixed
146 group). For the same-sex groups, the duration of the first part of the night was variable (range = 4-8h, mean
147 = 6h) and the experiment lasted eight nights for the male group and seven nights for the female group.

148 (d) Chasing behavior

149 We took the frequency of individuals chasing each other at the artificial flowers as an indicator of the
150 intensity of aggressive interactions between group members. We developed a method to automatically detect
151 and score chasing events using the computer-collected animal identification data from the RFID sensors
152 and flower sensors. In a previous pilot study (Wintergerst 2018), three mixed groups of bats were video
153 recorded for 24h over 14 nights, and the video data were synchronized to the computer-collected data.
154 During this pilot study flowers were not covered by plastic sheets so that all flowers and the surrounding
155 room were visible on video. From the analysis of the combined data we were able to identify the following
156 pattern of visitation events that reliably indicated a chasing event between two identified individuals:
157 (i) an identified bat visited a flower and (ii) its visit was instantaneously followed by the detection of a
158 second bat, the chaser, that was detected very briefly (<200ms) and only by the ID sensor (detection
159 range 5-7cm). Importantly, this second bat never attempted to drink and therefore did not insert its nose
160 into the artificial flower and interrupt the light barrier inside the flower head. This distinguished such
161 a chase from the occasional quick succession of two feeding visits by two bats at the same flower. This
162 automated detection of chasing events not saves considerable time for the experimenter, but also avoids the
163 human observer bias, a common drawback in video analysis. For the 24 hours of combined video data and
164 automatically logged data, all 89 chasing events detected in the computer-logged data were confirmed by
165 video. Therefore, we consider the algorithm for detecting chasing events in the logged data to be highly
166 reliable. Of course, chases did not only occur at the artificial flowers. Thus, our chase numbers are only
167 an indicator of chasing intensity between pairs of bats. For example, in one hour of video we observed 61
168 chasing events, but only five of those occurred during flower visits and were also automatically detected.
169 However, since with our algorithm (see below) we detected a total of 1811 chasing events (35.5 ± 12.3
170 events per night during the experiment and only 4.8 ± 3 during the training nights, mean \pm SD) for
171 the 36 participating bats, we considered the automated approach adequate for quantifying within-group
172 dominance relationships. The total number of individual detections per night constrains the number of
173 chasing opportunities detectable with our method. Therefore, we corrected our counts of chasing events by

174 dividing the number of observed chases for each bat by the total number of detections for that bat on each night.

175

176 (e) Statistical analysis

177 To investigate the difference in chasing behavior between males and females and between the resource
178 conditions (one versus two rewarding patches) a Bayesian generalized linear mixed model (`MCMCglmm`, Hadfield
179 2010) with a binomial error structure was used. Body weight as an approximation of size and the full
180 interaction between resource condition and sex were included as fixed effects and the influence of these fixed
181 effects on the proportion of chasing events was assessed. Experimental group and individual were included
182 as random effects. The same model structure was used to address the question if the proportion of being
183 chased was influenced by these independent variables. If one or more individuals start to defend flowers and
184 thus exclude others from drinking, nectar consumption should increasingly differ between individuals since
185 the successful chaser should gain a higher nectar intake thus reducing the intake of the chased individuals.
186 Therefore, the between-individual difference in nectar consumption over the course of the experiment was
187 compared between experimental groups and resource conditions (clumped vs. distributed). First, each
188 individual's total nectar consumption standardized by the number of hours of foraging during the clumped
189 (one rewarding patch) and distributed (two rewarding patches) resource condition was determined for each
190 experimental night. Then these data were used to calculate group standard deviations, separately for the
191 males and females of each group. In order to assess the influence of resource defense on the individual
192 differences in nectar consumption (standard deviation of nectar intake) we fit a `MCMCglmm` model with a
193 Gaussian error structure and the following fixed effects: sex, experimental night (centered), and resource
194 condition (clumped or distributed), as well as all two-way interactions. Again, we included group and
195 individual as random effects.

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

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

210 3. Results

211 (a) Example of nectar intake in one experimental group

212 The goal of our experiment was to investigate the sex-specific effects of resource defense in *Glossophaga*
213 *soricina*, in addition to the potential influence of interference competition on individual nectar intake. The
214 first striking observation we made was the uneven distribution of nectar consumed between the sexes and
215 individuals. For example, in the first mixed group of bats tested, after only two nights the nectar consumption
216 of two males was nearly reduced to zero, whereas the third male increased its consumption substantially (Fig.
217 2A). This pattern, however, only occurred during the clumped resource condition. Nectar consumption of
218 females did not change even during the clumped condition. On the same nights but during the second half of
219 the night, with resources distributed over two patches, nectar consumption of males and females converged at
220 the end of the experiment (Fig. 2B).

221 (b) Differences between sexes in frequency of chasing and being chased

222 In all mixed groups males chased other bats in front of flowers significantly more often than females did
 223 (Fig. 3A, Table 1). Notably, the frequency of females as active chasers in female-only groups was higher than
 224 chasing by females in the mixed groups (Fig. 3A). Although the rate of nectar availability remained constant
 225 throughout the night and only the spatial distribution of the resources changed, the number of chasing events
 226 was significantly lower during the distributed resource condition when rewards were available at both patches
 227 (Table 1). There was no significant difference between the sexes in how often a bat was chased by another
 228 individual (Fig. 3B) but individuals were chased less during the distributed resource condition (Table 1).
 229 Weight as an indicator of size had no significant effect on chasing frequency or the frequency of being chased
 230 (Table 1).

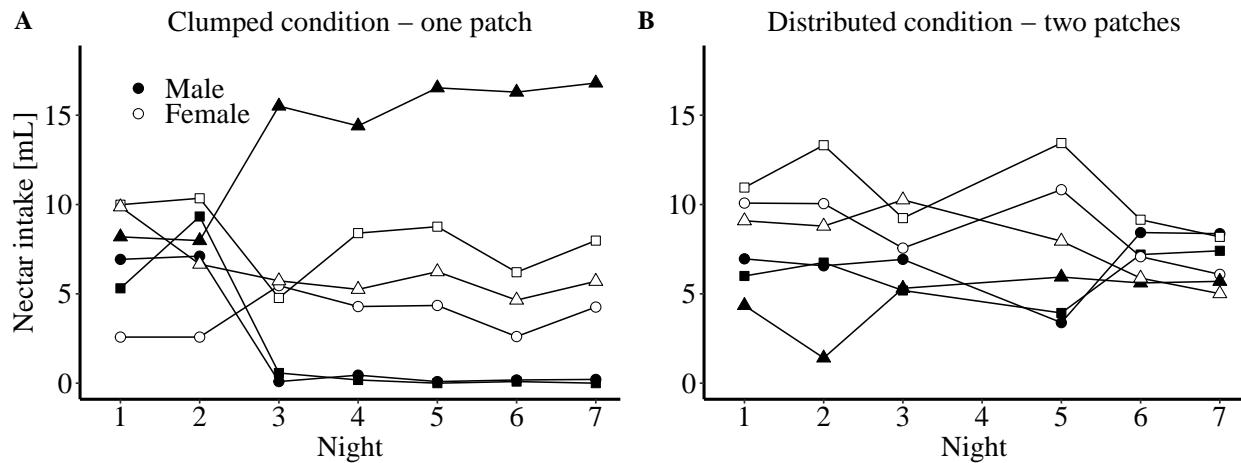


Figure 2: Change of individual nectar consumption from the clumped condition (A) to the distributed condition (B) during an experiment of one mixed group (3M, 3F, symbols show different individuals). (A). During the clumped resource condition (first part of the experimental night) rewards were only available 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 distributed resource condition (second part of the experimental night) rewards were available at both patches. Under this condition, 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.

