

¹ Sex-dependent resource defence in the nectar-feeding bat
² *Glossophaga*

³
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⁸ **Abstract**

⁹ Aggressive resource defence is frequently observed throughout the animal kingdom and although it is a
¹⁰ widespread phenomenon in nectar-feeding birds, reports of interference competition in nectarivorous bats are
¹¹ extremely rare. *Glossophaga soricina* has been observed to defend flowers of *Agave desmettiana* but not much
¹² is known about the social structure during resource defence and how interference competition leads to resource
¹³ monopolization and affects nectar intake. Here, we investigated the resource defence behaviour of *G. soricina*
¹⁴ in a laboratory setting. By using an experimental set-up consisting of two patches of computer-controlled
¹⁵ artificial flowers we tracked the nectar intake of every group member. Furthermore, we were able to establish
¹⁶ an automated method for flagging potentially aggressive interactions at proximity to the artificial flowers.
¹⁷ Theoretical models of interference competition predict that aggressive interactions increase when resources are
¹⁸ spatially more clumped. We varied resource distribution across two patches between clumped and distributed
¹⁹ to assess how resource density influences aggressive interactions. Resource defence behaviour was assessed
²⁰ in 36 individuals divided into one male and one female group, as well as four mixed-sex groups. Males
²¹ engaged in potentially aggressive interactions significantly more often than females and only males were
²² successful in defending artificial flowers. Subdominant males experienced a substantial decrease in nectar
²³ intake. However, females were only marginally affected by male aggression and maintained nectar intake.
²⁴ These results suggest that aggressive interactions and their effect on nectar intake are sex-dependent in *G.*
²⁵ *soricina*. Furthermore, as expected, aggressive interactions were more frequent and resource defence was
²⁶ only successful when resources were clumped. Our novel experimental set-up allowed us to perform a mostly
²⁷ automated experimental test of models of interference competition and resource defence with a mammal
²⁸ under the controlled conditions of the laboratory. This new approach may pave the way for further such
²⁹ studies with other groups of organisms.

³⁰ **Keywords:**

³¹ resource defence, economic defendability, bat

³² **1. Introduction**

³³ Competition for limited resources like food or mates is a ubiquitous phenomenon in the animal kingdom.
³⁴ Such competition can be indirect by exploiting a common resource and preventing others to benefit from it
³⁵ (Paton and Carpenter 1984) or it can be direct by aggressively defending a resource. The latter is known
³⁶ as interference competition (Amarasekare 2002). Aggressive resource defence establishes dominance and by
³⁷ exclusion of competitors leads to priority of access to those resources. In the extreme, dominance behaviour
³⁸ can lead to exclusive territoriality. Territoriality is a concept belonging to an indivisible continuum starting

39 with the transient monopolization of a preferred feeding opportunity to the longer-term defence of an area as
40 exclusive territory. The rules of economic defendability (Brown 1964) determine the adaptive compromise
41 to which a species' dominance behaviour will evolve and develop along this continuum. The establishment
42 of feeding territories is well known for nectar-feeding birds (Boyden 1978; Carpenter and Macmillen 1976;
43 Ewald and Carpenter 1978; Gill and Wolf 1975).

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

50 Within bats, the flower visitors have an additional advantage if they are intimately familiar with their
51 feeding area. Compared to an insect-hunting bat that must continually scan for elusive prey by active
52 echolocation, a flower visitor can approach a target with minimal echolocation when seeking specific flowers
53 at known locations (Thiele and Winter 2005; Winter and Stich 2005; Gonzalez-Terrazas et al. 2016; Rose et
54 al. 2016). Thus, it is not surprising that the longer-term defence of extensive feeding territories as commonly
55 observed in nectar-feeding birds is not known for glossophagine, nectar-feeding bats (but see Watzke 2006 for
56 *Megalopsglossus* paleotropical nectar-feeding flying foxes). Nonetheless, several observations have documented
57 aggressive food defence by glossophagine bats. The inflorescences of *Agave desmettiana* with their copious
58 nectar (Lemke 1985) may be defended by males or females of *Glossophaga soricina* against conspecifics but
59 only during some hours of the night (Lemke 1984, 1985). When left unguarded, intruders quickly exploited
60 the opportunity to feed from the previously defended plants. The Costa Rican bat *Glossophaga commissarisi*
61 occasionally defends and temporarily monopolizes single inflorescences of the understory palm *Calyptrogyne*
62 *ghiesbreghtiana* against other hovering bats, perching bats and katydids (Tschapka 2003). A commonality in
63 these reports was that the defence did not cover the area of a typical feeding range but was restricted to a
64 single or a few flowering plants and was also limited to a small number of hours during the night.
65 Thus, glossophagine bats can show aggressive resource defence to establish dominance. In this study, we
66 investigated for a nocturnal, nectar-feeding mammal the flower-visiting bat *Glossophaga soricina*, the role of
67 aggressive interactions for gaining access to nectar food. We tested the predictions of models of resource
68 defence (Grant et al. 2002) and interference competition (Grant 1993) during a naturalistic foraging paradigm
69 in the laboratory. The occurrence of resource defence is predicted to be highest at intermediate levels of food
70 abundance (Grant et al. 2002). In line with this prediction, the transient nature of nightly defence behaviour
71 observed in the field suggests that changes in food-abundance or food-requirements that occur within the
72 night affected the strength of the observed behaviour. To mimic the natural situation of flowers that provide
73 nectar at steady rates of secretion we programmed artificial flowers to provide nectar with a fixed interval
74 reward schedule. Once a nectar reward had been taken by any bat, the fixed interval had to pass before the
75 next reward was available at this flower.
76 Furthermore, theoretical models of interference competition predict that clumped resources lead to more
77 agonistic behaviour and resource defence than evenly distributed resources (Grant 1993). To include a test
78 of these predictions in our experimental design, we spatially subdivided our flower field into two patches
79 and programmed them to automatically change during the night the spatial distribution of available nectar
80 resources. We performed our study with 36 individuals of male and female *G. soricina*. By using artificial
81 flowers in a closed environment, we could track all flower visits and total nectar consumption of every
82 individual in the group. Each individual carried an electronic ID tag and flowers were equipped with ID
83 sensors. This also enabled us to detect and quantify a typical class of aggressive interactions between pairs of
84 individuals directly at the artificial flowers fully automatically.
85 Our novel experimental set-up thus allowed us to perform a mostly automated experimental test of models
86 of interference competition and resource defence with a mammal under the controlled conditions of the
87 laboratory. This new approach may pave the way for further such studies with other groups of organisms.