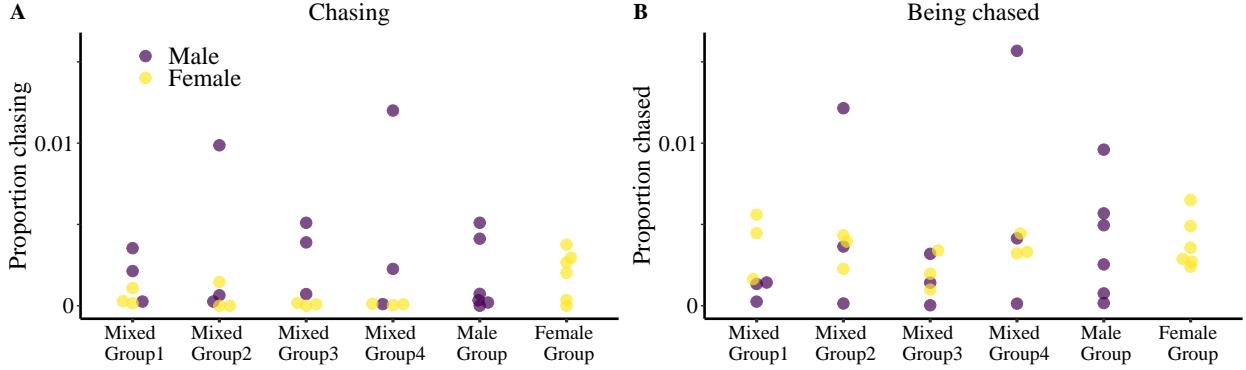


Figure 3: Sexes differed in the frequency of chasing or being chased during the clumped resource condition. (A) Males (dark symbols) chased others significantly more than females did (light symbols, Table 1). Shown are the individual proportions of chasing events over the whole experiment. Notably, in the females-only group 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), but the variance of being chased was much higher for males.

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
Chasing				
	(Intercept)	-6.52	(-18.06, 5.46)	0.252
	sex (female)	-2.09	(-3.47, -0.65)	0.001
	condition (distributed)	-0.49	(-0.76, -0.23)	0.001
	weight	-0.01	(-1.34, 1.1)	0.962
	sex (female):condition (distributed)	-0.29	(-0.75, 0.19)	0.228
Being chased				
	(Intercept)	-2.93	(-11.98, 4.61)	0.496
	sex (female)	0.90	(-0.12, 1.86)	0.078
	condition (distributed)	-0.98	(-1.24, -0.74)	0.001
	weight	-0.40	(-1.26, 0.44)	0.326
	sex (female):condition (distributed)	-0.13	(-0.48, 0.24)	0.440

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

231 (c) Differences in nectar intake over time and between sexes and conditions

232 Resource defense should lead to a larger between-individual difference in nectar consumption (Brown 1964).
 233 Differences in nectar consumption were quantified as the standard deviation of nectar intake in each group,

separately for males and females. During the clumped resource condition, the standard deviation increased significantly over time for males (Table 2, Fig. S1) and was generally higher for males than for females (Table 2, Fig. S1). For females in the clumped resource condition the increase in standard deviation was significantly smaller than in males (significant interaction between sex and night, Table 2), and was not itself significant (estimate = 0.03, 95% CI = -0.02, 0.07). Compared to the clumped resource condition, in the distributed resource condition the effect of experimental night was significantly lower for males (interaction between condition and night, Table 2), but not for females (estimate = 0, 95% CI = -0.03, 0.02). Moreover, in the distributed resource condition there was no significant change over the course of the experiment in males (estimate = 0.01, 95% CI = -0.03, 0.05) nor in females (estimate = 0.03, 95% CI = -0.02, 0.06). Overall, for both males (significant effect of condition) and females (estimate = -0.07, 95% CI = -0.14, -0.02) the standard deviations were higher in the clumped than in the distributed resource conditions.

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)	0.52	(0.37, 0.68)	0.001
sex (female)	-0.20	(-0.26, -0.14)	0.001
condition (distributed)	-0.23	(-0.29, -0.17)	0.001
night	0.06	(0.01, 0.1)	0.022
sex (female):condition (distributed)	0.15	(0.06, 0.23)	0.001
sex (female):night	-0.03	(-0.06, -0.01)	0.015
condition (distributed):night	-0.04	(-0.07, -0.02)	0.001
sex (female):condition (distributed):night	0.04	(0.01, 0.08)	0.020

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

245 (d) Social status and its effects on nectar intake

246 When plotting chasing events against nectar consumption the data for males fall into two non-overlapping
 247 groups. The males of one cluster (Fig. 4A, inside dashed oval) chased other individuals and consumed more
 248 nectar than the other males. This cluster included only one male from each of the four mixed groups but
 249 two males from the single males-only group. These six males were categorized as “dominant.” The second
 250 cluster of males (Fig. 4A, outside and below dashed oval) was characterized by a low frequency of chasing
 251 and low nectar consumption. These males were categorized as “subordinate.” In females such a pattern did
 252 not emerge (Fig. 4B). This classification was also supported by the Glicko ratings in each group (Fig. S2)
 253 and the observation that there was generally an inverse relationship between the frequency of chasing and the
 254 frequency of being chased, especially in males (Fig. S3). While in the females-only group four females chased
 255 other females more frequently, only one of these females would be classified as dominant using the same
 256 cut-off criteria we used for the males (Fig. 4B), but this was not the female with the highest Glicko rating
 257 (Fig. S2). During the last two nights of the experiment in the clumped resource condition, the highest nectar
 258 intake was observed in dominant males, with an intermediate intake in females, and lowest nectar intake
 259 in subordinate males (Fig. 5). In contrast, in the distributed resource condition there were no detectable
 260 differences between the nectar intake of dominant and subordinate males at any stage of the experiment (Fig.
 261 5), while the subordinate males had a significantly lower nectar intake than females in the first two, but not
 262 in the last two experimental nights (Fig. 5). Finally, the subordinate males increased their nectar intake from
 263 the clumped to the distributed condition, but the difference was only significant for the last two experimental
 264 nights (Fig. 5). While there was a correspondent decrease in the nectar intake of dominant males, it was not
 265 significant, most likely due to the small sample size ($n = 6$, Fig. 5). Again, in females there was no change in
 266 nectar intake between the resource conditions (Fig. 5)

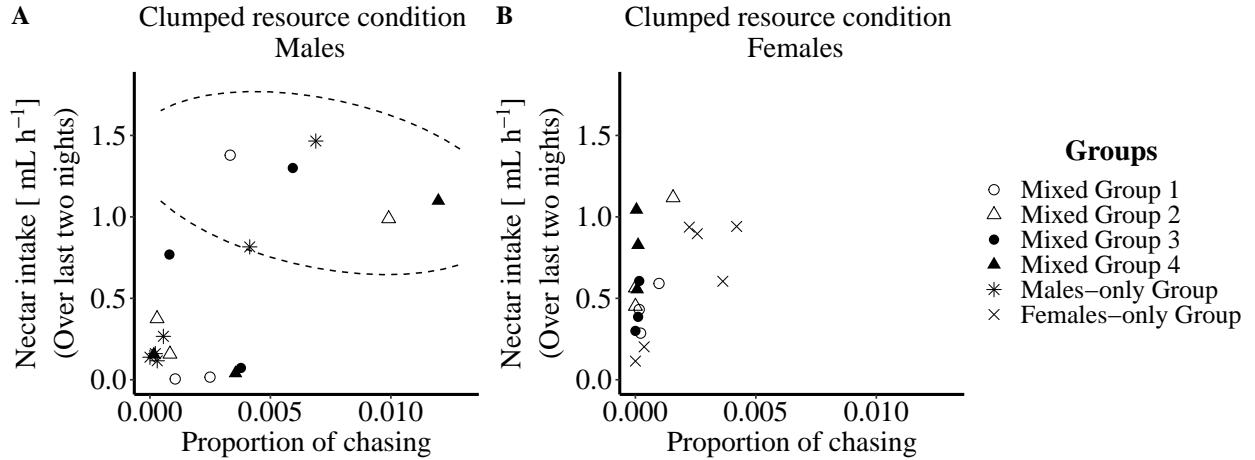


Figure 4: Influence of chasing frequency on nectar intake in the clumped resource condition during the last two nights of the experiment. **(A)** Males that more often chased other males also consumed more nectar. Males were divided into two non-overlapping groups by considering the chasing frequency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

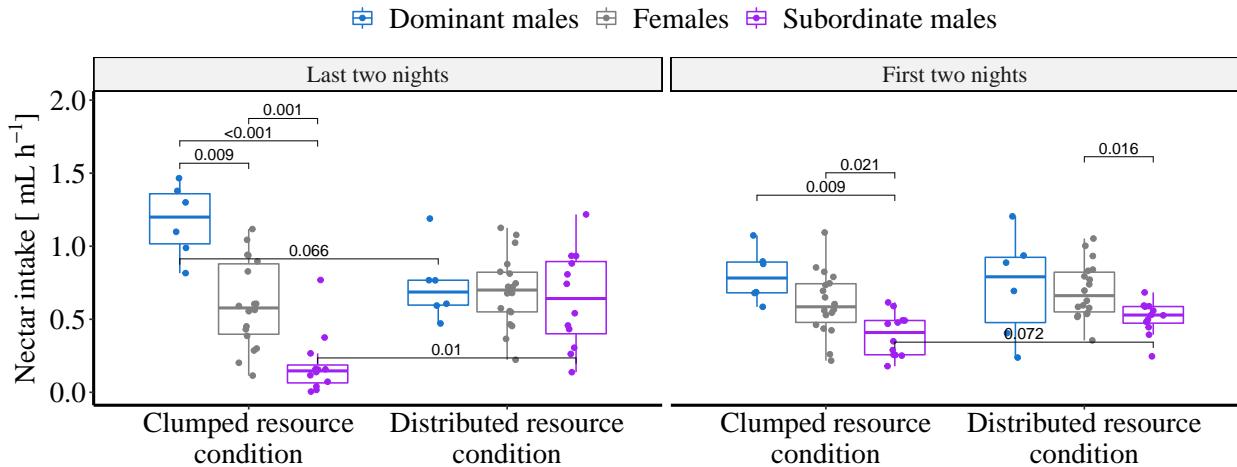


Figure 5: Comparison of nectar intake during the first and last two nights of the experiment depending on sex and social status. During the clumped resource distribution (left in each panel), already at the beginning of the experiment (right panel) subordinate males collected significantly less nectar than dominant males and females. At the end of the experiment (left panel), females, dominant and subordinate males differed to a large extent in their nectar consumption. During the distributed resource condition at the beginning of the experiment subordinate males received less nectar than females, but these differences 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 conditions were from paired Welch's tests. For clarity, only p values smaller than 0.1 are shown.

267 (e) Behavioral observations

268 Qualitative behavioral observations of four hours of video recordings revealed several behaviors that seem to
 269 be characteristic for dominant males. Instead of just visiting the flowers and leaving the patch as the other
 270 individuals did, dominant males remained hanging between the flowers within the patch for a significant
 271 amount of time (Fig. S4). When other individuals came close due to visits of directly adjacent flowers,
 272 dominant males often spread one wing in the direction of the other individual which could be interpreted as
 273 a threatening posture. Some individuals were attacked and chased away by dominant males while visiting
 274 artificial flowers. In this case, dominant males mostly attacked from above with their mouth wide open, and
 275 followed the intruder for a short distance. Sometimes the chasing escalated into fighting with both bats
 276 tumbling towards the ground and resuming their flight only shortly above the floor. In rare cases, these fights
 277 might have led to small injuries. One subordinate male had several fresh scratches on its wing that were not
 278 present before the experiment and that were possibly caused by bites (Fig. S5). After a successful flower
 279 defense, the dominant male normally visited most of the five flowers within the patch before returning to its
 280 hanging position between the flowers.

281 4. Discussion

282 Similar to observations in free-living *Glossophaga* populations, in this experiment *G. mutica* competed for
 283 nectar not only by exploitation but also by interference competition. However, the results show that the
 284 predisposition to defend resources and the influence of interference competition on individual nectar intake
 285 differed significantly between the sexes. Only a subset of individuals, exclusively males in the mixed-sex groups,
 286 successfully defended flower patches. Dominant individuals were characterized by the highest frequency of
 287 chasing other individuals away from profitable flowers, by the highest Glicko ratings, and by a substantial
 288 increase in nectar intake during the time periods of active defense by the end of the experimental run.

289 Although the dominant males in the mixed groups chased females and other males equally often, only the
290 nectar intake of subordinate males but not of the females was affected by this behavior. Thus, male-initiated
291 interference competition increased the difference in nectar intake between males but did not affect females.
292 The frequency of aggressive interactions was higher, and males only defended resources successfully when
293 the available nectar was concentrated at only one flower patch. This supports the hypothesis that clumped
294 resources favor an increase in aggressive interactions (Grant 1993).

295 **(a) Sex-dependent resource defense and its differential effect on nectar intake,
296 depending on social status**

297 To our knowledge, this study is the first report of sex-dependent differences in resource defense behavior of
298 neotropical nectar-feeding bats. In mixed sex groups, females seemed to be much less affected by the behavior
299 of dominant males whereas subordinate males were excluded at least partially from the defended flower patch.
300 This finding is consistent with observations of free-flying *G. commissarisi*, in which males visited on average
301 a smaller number of artificial flowers than females did (Nachev and Winter 2019), presumably because of
302 interactions with other males. There are two possible explanations for this differential effect on subordinate
303 males and females. On the one hand, dominant males might just not be capable of excluding females. On
304 the other hand, dominant males could tolerate females in their defended patch because they might receive
305 additional benefits, for example tolerating females could lead to an increase in (future) mating opportunities.
306 Similar social dynamics have been described in the insectivorous bat species *Myotis daubentonii* (Senior,
307 Butlin, and Altringham 2005). Dominant males of this species temporarily exclude other males from profitable
308 habitats whereas females are tolerated and in addition to securing access to resources, the successful exclusion
309 of other males has been shown to increase the reproductive success of dominant males (Senior, Butlin, and
310 Altringham 2005). Similarly, it has been observed that male purple-throated carib hummingbirds (*Eulampis*
311 *jugularis*), which successfully defend highly profitable feeding-territories against other males while sharing the
312 available resources with females, experienced an increase in their mating success (Temeles and Kress 2010).
313 However, in our experiment dominant males chased females about as often as they chased subordinate males
314 (Table 1). If females were able to feed in the defended patch because dominant males tolerated them due
315 to potential additional benefits, it could be that the detected chasing events by dominant males differed in
316 quality depending on the sex of the intruder. This was not further quantified in the current study but could
317 potentially be investigated using audio recordings (Knörnschild, Glöckner, and Helversen 2010). We extracted
318 the frequency of chasing events from data automatically recorded at artificial flowers (successive detection
319 of two different IDs while and after the first was feeding at the flower). Therefore, it was not possible to
320 determine if males showed behavioral differences when chasing other males in comparison to chasing females.
321 The recorded videos revealed that individuals chased each other not only directly at the artificial flowers but
322 also in other areas of the flower patch. Since individuals could only be identified by their ID tags directly at
323 the ID reader attached to artificial flowers the sex of individuals chasing each other in other areas of the
324 experimental room remained unknown. However, after the experiment some subordinate individuals showed
325 marks from small injuries at their wings (see example in Fig. S5) and such marks were only observed in males.
326 This could be an indication that dominant males directed more aggression (biting) towards subordinate
327 males than towards females. Such sexual dimorphism in aggressive resource defense is also known from other
328 nectar-feeding vertebrates, like hummingbirds. The beaks of the males of some territorial hummingbirds seem
329 to be specifically adapted as intrasexually selected weapons (Rico-Guevara et al. 2019).

330 **(b) Some observations from the single-sex groups**

331 Generally, females showed lower chasing frequencies, but, surprisingly, some females in the females-only group
332 showed an increased nectar consumption and chasing frequency, compared to the females in the mixed groups
333 (Fig. 4B). Thus it appears that in the absence of male individuals, some females exerted dominant behavior
334 over the other females, similar to males. These findings are similar to the social structure of resource defense
335 found in some nectar-feeding bird species. For example, in free-living ruby-throated hummingbirds females
336 also have lower levels of defense (Rousseau, Charette, and Bélisle 2014). Moreover, although both male and
337 female *Eulampis jugularis* hummingbirds defend feeding territories during the non-breeding season, males are
338 always dominant over females (Wolf and Hainsworth 1971; Temeles, Goldman, and Kudla 2005). It would be

339 interesting to better understand why females were less affected by the aggressive resource defense behavior of
340 dominant males compared to subordinate males and why females themselves did not consistently monopolize
341 the profitable patch against other females, not even in the females-only group. Of course, as there was but a
342 single females-only group, the latter observation needs to be confirmed with more data. One possibility is
343 that females do not need to defend flowers when a dominant male is already reducing the number of flower
344 visitors and thus increasing the amount of food available.