88 **2. Materials and Methods**

89 **(a) Subjects and housing**

90 Experiments were conducted with 36 individuals of the 9-10g neotropical nectarivorous bat species *Glossophaga*
91 *soricina* (Pallas's long-tongued bat). Bats came from a captive colony (founders originating from Mexico,
92 1988) and were older than one year as judged by finger joint ossification (Brunet-Rossini and Wilkinson
93 2009). Bats carried Radio Frequency Identification (RFID) tags attached to cable tie collars (total weight
94 of collar and RFID tag = 0.2g, max. 2.4% of the body weight) that were removed after the experiment.
95 Additionally, bats had numbered plastic split rings (A C Hughes Ltd., Middlesex, UK) around the forearm
96 for visual identification. Temperature in the experimental and colony room was kept at 20-25°C and air
97 humidity at 65-75%.

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

99 In the experimental room ten artificial flowers with automated nectar delivery (Winter and Stich 2005) were
100 mounted along a 4.2m bar at a height of 1.20m (Fig. 1). The distance between flowers was 0.4m. Flowers were
101 divided into two groups of five to simulate two flower patches. Each patch was enclosed by a sheet-covered
102 frame to separate the groups of flowers spatially (Fig. 1). The only entrance to the patches was a 40cm gap
103 between the ground and the bottom end of the enclosure (Fig. 1, dashed line). From this entrance bats had
104 to fly up vertically to reach the flowers. A syringe pump delivered nectar via tubes and pinch valves to the
105 artificial flowers. Nectar rewards were triggered by the interruption of an infrared light beam at the flower
106 opening. The RFID reader below the flower head identified a bat's ID code. Visits were recorded for all
107 flowers during every experimental night from 16h to 4h. The reward schedule was configured using PhenoSoft
108 Control (Phenosys GmbH, Berlin, Germany). Every detected event at a flower (including date, time, identity
109 of the individual, duration of the event and amount of nectar delivered) was recorded for data analysis.

110 **(c) Experimental procedure**

111 Six bats were randomly caught from the colony and were tested simultaneously as a group. Four experimental
112 groups consisted of three males and three females (mixed groups), whereas one group consisted of six males,
113 and another of six females. All bats were weighed before the experiment.

114 During the nightly experiments, in addition to the nectar provided by artificial flowers, bats had access to
115 pollen and water and to 6mL of additional food containing 200mg NektarPlus (Nekton, Keltern, Germany)
116 and 300mg milk powder (Milasan Folgemilch 2, Sunval Baby Food GmbH, Mannheim, Germany) dissolved in
117 water. Rewards at flowers consisted always of 30 μ L nectar (15% w/w sugar concentration, sucrose: fructose
118 1:2). Before the experimental schedule started, individuals were allowed to familiarize themselves with the
119 set-up and the artificial flowers. Since during this phase the cover was removed, the two flower patches were
120 not spatially separated and every flower visit was rewarded. This phase lasted for one to four nights until
121 each bat visited the flowers regularly. One female of the first mixed group did not visit any artificial flower
122 during the first night and was replaced by another female.

123 During the main experiment, the two flower patches were covered and spatially separated. Experimental
124 nights were divided into two phases. During the first phase of the night only one of the two flower patches
125 was rewarding, and therefore the resources were spatially clumped. The fixed time interval between rewards
126 was 60s. During the second phase of the night both patches gave rewards, resources were evenly distributed
127 across the patches, and the fixed time interval between two rewards at a flower was increased to 120s.
128 Therefore, the amount of food available per unit time did not change during the whole night; only the spatial
129 distribution of food changed from the clumped resource condition with one patch rewarding (five flowers)
130 during the first phase of the night to the distributed resource condition with two patches rewarding (ten
131 flowers) during the second phase of the night. With this experimental schedule, the maximal amount of
132 nectar the bats could collect was 108mL, which corresponds to 18mL nectar per individual per night. The
133 rewarding patch during the first phase of the night was chosen pseudo-randomly and the same patch was
134 never chosen in more than two consecutive nights. For the mixed groups, the duration of the clumped
135 resource condition was six hours and the experiment lasted nine nights (seven nights for the first mixed
136 group). The duration of the first part of the night was more variable (4-8h) in the same-sex groups and the

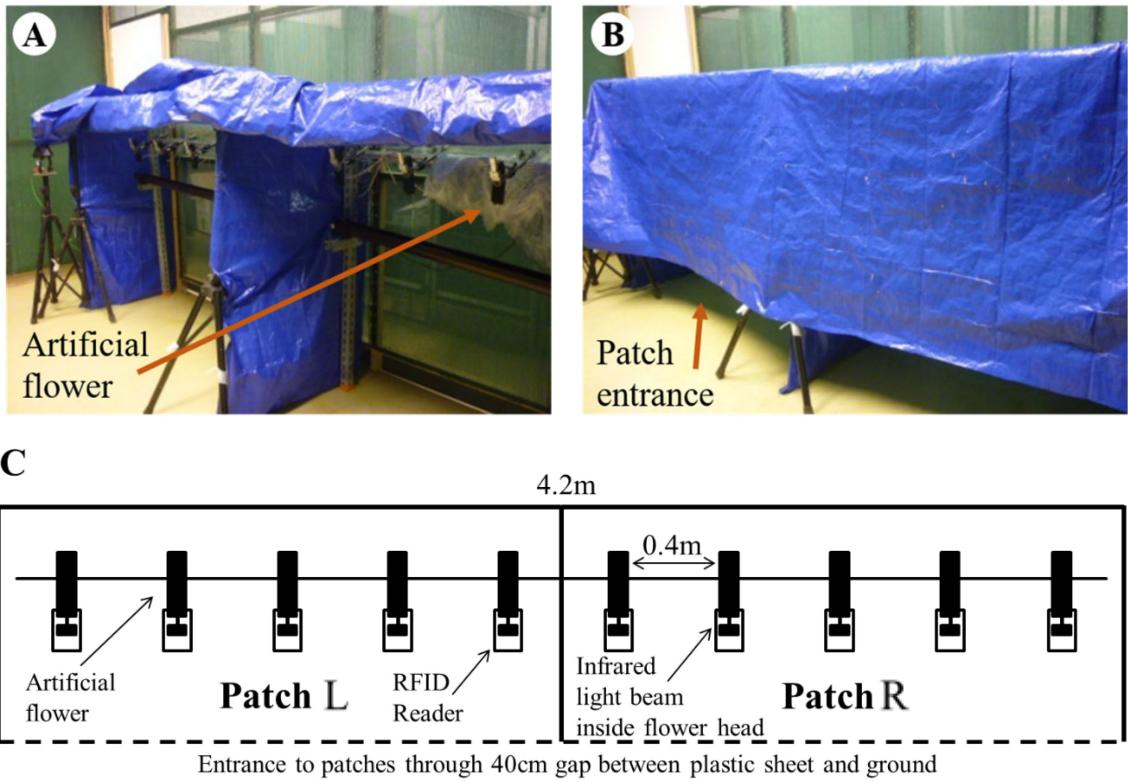


Figure 1: Experimental set-up consisting of two spatially separated flower patches. (A) The flowers were mounted 1.2m above ground. These ten flowers were divided into two patches (L and R) with five flowers each. (B) The patches were spatially separated by using a wooden frame covered with plastic sheet. To make it more demanding for bats to enter the patch, the only entrance was close to the ground in front of the flowers through a gap of 0.4 m from the ground to the lower rim of the plastic foil. (C) Schematic drawing of the experimental set-up from above. The dashed line indicates the side with the patch entrance.