345 In all mixed sex groups, only one male per group became dominant and successfully defended flowers, whereas
346 in the males-only group two males exhibited dominant behavior (Fig. 4A). A closer look at the nectar
347 consumption at each flower revealed that on the last night of the experiment these two males had nearly
348 monopolized different flowers within the same patch rather than sharing access to the same flowers (Fig. S6).
349 Such flower partitioning was also observed in the females-only group (Fig. S7), but rarely seen in the mixed
350 groups (Figs. S8-S11). The successful resource defense by two individuals in the male-only group showed
351 that resource defense can occur independent of the presence of females, but, again, this was only based on a
352 single observation.

353 (c) Social status and social hierarchy

354 Although the position of the rewarding patch during the clumped resource condition changed between the
355 nights between the left and right, usually the same male continued to successfully defend the patch, especially
356 in the mixed-sex groups (Figs. S6-S11). This means that males defended the resources themselves and not a
357 particular location. Furthermore, this shows that even after changing the location of the defended patch
358 the same individuals were usually able to succeed in re-establishing their dominance against other males,
359 indicating a stable hierarchy at least for the duration of the experiment.

360 The ability of an individual to successfully defend and monopolize resources is often correlated with distinct
361 physical characteristics for example body size (Searcy 1979). However, in our results weight as an approxima-
362 tion of size did not correlate significantly with the chasing frequency of individuals (Table 1) and therefore
363 did not predict which male succeeded to defend a flower patch. Another factor that could influence the
364 success in defending flowers is age and therefore experience (Arcese 1987; Yasukawa 1979). Since we could
365 only discriminate between young and adult animals, we cannot dismiss age and experience as a predictor of
366 successful flower defense.

367 In this study, subordinate males received considerably less nectar than dominant males and females (Fig. 5).
368 However, except in mixed group 1, subordinate males were rarely completely excluded from the flower patch
369 and their average nectar intake during the clumped resource condition was still $0.3 \pm 0.18 \text{ mL h}^{-1}$ (mean \pm
370 SD). This result is in accordance with observations of free-living *G. soricina* in Colombia. There, subordinate
371 bats exploited the flowers defended by other individuals as soon as the dominant bat temporarily ceased
372 defending (Lemke 1984). Furthermore, in our study the frequency of chasing events decreased significantly
373 during the distributed resource condition in the second part of the night (Table 1). This supports the
374 theoretical prediction that aggressive defense behavior increases when resources are spatially concentrated
375 (Grant and Guha 1993), with the important caveat that the sequence of conditions was not controlled in this
376 experiment. With the current data we cannot answer whether the dominant males would successfully defend
377 a patch if the condition changed from distributed to clumped, but we believe this is a different question that
378 should be addressed separately. Resource defense should only occur when the energy gain outweighs the
379 cost of aggressive interactions (Brown 1964). Thus, our results could be explained by the decrease in quality
380 of the defended patch once its nectar supply rate dropped to half. This is also supported by the very low
381 number of chases observed during training when the flowers gave unrestricted rewards and were not separated
382 in discrete patches. Together, these results suggest that along the different degrees of territorial behavior,
383 resource defense observed in *Glossophaga* seems to represent a transient monopolization of resources instead
384 of a longer-term permanent exclusion of intruders.

385 (d) Conclusion

386 Although flower defense behavior of *G. mutica* was investigated in a laboratory setting, we observed similar
387 behavior as described in free-living *Glossophaga* populations. Our results revealed a sexual dimorphism in
388 flower defense behavior in mixed-sex groups. Only males successfully defended flower patches and excluded

389 other males from their defended resource, whereas females remained unaffected by this male behavior and
390 continued to visit the flowers guarded by a male. This observed pattern is similar to resource defense behavior
391 observed in other nectar-feeding vertebrates. Furthermore, we could show that the frequency of aggressive
392 interactions was, as predicted, higher when resources were clumped in one patch and transient. Future studies
393 with free-living populations have to be conducted to assess how frequent and important resource defense in
394 these nectar-feeding bats is and if males that are successful in defending resources have additional fitness
395 advantages.

396 **Supplementary material**

397 **Video analysis**

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

403

404 $f \rightarrow f$ appear to be less aggressive

405 $f \rightarrow m$ appear aggressive

406 $m \rightarrow f$ appear aggressive

407 $m \rightarrow m$ appear aggressive

408

409 **Supplementary figures**

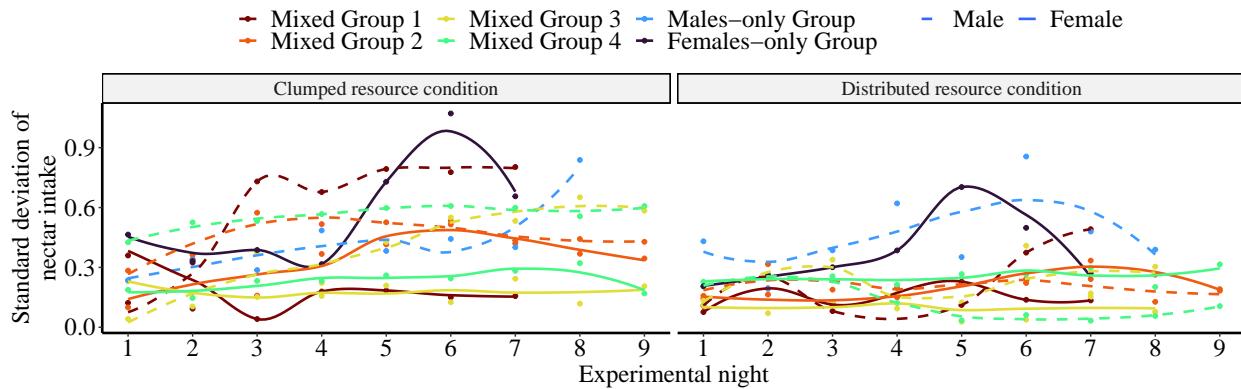


Figure S1: The standard deviation of group nectar consumption was used to measure the between individual differences in nectar intake. It was calculated for the clumped (left panel) and the distributed (right panel) resource conditions, separately for males (dashed lines) and females (continuous lines) 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).

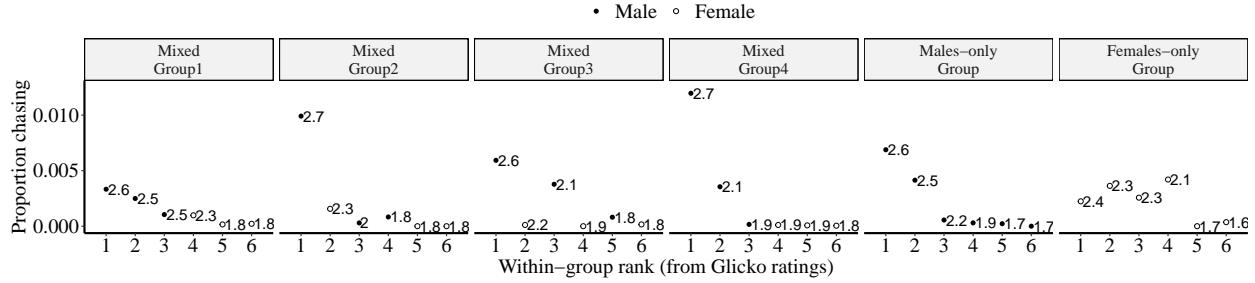


Figure S2: Glicko ratings within the six experimental groups. Over the last two experimental nights, the males (closed symbols) with the highest proportion of chasing events were also the individuals with the highest Glicko rating in each group (panels) during the clumped resource condition. There was no such correspondence for females in the female-only group (right panel). Numbers at symbols give the Glicko rating in thousands.

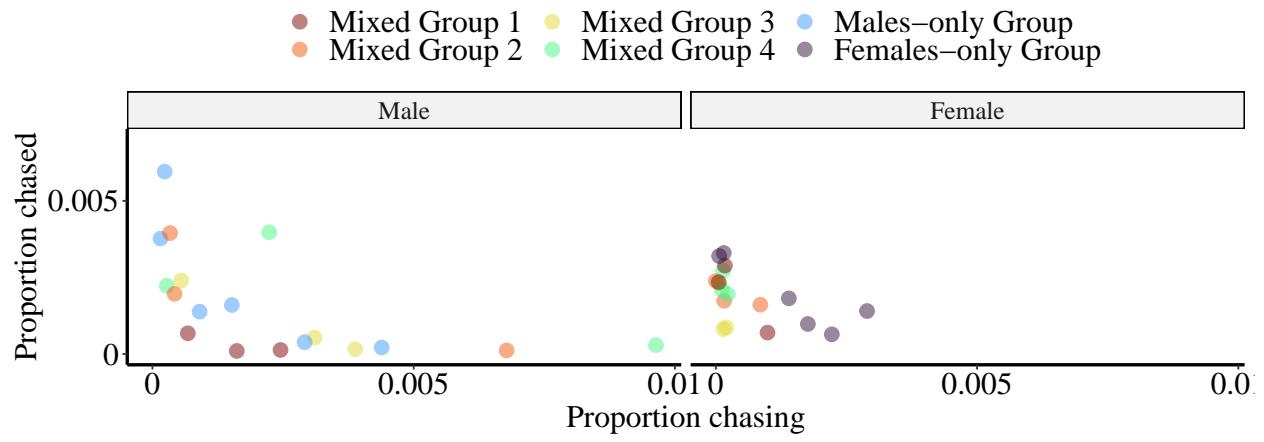


Figure S3: The relationship between proportion of chases versus the proportion of being chased out of all detections for female (right) and male (left) individuals in the six experimental groups (different colors).

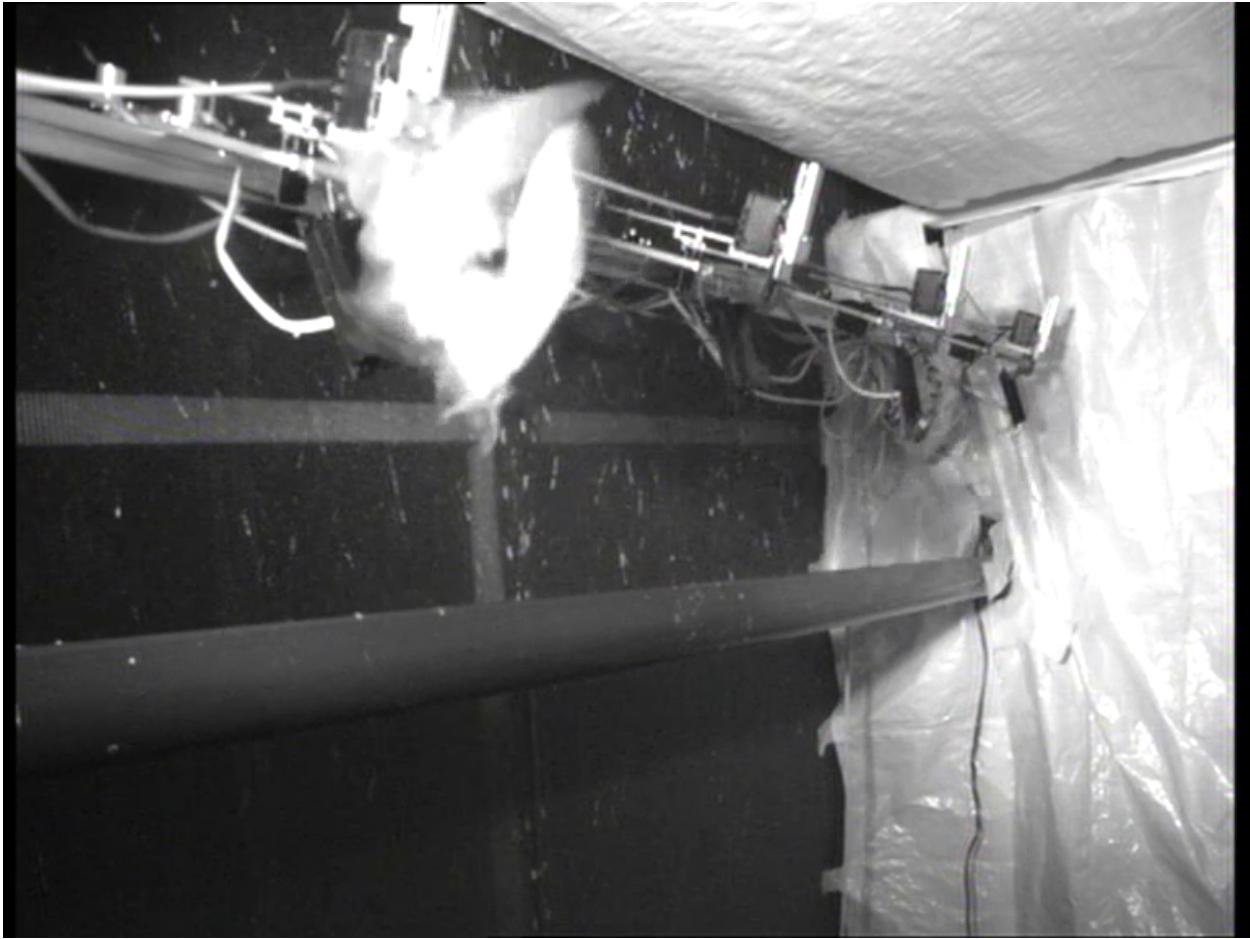


Figure S4: Video of the dominant male in mixed group 3 chasing all bats approaching the rewarding flowers in the rewarding patch during the clumped resource condition.

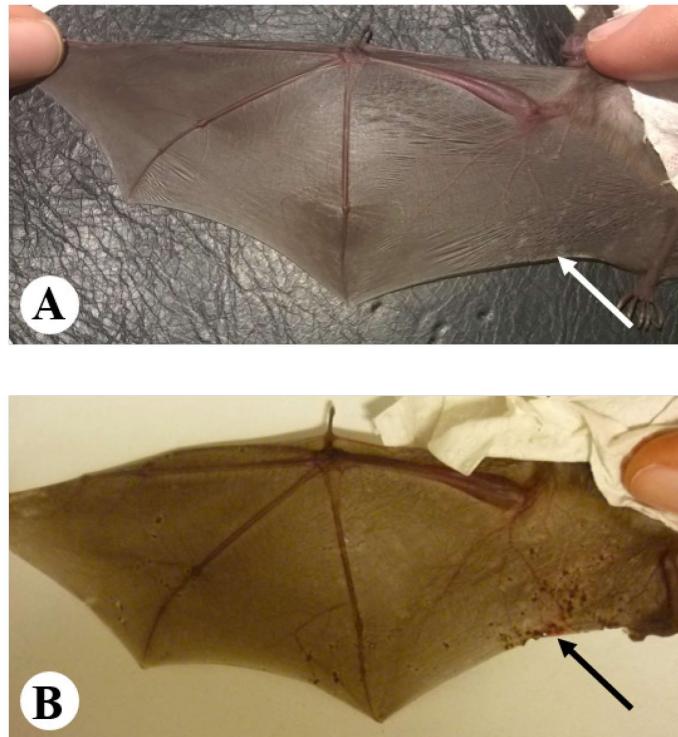


Figure S5: Wing images of a subordinate male from mixed group 4. The same individual was photographed before (**A**) and after the experiment (**B**). The black arrow points to the scarred location due to wing injuries, purportedly caused by the dominant male.

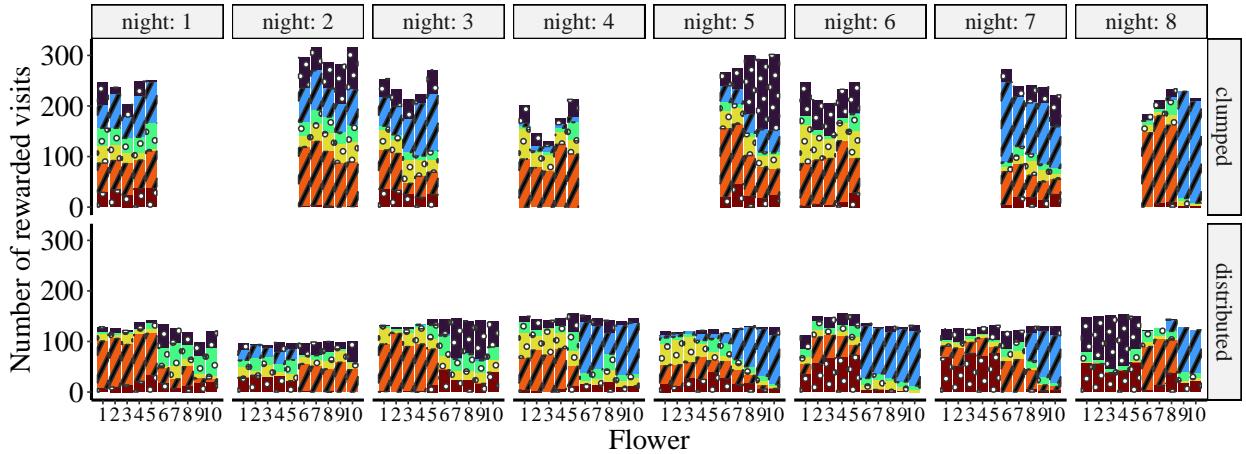


Figure S6: Distribution of rewarded visits across flowers for the six bats in the males-only group. The colored bars give the number of rewarded visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns). The dominant males are shown with black stripes and the subordinate males are shown with white 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.