137 experiment lasted eight nights for the male group and nine nights for the female group).

138

139 (d) Chasing behaviour

140 We took the chasing frequency of individuals at the artificial flowers as an indicator of the intensity of
 141 aggressive interactions between group members. We developed a method to automatically detect and
 142 score chasing events using the computer-collected animal identification data from the RFID sensors and
 143 flower sensors. In a previous pilot study [Wintergerst (2018); Appendix], three mixed groups of bats were
 144 video recorded for 24h over 14 nights, and the video data were synchronized to the computer-collected
 145 data. From the analysis of the combined data we were able to identify the following pattern of visitation
 146 events that reliably indicated a chasing event between two identified individuals: (i) an identified bat
 147 collected a reward at a flower, (ii) its visit ended and (iii) was immediately followed by a very brief
 148 (<200ms) RFID detection of a second bat, the chaser. Importantly, this second bat never attempted
 149 to drink and therefore did not insert its nose into the artificial flower and interrupt the light barrier
 150 inside the flower head. This distinguished such a chase from the occasional quick succession of two
 151 drinking visits by two bats at the same flower. The automated detection of chasing events not only offers
 152 a considerable time profit for the experimenter, but also avoids the human observer bias, a common
 153 drawback in video analysis. For the 24 hours of combined video data and automatically logged data, all
 154 89 chasing events detected in the computer-logged data were confirmed by video. Therefore, we consider

155 the algorithm for detecting chasing events in the logged data to be highly reliable. Of course, chases did
156 not only occur at the artificial flowers. Thus, our chase numbers are only an indicator of chasing intensity
157 between pairs of bats. For example, in one hour of video we observed 61 chasing events, but only five of
158 those occurred during flower visits and were also automatically detected. However, since we detected a
159 total of 1757 chasing events with our algorithm (see below) for the 36 participating bats, we considered
160 the automated approach adequate for quantifying the within-group dominance relationships. The total
161 number of flower visits per night constrains the number of chasing opportunities. Therefore, we corrected
162 our counts of chasing events by dividing observed chases by the total number of visits for each bat on each night.
163

164 (e) Statistical analysis

165 To investigate the difference in chasing behaviour between males and females and between the resource
166 conditions (one versus two rewarding patches) a Bayesian generalized linear mixed model (MCMCglmm, Hadfield
167 2010) with a binomial error structure was used. Body weight as an approximation of size and the full
168 interaction between resource condition and sex were included as fixed effects and the influence of these fixed
169 effects on the proportion of chasing events was assessed. Experimental group and individual were included
170 as random effects. The same model structure was used to address the question if the proportion of being
171 chased was influenced by these independent variables. If one or more individuals start to defend flowers and
172 thus exclude others from drinking, nectar consumption should increasingly differ between individuals since
173 the successful chaser should gain a higher nectar intake thus reducing the intake of the chased individuals.
174 Therefore, the between-individual difference in nectar consumption over the course of the experiment was
175 compared between experimental groups and resource conditions (clumped vs. distributed). First, each
176 individual's total nectar consumption standardized by the number of hours of foraging during the clumped
177 (one rewarding patch) and distributed (two rewarding patches) resource condition was determined for each
178 experimental night. Then these data were used to calculate group standard deviations, separately for the
179 males and females of each group. In order to assess the influence of resource defence on the individual
180 differences in nectar consumption (standard deviation of nectar intake) we fit a MCMCglmm model with a
181 Gaussian error structure and the following fixed effects: sex, experimental night, and resource condition
182 (clumped or distributed), as well as all two-way interactions. Again, we included group and individual as
183 random effects.

184 By plotting individual nectar consumption during the last two nights of the experiment against the frequency
185 of chasing other individuals, two non-overlapping groups of males were obtained, which were labeled dominant
186 and subdominant males, respectively. Such a clear pattern was not observed in females. Therefore, each
187 mixed group contained individuals belonging to one of three different types of social status: female, dominant
188 male, and subdominant male. To address the question whether nectar consumption varied depending on
189 social status during the early and late stages of the experiment we used Welch tests and adjusted the p
190 values using the Holms method for multiple comparisons.

191 All statistical analyses were conducted using R (Team 2021). All data and code are available in the Zenodo
192 repository: xxx.
193

194 2. Results

195 The goal of these experiments was to investigate the social structure of resource defence in *Glossophaga*
196 *soricina*, in addition to the potential influence of interference competition on individual nectar intake. The
197 first striking observation we made was the uneven distribution of nectar consumed between the sexes and
198 individuals. For example, in the first mixed group of bats tested, after only two nights the nectar consumption
199 of two males was nearly reduced to zero, whereas the third male increased its consumption substantially
200 (Fig. 2A). This pattern, however, only occurred during the condition when resources were clumped. Nectar
201 consumption of females did not change even during the clumped condition. On the same nights but during
202 the second half of the night, with resources distributed over two patches, nectar consumption of males and
203 females converged at the end of the experiment (Fig. 2B).

204 In total 1757 chasing events were identified within the data. In all mixed groups males chased other bats

205 in front of flowers significantly more often than females did (Fig. 3A, Table 1). Notably, the frequency of
 206 females as active chasers in female-only groups was higher than chasing by females in the mixed groups
 207 (Fig. 3A). Although the rate of nectar availability remained constant throughout the night and only the
 208 spatial distribution of the resources changed, the number of chasing events was significantly lower during
 209 the distributed resource condition when rewards were available at both patches (Table 1). There was no
 210 significant difference between the sexes in how often a bat was chased by another individual but individuals
 211 were chased less during the distributed resource condition (Fig. 3B, Table 1). Weight as an indicator of size
 212 had no significant effect on chasing frequency or the frequency of being chased (Table 1).