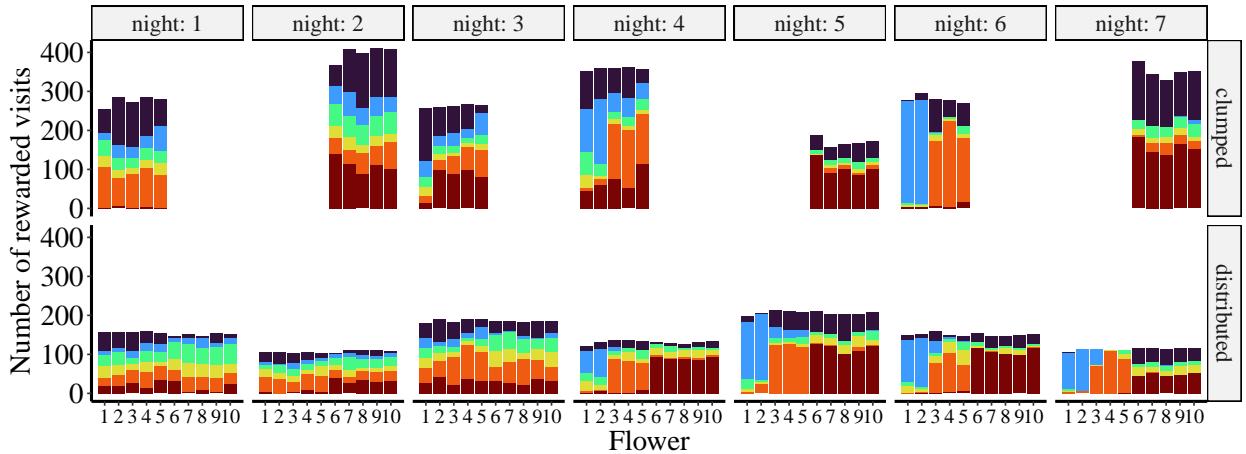


Figure S7: Distribution of rewarded visits across flowers for the six bats in the females-only group. The colored bars give the number of rewarded visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns). Females in this group exhibited the highest frequency of chasing behavior compared to all other females. This is also the only group, in which females nearly monopolized flower patches or flowers within a patch.

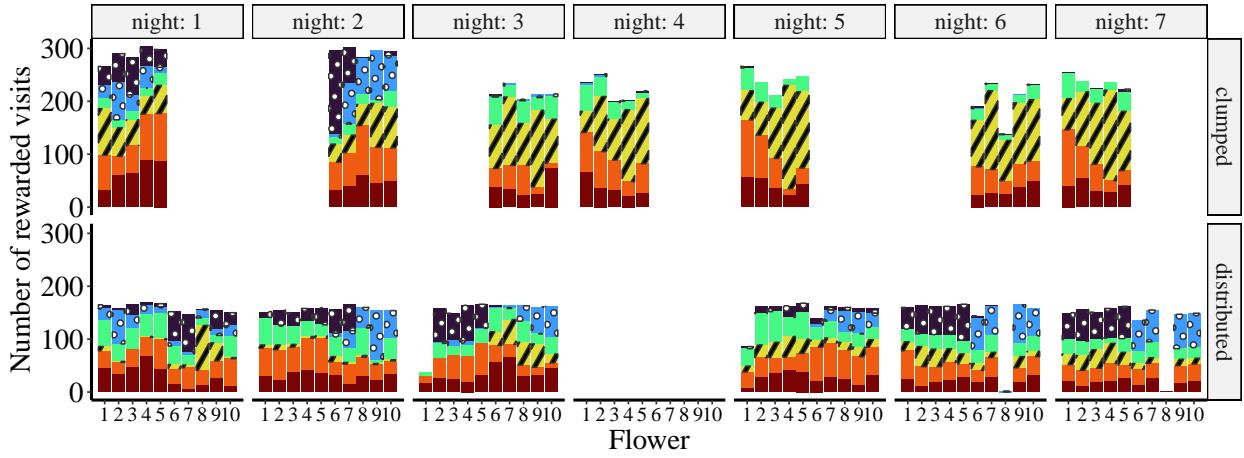


Figure S8: Distribution of rewarded visits across flowers for the six bats in mixed group 1. The colored bars give the number of rewarded visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns). The dominant male is shown with black stripes, the subordinate males are shown with white dots, and the females are shown with solid bars. Due to a technical malfunction on night 4, there were no rewards delivered in the distributed resource condition and the data were excluded from analysis.

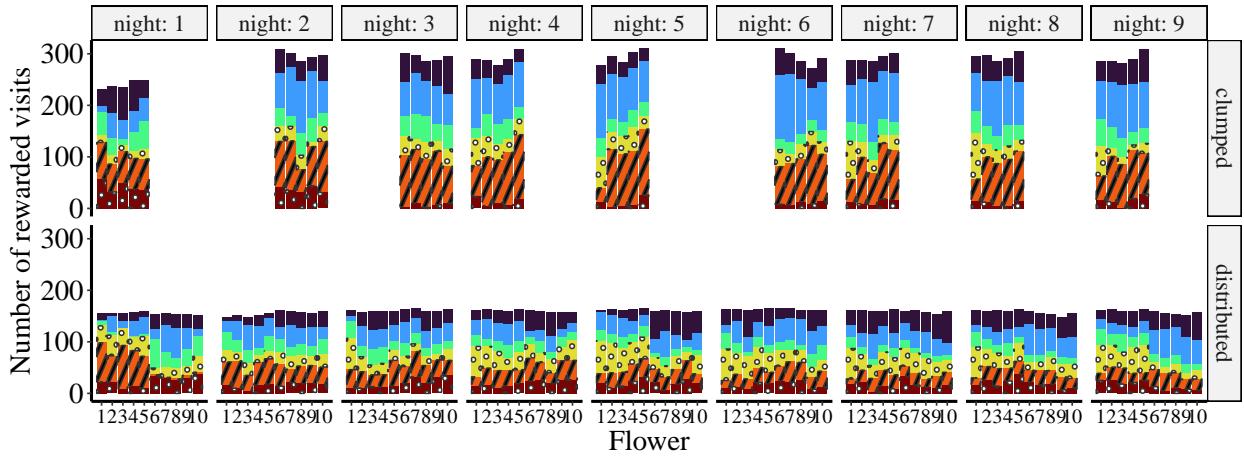


Figure S9: Distribution of rewarded visits across flowers for the six bats in mixed group 2. Same notation as in Fig. S8, but the colors correspond to different individuals.

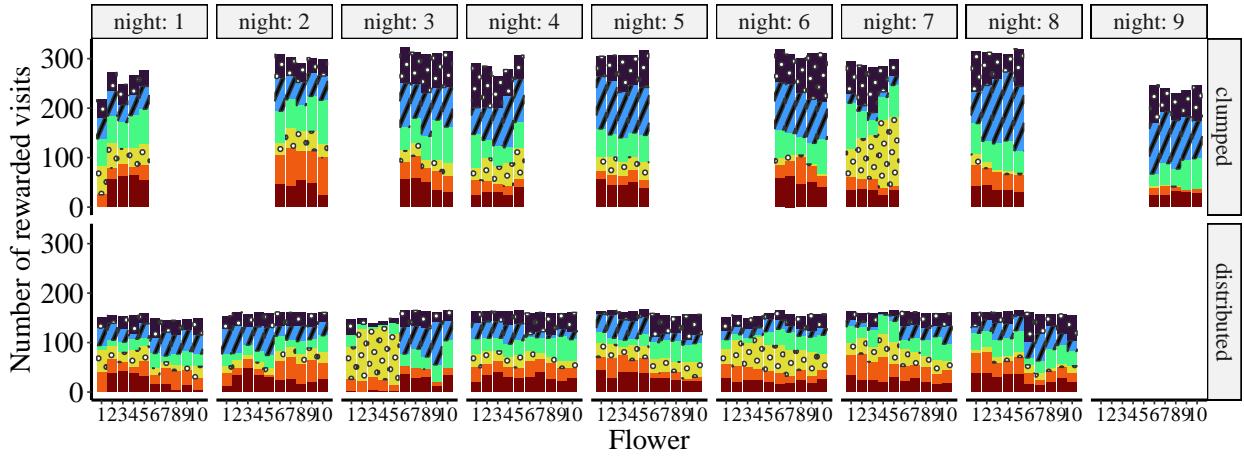


Figure S10: Distribution of rewarded visits across flowers for the six bats in mixed group 3. Same notation as in Fig. S8, but the colors correspond to different individuals. Due to a technical malfunction on night 9, there were no rewards delivered in the distributed resource condition and the data were excluded from analysis.