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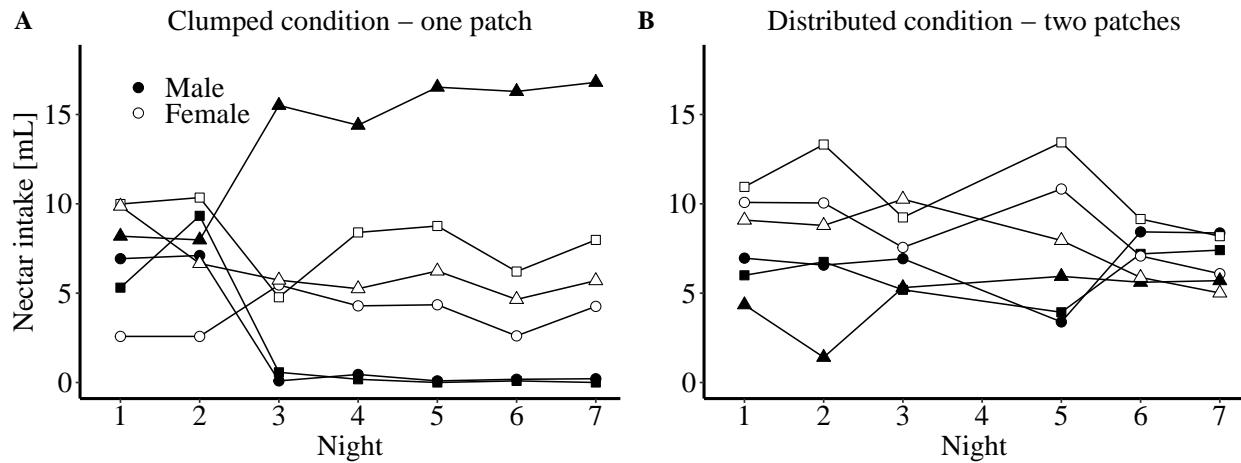


Figure 2: Exemplary change of individual daily nectar consumption during the experiment of one mixed experimental group consisting of three males and three females (symbols show different individuals). **(A)** During the clumped resource condition (first part of the experimental night) rewards were only available concentrated at one patch. The nectar consumption of two males approached zero after only two nights, whereas the third male received considerably more nectar than at the beginning of the experiment (males filled symbols). Females on the other hand maintained their level of daily nectar consumption (females open symbols). **(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 consumption over the course of the experiment. The second part of night 4 was excluded due to technical problems.

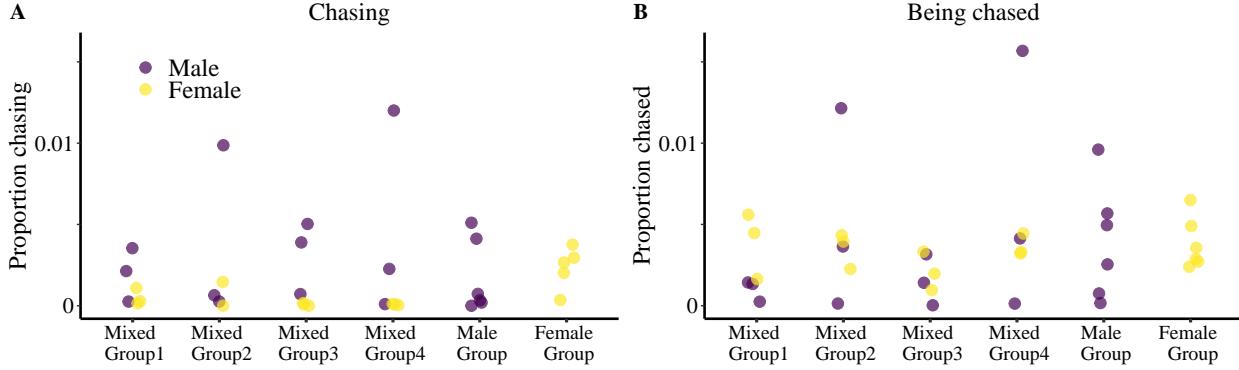


Figure 3: Sexes differed in the frequency of chasing other individuals. (A) Males (dark symbols) chased others significantly more than females did (light symbols, Table 1). Single sex groups for comparison. Shown are the individual proportions of chasing events over the whole experiment. Notably, in 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 during the clumped resource condition (Table 1), but the variance 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

214 Resource defence should lead to a larger between-individual difference in nectar consumption. Between-
 215 individual differences in nectar consumption was quantified as the standard deviation of nectar intake in
 216 each group, separately for males and females. During the clumped resource condition, the standard deviation

increased significantly (Fig. 4, Table 2) for both sexes and males had higher standard deviations of nectar intake (Table 2). However, during the distributed resource condition the standard deviation of mean nectar consumption was significantly lower (Fig. 4, Table 2), there was no difference between the sexes (estimate = 0.01, 95% CI = (-0.07, 0.14)) and there was no significant change over the course of the experiment (estimate = 0.02, 95% CI = (-0.02, 0.07)).

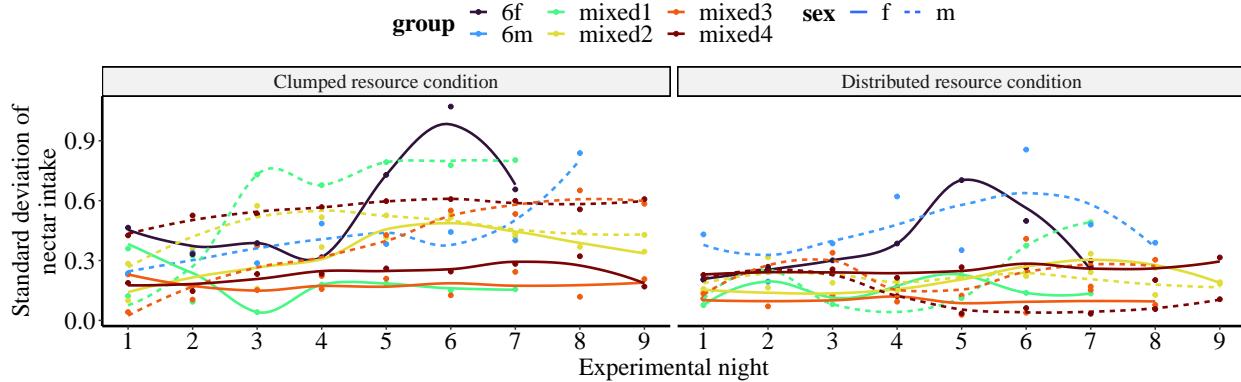


Figure 4: The standard deviation of group nectar consumption was used to measure the between individual differences in nectar intake. It was calculated for the clumped (left panel) and the distributed (right panel) resource conditions, separately for males and females (line types) of each experimental group (different colors). For visualization only, lines give the corresponding fits based on locally weighted scatterplot smoothing (loess).