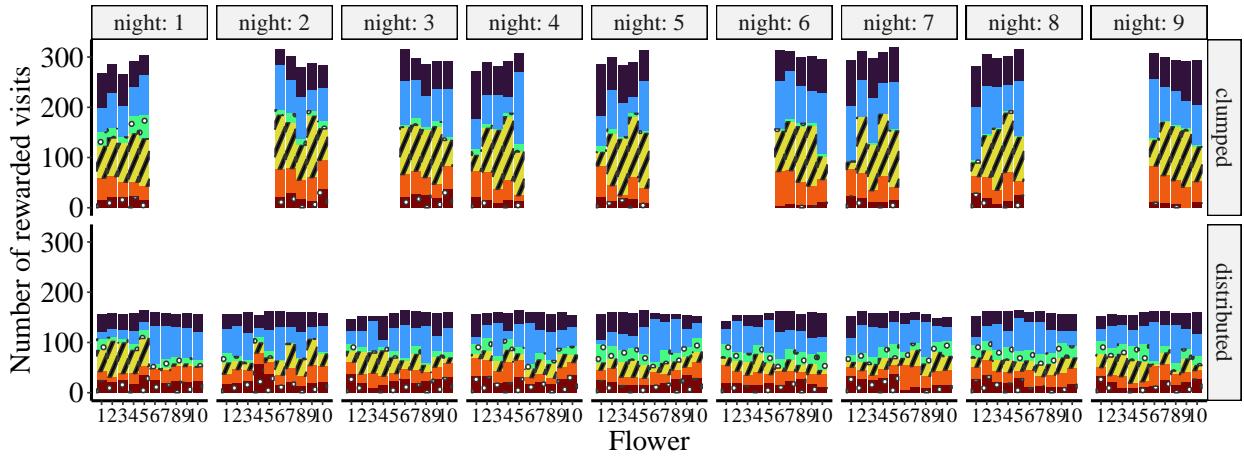


Figure S11: Distribution of rewarded visits across flowers for the six bats in mixed group 4. Same notation as in Fig. S8, but the colors correspond to different individuals.

⁴¹⁰ **Authors' contributions**

⁴¹¹ S.W. Conceptualization, Methodology, Software, Data collection, Formal Analysis, Video Analysis, Writing—
⁴¹² original draft. V.N. Conceptualization, Methodology, Software, Formal Analysis, Data curation, Writing—
⁴¹³ review and editing, Visualization, Supervision, Project Administration.
⁴¹⁴ Y.W. Conceptualization, Resources, Methodology, Software (data acquisition), Writing—review and editing,
⁴¹⁵ Supervision, Funding.

⁴¹⁶ **Competing interests**

⁴¹⁷ We declare we have no competing interests.

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⁴²⁵ **Data Availability**

⁴²⁶ All data and code are available in the Zenodo repository: <https://doi.org/10.5281/zenodo.5205511>.

427 **References**

- 428 Amarasekare, Priyanga. 2002. "Interference Competition and Species Coexistence." *Proceedings of the Royal
429 Society of London. Series B: Biological Sciences* 269 (1509): 2541–50. <https://doi.org/10.1098/rspb.2002.2181>.
- 431 Arcese, Peter. 1987. "Age, Intrusion Pressure and Defence Against Floaters by Territorial Male Song
432 Sparrows." *Animal Behaviour* 35 (3): 773–84. [https://doi.org/10.1016/S0003-3472\(87\)80114-8](https://doi.org/10.1016/S0003-3472(87)80114-8).
- 433 Boyden, Thomas C. 1978. "Territorial Defense Against Hummingbirds and Insects by Tropical Hummingbirds."
434 *The Condor* 80 (2): 216–21. <https://doi.org/10.2307/1367921>.
- 435 Brown, Jerram L. 1964. "The Evolution of Diversity in Avian Territorial Systems." *The Wilson Bulletin* 76
436 (2): 160–69. <https://www.jstor.org/stable/4159278>.
- 437 Brunet-Rossini, Anja K., and Gerald S. Wilkinson. 2009. "Methods for Age Estimation and the Study
438 of Senescence in Bats." In *Ecological and Behavioral Methods for the Study of Bats.*, 2nd. ed, 315–25.
439 Baltimore, MD: Johns Hopkins University Press.
- 440 Calahorra-Oliart, Adriana, Sandra M Ospina-Garcés, and Livia León-Paniagua. 2021. "Cryptic Species in
441 *Glossophaga Soricina* (Chiroptera: Phyllostomidae): Do Morphological Data Support Molecular Evidence?"
442 *Journal of Mammalogy* 102 (1): 54–68. <https://doi.org/10.1093/jmammal/gyaal16>.
- 443 Carpenter, F. L., and R. E. Macmillen. 1976. "Threshold Model of Feeding Territoriality and Test with a
444 Hawaiian Honeycreeper." *Science (New York, N.Y.)* 194 (4265): 639–42. <https://doi.org/10.1126/science.194.4265.639>.
- 446 Chase, Ivan D., Craig Tovey, Debra Spangler-Martin, and Michael Manfredonia. 2002. "Individual Differences
447 Versus Social Dynamics in the Formation of Animal Dominance Hierarchies." *Proceedings of the National
448 Academy of Sciences* 99 (8): 5744–49. <https://doi.org/10.1073/pnas.082104199>.
- 449 Ewald, Paul W., and F. Lynn Carpenter. 1978. "Territorial Responses to Energy Manipulations in the Anna
450 Hummingbird." *Oecologia* 31 (3): 277–92. <https://doi.org/10.1007/BF00346248>.
- 451 Gill, Frank B., and Larry L. Wolf. 1975. "Economics of Feeding Territoriality in the Golden-Winged Sunbird."
452 *Ecology* 56 (2): 333–45. [https://doi.org/https://doi.org/10.2307/1934964](https://doi.org/10.2307/1934964).
- 453 Glickman, Mark E. 1999. "Parameter Estimation in Large Dynamic Paired Comparison Experiments."
454 *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 48 (3): 377–94. [https://doi.org/10.1111/1467-9876.00159](https://doi.org/https://doi.org/10.1111/1467-9876.00159).
- 456 Gonzalez-Terrazas, Tania P., Carlos Martel, Paulo Milet-Pinheiro, Manfred Ayasse, Elisabeth K. V. Kalko,
457 and Marco Tschapka. 2016. "Finding Flowers in the Dark: Nectar-Feeding Bats Integrate Olfaction
458 and Echolocation While Foraging for Nectar." *Royal Society Open Science* 3 (8): 160199. <https://doi.org/10.1098/rsos.160199>.
- 460 Grant, James W. A. 1993. "Whether or Not to Defend? The Influence of Resource Distribution." *Marine
461 Behaviour and Physiology* 23 (1-4): 137–53. <https://doi.org/10.1080/10236249309378862>.
- 462 Grant, James W. A., Isabelle L. Girard, Cindy Breau, and Laura K. Weir. 2002. "Influence of Food
463 Abundance on Competitive Aggression in Juvenile Convict Cichlids." *Animal Behaviour* 63 (2): 323–30.
464 <https://doi.org/10.1006/anbe.2001.1891>.
- 465 Grant, James W. A., and Rabi T. Guha. 1993. "Spatial Clumping of Food Increases Its Monopolization
466 and Defense by Convict Cichlids, *Cichlasoma Nigrofasciatum*." *Behavioral Ecology* 4 (4): 293–96.
467 <https://doi.org/10.1093/beheco/4.4.293>.
- 468 Hadfield, Jarrod D. 2010. "MCMC Methods for Multi-Response Generalized Linear Mixed Models: The
469 MCMCglmm R Package." *Journal of Statistical Software* 33 (2): 1–25.
- 470 Howell, D. J. 1974. "Acoustic Behavior and Feeding in Glossophagine Bats." *Journal of Mammalogy* 55 (2):
471 293–308. <https://doi.org/10.2307/1378999>.

- 472 Hörmann, David, Marco Tschapka, Andreas Rose, and Mirjam Knörnschild. 2020. "Distress Calls of
 473 Nectarivorous Bats (*Glossophaga Soricina*) Encode Individual and Species Identity." *Bioacoustics* 0 (0):
 474 1–19. <https://doi.org/10.1080/09524622.2020.1720815>.
- 475 Knörnschild, Mirjam, Volker Glöckner, and Otto von Helversen. 2010. "The Vocal Repertoire of Two Sympatric Species of Nectar-Feeding Bats (*Glossophaga Soricina* and *G. Commissarisi*)."
 476 *Acta Chiropterologica* 12 (1): 205–15. <https://doi.org/10.3161/150811010X504707>.
- 477 Lemke, Thomas O. 1984. "Foraging Ecology of the Long-Nosed Bat, *Glossophaga Soricina*, With Respect to
 478 Resource Availability." *Ecology* 65 (2): 538–48. <https://doi.org/10.2307/1941416>.
- 479 ———. 1985. "Pollen Carrying by the Nectar-Feeding Bat *Glossophaga Soricina* in a Suburban Environment."
 480 *Biotropica* 17 (2): 107–11. <https://doi.org/10.2307/2388502>.
- 481 Nachev, Vladislav, and York Winter. 2019. "Behavioral Repeatability and Choice Performance in Wild
 482 Free-Flying Nectarivorous Bats (*Glossophaga Commissarisi*)."
 483 *Behavioral Ecology and Sociobiology* 73 (2): 24. <https://doi.org/10.1007/s00265-019-2637-4>.
- 484 Paton, David C., and F. Lynn Carpenter. 1984. "Peripheral Foraging by Territorial Rufous Hummingbirds:
 485 Defense by Exploitation." *Ecology* 65 (6): 1808–19. <https://doi.org/10.2307/1937777>.
- 486 Rico-Guevara, A, M A Rubega, K J Hurme, and R Dudley. 2019. "Shifting Paradigms in the Mechanics
 487 of Nectar Extraction and Hummingbird Bill Morphology." *Integrative Organismal Biology* 1 (oby006).
 488 <https://doi.org/10.1093/iob/oby006>.
- 489 Rose, Andreas, Miriam Kolar, Marco Tschapka, and Mirjam Knörnschild. 2016. "Learning Where to Feed:
 490 The Use of Social Information in Flower-Visiting Pallas' Long-Tongued Bats (*Glossophaga Soricina*)."
 491 *Animal Cognition* 19 (2): 251–62. <https://doi.org/10.1007/s10071-015-0930-9>.
- 492 Rousseau, François, Yanick Charette, and Marc Bélisle. 2014. "Resource Defense and Monopolization in a
 493 Marked Population of Ruby-Throated Hummingbirds (*Archilochus Colubris*)."
 494 *Ecology and Evolution* 4 (6): 776–93. [https://doi.org/https://doi.org/10.1002/ece3.972](https://doi.org/10.1002/ece3.972).
- 495 Searcy, William A. 1979. "Morphological Correlates of Dominance in Captive Male Red-Winged Blackbirds."
 496 *Condor* 81 (4): 417–20.
- 497 Senior, Paula, Roger K Butlin, and John D Altringham. 2005. "Sex and Segregation in Temperate Bats."
 498 *Proceedings of the Royal Society B: Biological Sciences* 272 (1580): 2467–73. <https://doi.org/10.1098/rsb.2005.3237>.
- 499 So, Nina, Becca Franks, Sean Lim, and James P. Curley. 2015. "A Social Network Approach Reveals
 500 Associations Between Mouse Social Dominance and Brain Gene Expression." *PLOS ONE* 10 (7): e0134509.
 501 <https://doi.org/10.1371/journal.pone.0134509>.
- 502 Stephenson, Alec, and Jeff Sonas. 2020. "PlayerRatings: Dynamic Updating Methods for Player Ratings
 503 Estimation." <https://rdrr.io/cran/PlayerRatings/>.
- 504 Team, R Core. 2021. "R: A Language and Environment for Statistical Computing." Vienna, Austria: R
 505 Foundation for Statistical Computing. <http://www.R-project.org>.
- 506 Temeles, Ethan J., Robin S. Goldman, and Alexei U. Kudla. 2005. "Foraging and Territory Economics of
 507 Sexually Dimorphic Purple-Throated Caribs (*Eulampis Jugularis*) on Three Heliconia Morphs." *The Auk*
 508 122 (1): 187–204. <https://doi.org/10.1093/auk/122.1.187>.
- 509 Temeles, Ethan J., and W. John Kress. 2010. "Mate Choice and Mate Competition by a Tropical Hummingbird
 510 at a Floral Resource." *Proceedings of the Royal Society B: Biological Sciences* 277 (1687): 1607–13.
 511 <https://doi.org/10.1098/rspb.2009.2188>.
- 512 Thiele, Johannes, and York Winter. 2005. "Hierarchical Strategy for Relocating Food Targets in Flower Bats:
 513 Spatial Memory Versus Cue-Directed Search." *Animal Behaviour* 69 (2): 315–27. <https://doi.org/10.1016/j.anbehav.2004.05.012>.

- 517 Tschapka, Marco. 2003. "Pollination of the Understorey Palm *Calyptrogyne Ghiesbreghtiana* by Hovering and
518 Perching Bats." *Biological Journal of the Linnean Society* 80 (2): 281–88. <https://doi.org/10.1046/j.1095-8312.2003.00235.x>.
- 520 Tschapka, Marco, and Otto von Helversen. 2007. "Phenology, Nectar Production and Visitation Behaviour
521 of Bats on the Flowers of the Bromeliad *Werauhia Gladioliflora* in a Costa Rican Lowland Rain Forest."
522 *Journal of Tropical Ecology* 23 (04): 385–95. <https://doi.org/10.1017/S0266467407004129>.
- 523 Watzke, Steffen. 2006. "Nahrung Und Paarung – Vom „Kleinen“ Unterschied Der Ressourcennutzung
524 Des Flughundes *Macroglossus Minimus* – Sind Blüten Mehr Als Nur Eine Nahrungsquelle?" In
525 *Ressourcennutzung Und Paarungssystem Der Nektarivoren Flughundart Macroglossus Minimus (Pteropodidae: Macroglossinae) in West-Malaysia*, 82–171. Munich, Germany: Ludwig-Maximilians-Universität
526 München. <https://edoc.ub.uni-muenchen.de/6174/>.
- 528 Winter, York, and Otto von Helversen. 2001. "Bats as Pollinators: Foraging Energetics and Floral
529 Adaptations." In *Cognitive Ecology of Pollination: Animal Behaviour and Floral Evolution*, edited
530 by James D. Thomson and Lars Chittka, 148–70. Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511542268.009>.
- 532 Winter, York, and Kai Petra Stich. 2005. "Foraging in a Complex Naturalistic Environment: Capacity of
533 Spatial Working Memory in Flower Bats." *The Journal of Experimental Biology* 208 (Pt 3): 539–48.
534 <https://doi.org/10.1242/jeb.01416>.
- 535 Wintergerst, Sabine. 2018. "Modulators of Foraging Behavior by Nectar-Feeding Bats (Glossophaginae),"
536 January. <https://doi.org/10.18452/18673>.
- 537 Wolf, Larry L., and F. Reed Hainsworth. 1971. "Time and Energy Budgets of Territorial Hummingbirds."
538 *Ecology* 52 (6): 980–88. <https://doi.org/https://doi.org/10.2307/1933803>.
- 539 Yasukawa, Ken. 1979. "Territory Establishment in Red-Winged Blackbirds: Importance of Aggressive
540 Behavior and Experience." *The Condor* 81 (3): 258–64. <https://doi.org/10.2307/1367628>.
- 541 Yoh, Natalie, Peter Syme, Ricardo Rocha, Christoph F. J. Meyer, and Adrià López-Baucells. 2020. "Echolocation of Central Amazonian 'Whispering' Phyllostomid Bats: Call Design and Interspecific Variation."
542 *Mammal Research* 65 (3): 583–97. <https://doi.org/10.1007/s13364-020-00503-0>.