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) | 0.30 (0.2, 0.43) | | 0.001 |
| sex (female) | -0.14 (-0.24, -0.03) | | 0.006 |
| condition (distributed) | -0.12 (-0.21, -0.02) | | 0.020 |
| night | 0.05 (0.01, 0.1) | | 0.030 |
| sex (female):condition (distributed) | 0.14 (0.05, 0.23) | | 0.001 |
| condition (distributed):night | -0.02 (-0.04, -0.01) | | 0.010 |
| sex (female):night | -0.01 (-0.03, 0.01) | | 0.188 |

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

When plotting chasing events against nectar consumption the data for males fall into two non-overlapping groups. The males of one cluster (Fig. 5A, inside dashed oval) chased other individuals and consumed more nectar than the other males. This cluster included only one male from the mixed groups but two males from the males-only group. These males were categorized as “dominant.” The second cluster of males (Fig. 5A, outside and below dashed oval) was characterized by a low frequency of chasing and low nectar consumption. These males were categorized as “subdominant.” In females such a pattern did not emerge (Fig. 5B). While

228 in the females-only group four females chased other females more frequently, only one of these females would
 229 be classified as dominant using the same cut-off criteria we used for the males (Fig. 5B). During the first two
 230 nights of the experiment in the clumped resource condition, there was a difference in nectar intake between
 231 dominant and subdominant males and between subdominant males and females (Fig. 6). During the last two
 232 nights of the experiment in the clumped resource condition, the three groups clearly differed, with the highest
 233 nectar intake in dominant males, an intermediate intake in females, and lowest nectar intake in subdominant
 234 males (Fig. 6). In contrast, in the distributed resource condition there were no differences between the nectar
 235 intake of dominant and subdominant males in any stage of the experiment (Fig. 6). The subdominant males
 236 had a significantly lower nectar intake than females in the first two, but not in the last two experimental
 237 nights (Fig. 6).

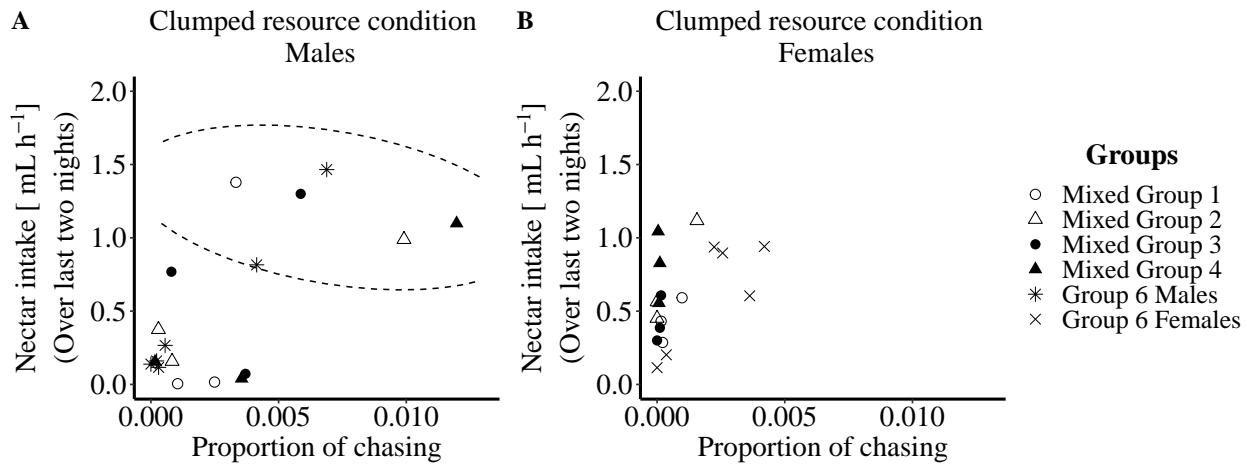


Figure 5: Influence of chasing frequency on nectar intake in the clumped resource condition during the last two nights of the experiment. (A) Males that more often chased other males also consumed more nectar. Males were divided into two non-overlapping groups by considering the chasing frequency and 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 subdominant males. (B) Nectar consumption of females did not depend on chasing frequency during the clumped resource condition and non-overlapping groups did not emerge.

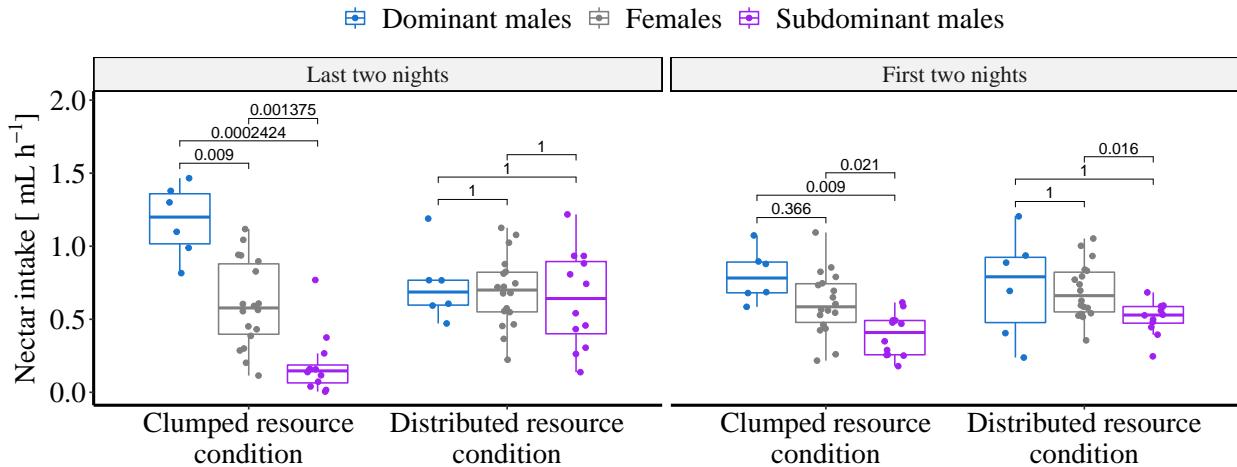


Figure 6: Comparison of nectar consumption during the first and last two nights of the experiment depending on sex and social status. During the clumped resource distribution (left panel), already at the beginning of the experiment subdominant males collected significantly less nectar than dominant males and females. At the end of the experiment, females, dominant and subdominant males differed to a large extent in their nectar consumption. During the distributed resource condition at the beginning of the experiment subdominant 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.

238 Behavioural observations

239 Qualitative behavioural observations of four hours of video recordings revealed several behaviours that seem
 240 to be characteristic for dominant males. Instead of just visiting the flowers and leaving the patch as the other
 241 individuals did, dominant males remained hanging between the flowers within the patch for a significant
 242 amount of time (Appendix Fig. A1). When other individuals came close due to visits of directly adjacent
 243 flowers, dominant males often spread one wing in the direction of the other individual which could be
 244 interpreted as a threatening posture. Some individuals were attacked and chased away by dominant males
 245 while visiting artificial flowers. In this case, dominant males mostly attacked from above with their mouth
 246 wide open, and followed the intruder for a short distance. Sometimes the chasing escalated into fighting with
 247 both bats tumbling towards the ground and resuming their flight only shortly above the floor. In rare cases,
 248 these fights might have led to small injuries. One subdominant male had several fresh scratches on its wing
 249 that were not present before the experiment and that were possibly caused by teeth or claws (Appendix Fig.
 250 A2). After a successful flower defence, the dominant male normally visited most of the five flowers within the
 251 patch before returning to its position between the flowers.

252 3. Discussion

253 Similar to observations in free-living populations, in this experiment *Glossophaga soricina* competed for
 254 nectar not only by exploitation but also by interference competition. However, the results show that the
 255 predisposition to defend resources and the influence of interference competition on individual nectar intake
 256 differed significantly between the sexes. Only a subset of males successfully defended flower patches. These
 257 dominant males were characterized by the highest frequency of chasing other individuals away from profitable
 258 flowers and by a substantial increase in nectar intake by the end of the experimental run. Although these
 259 dominant males chased females and other males equally often, only the nectar intake of subdominant males but
 260 not of the females was affected by this behaviour. Thus, male-initiated interference competition increased the

261 difference in nectar intake between males but did not affect females. The frequency of aggressive interactions
262 was higher and males only defended resources successfully when the available nectar was concentrated at
263 only one flower patch. This supports the hypothesis that clumped resources favour an increase in aggressive
264 interactions (Grant 1993).

265 To the best of our knowledge, this study is the first report of sex-dependent differences in the resource defence
266 behaviour of neotropical nectar-feeding bats. In mixed sex groups, females seemed to be unaffected by the
267 behaviour of dominant males whereas subdominant males were excluded at least partially from the defended
268 flower patch. There are two possible explanations for this differential effect on subdominant males and
269 females. On the one hand, dominant males might just not be capable of excluding females. On the other hand,
270 dominant males could tolerate females in their defended patch because they might receive additional benefits,
271 for example tolerating females could lead to an increase in mating opportunities. Similar social dynamics
272 have been described in the insectivorous bat species *Myotis daubentonii* (Senior, Butlin, and Altringham
273 2005). Dominant males of this species temporarily exclude other males from profitable habitats whereas
274 females are tolerated and in addition to securing access to resources, the successful exclusion of other males
275 has been shown to increase the reproductive success of dominant males (Senior, Butlin, and Altringham
276 2005). Similarly, it has been observed that male *Eulampis jugularis* hummingbirds, which successfully defend
277 highly profitable feeding-territories against other males while sharing the available resources with females,
278 experienced an increase in their mating success (Temeles and Kress 2010).

279 However, in our experiment dominant males chased females about as often as they chased subdominant males
280 (Table 1). If females were able to feed in the defended patch because dominant males tolerated them due
281 to potential additional benefits, it could be that the detected chasing events by dominant males differed
282 in quality depending on the sex of the intruder. However, this was not further quantified in the current
283 study. We extracted the frequency of chasing events from data automatically recorded at artificial flowers
284 (successive detection of two different IDs while the first was feeding at the flower). Therefore, it was not
285 possible to determine if males showed behavioural differences when chasing other males in comparison to
286 chasing females. However, the recorded video revealed that individuals chased each other not only directly at
287 the artificial flowers but also in other areas of the flower patch. Since individuals could only be identified by
288 their RFID tag directly at the RFID reader attached to artificial flowers the sex of individuals chasing each
289 other in other areas of the experimental room remains unknown. However, some subdominant individuals
290 showed marks from small injuries at their wings after the experiment (see example in Appendix Fig. A2)
291 and such marks were only observed in males. This could be an indication that dominant males could direct
292 more aggression towards subdominant males besides the interactions observed directly at the flowers. This
293 could explain why subdominant males were more affected than females by the aggressive resource defence
294 behaviour of dominant males. Such sexual dimorphism in aggressive resource defence is known from other
295 nectar-feeding vertebrates, like hummingbirds. It is thought that the beaks of the males of some territorial
296 species are specifically adapted as intrasexually selected weapons (Rico-Guevara et al. 2019).

297 Generally, females showed lower chasing frequencies, but, surprisingly, some females in the females-only
298 group showed an increased nectar consumption and chasing frequency, compared to the females in the mixed
299 groups (Fig. 5B). Thus it appears that in the absence of male individuals, some females begin to exert
300 dominant behaviour over the other females. These findings are similar to the social structure of resource
301 defence found in some nectar-feeding bird species. For example, in free-living ruby-throated hummingbirds
302 females also have lower levels of defence (Rousseau, Charette, and Bélisle 2014). Moreover, although both
303 male and female *Eulampis jugularis* hummingbirds defend feeding territories during the non-breeding season,
304 males are always dominant over females (Wolf and Hainsworth 1971; Temeles, Goldman, and Kudla 2005). It
305 would be interesting to better understand why females are less affected by the aggressive resource defence
306 behaviour of dominant males compared to subdominant males and also why females themselves were not able
307 to completely monopolize the profitable patch against other females.

308 In all mixed sex groups, only one male per group became dominant and successfully defended flowers, whereas
309 in the males-only group two males exhibited dominant behaviour (Fig. 5A). A closer look at the nectar
310 consumption at each flower revealed that on the last night of the experiment the two males had nearly
311 monopolized different flowers within the same patch rather than sharing access to the same flowers (Appendix
312 Fig. A3). Such flower partitioning was also observed in the females-only group (Appendix Fig. A4), but
313 rarely seen in the mixed groups (Appendix Figs. A5-A8). The successful resource defence by two individuals

314 in the male-only group showed that resource defence can occur independent of the presence of females.
315 Although the position of the rewarding patch during the clumped resource condition changed between the
316 nights between the left and right, usually the same male continued to successfully defend the patch (Appendix
317 Figs. A3-A8). This means that males defended the resources themselves and not a particular location.
318 Furthermore, this shows that even after changing the location of the defended patch the same individuals
319 were able to succeed in monopolizing the resources, indicating a stable hierarchy at least for the duration of
320 the experiment.
321 The ability of an individual to successfully defend and monopolize resources is often correlated with distinct
322 physical characteristics for example body size (Searcy 1979). However, the results show that weight as an
323 approximation of size did not correlate significantly with the chasing frequency of individuals (Table 1) and
324 therefore did not predict which male succeeded to defend a flower patch during this study. Another factor that
325 could influence the success in defending flowers is age and therefore experience (Arcese 1987; Yasukawa 1979).
326 Since we could only discriminate between young and adult animals, we cannot dismiss age and experience as
327 a predictor of successful flower defence.
328 In this study, subdominant males received considerably less nectar than dominant males and females (Fig. 6).
329 However, except in mixed group 1, subdominant males were rarely completely excluded from the flower patch
330 and their average nectar intake during the clumped resource condition was still $0.3 \pm 0.18 \text{ mL h}^{-1}$ (mean \pm
331 SD). This result is in accordance with observations of free-living *G. soricina* in Colombia. There, subdominant
332 bats exploited the flowers defended by other individuals as soon as the dominant bat temporarily ceased
333 defending (Lemke 1984). Furthermore, in our study the frequency of chasing events decreased significantly
334 during the distributed resource condition in the second part of the night (Table 1). This supports the
335 theoretical prediction that aggressive defence behaviour increases when resources are spatially concentrated
336 (Grant and Guha 1993). Resource defence should only occur when the energy gain outweighs the cost of
337 aggressive interactions (Brown 1964). Therefore, a possible explanation for this observation could be the
338 decrease in quality of the defended patch once its nectar supply dropped to half. Together, these results
339 suggest that along the different degrees of territorial behaviour, resource defence observed in *G. soricina*
340 seems to represent a transient monopolization of resources instead of a longer-term permanent exclusion of
341 intruders.

342 4. Conclusion

343 Although flower defence behaviour of *G. soricina* was investigated in a laboratory setting, we observed
344 similar behaviour as described in free-living populations. Our results revealed a sexual dimorphism in flower
345 defence behaviour. Only males successfully defended flower patches and excluded other males from their
346 defended resource, whereas females remained unaffected by this male behaviour and continued to visit the
347 flowers guarded by a male. This observed pattern is similar to resource defence behaviour observed in other
348 nectar-feeding vertebrates. Furthermore, we could show that the frequency of aggressive interactions was, as
349 predicted, higher when resources were clumped in one patch. Future studies with free-living populations have
350 to be conducted to assess how frequent and important resource defence in these nectar-feeding bats is and if
351 males that are successful in defending resources have additional advantages.

352 **Appendix**

353 **Video analysis**

354 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).
355 Every time the algorithm marked an event as a chase event, there were two individuals following each other.
356 Some chase sequences did not get detected. The individual that chased never drank immediately after the
357 chase at the same flower location where the chase occurred. There were 16 incidences that were difficult to
358 classify by observation or did not appear to be aggressive interactions.

359

360 $f \rightarrow f$ appear to be less aggressive

361 $f \rightarrow m$ appear aggressive

362 $m \rightarrow f$ appear aggressive

363 $m \rightarrow m$ appear aggressive

364

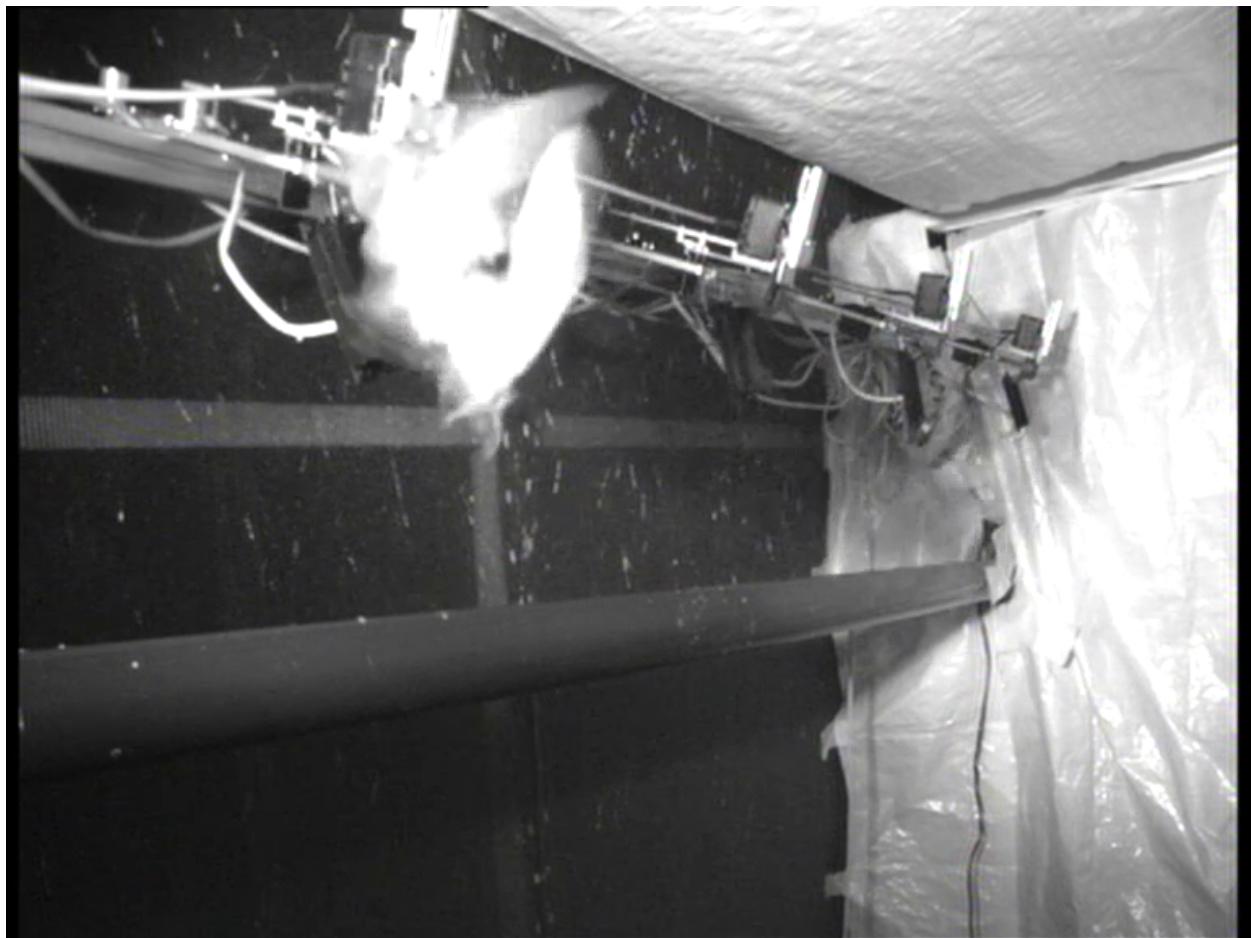


Figure A1: Video of the dominant male in mixed group 3 chasing all bats approaching the rewarding flowers in the rewarding patch during the clumped resource condition.

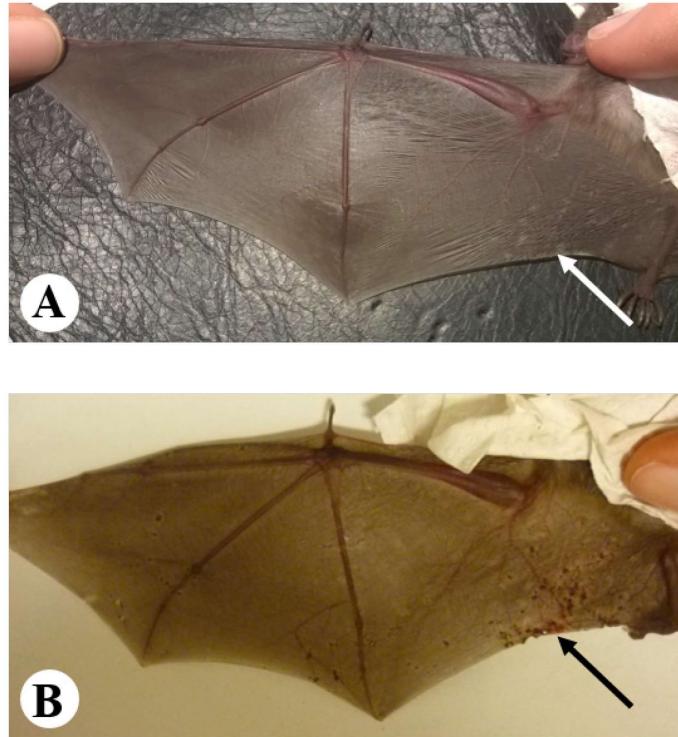


Figure A2: Wing images of a subordinate male from mixed group 4. The same individual was photographed before (**A**) and after the experiment (**B**). The black arrow points to the scarred location due to wing injuries, purportedly caused by the dominant male.

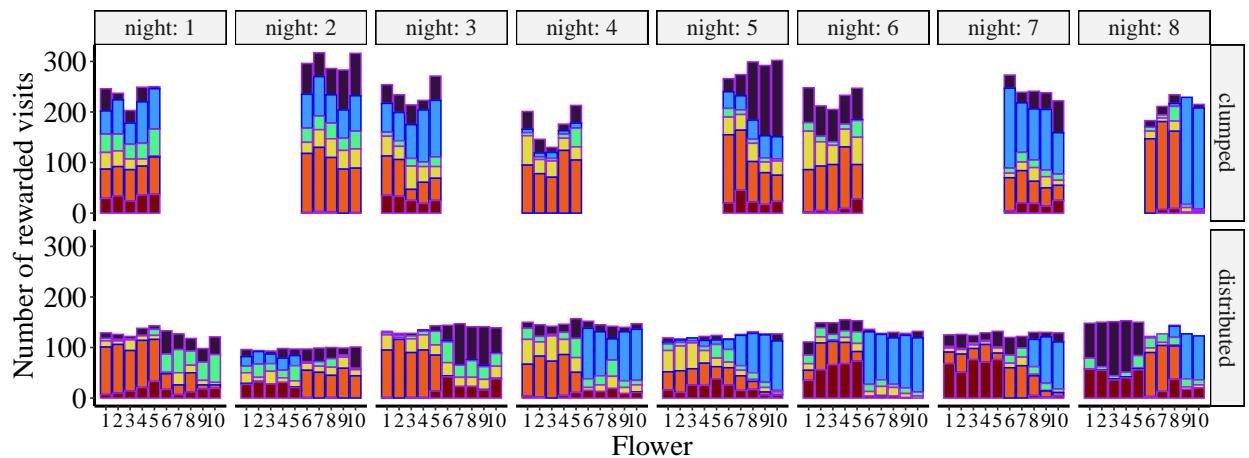


Figure A3: Distribution of visits across flowers for the six bats in the males-only group. The coloured bars give the number of visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns). The dominant males are shown with a blue border and the subdominant males are shown with a purple border. 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.

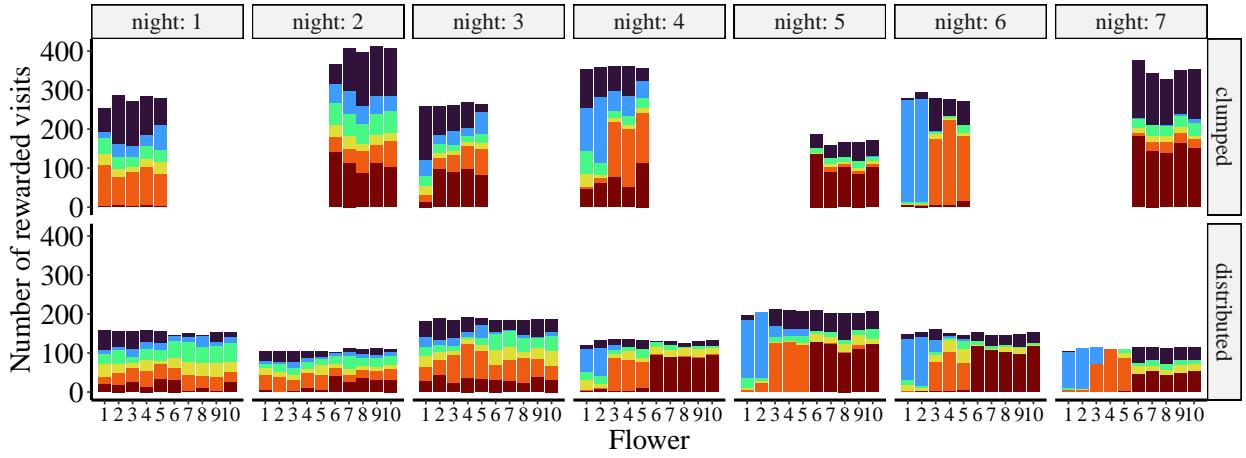


Figure A4: Distribution of visits across flowers for the six bats in the females-only group. The colored bars give the number of visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns). Females in this group exhibited the highest frequency of chasing behaviour compared to all other females. This is also the only group, in which females nearly monopolized flower patches or flowers within a patch.

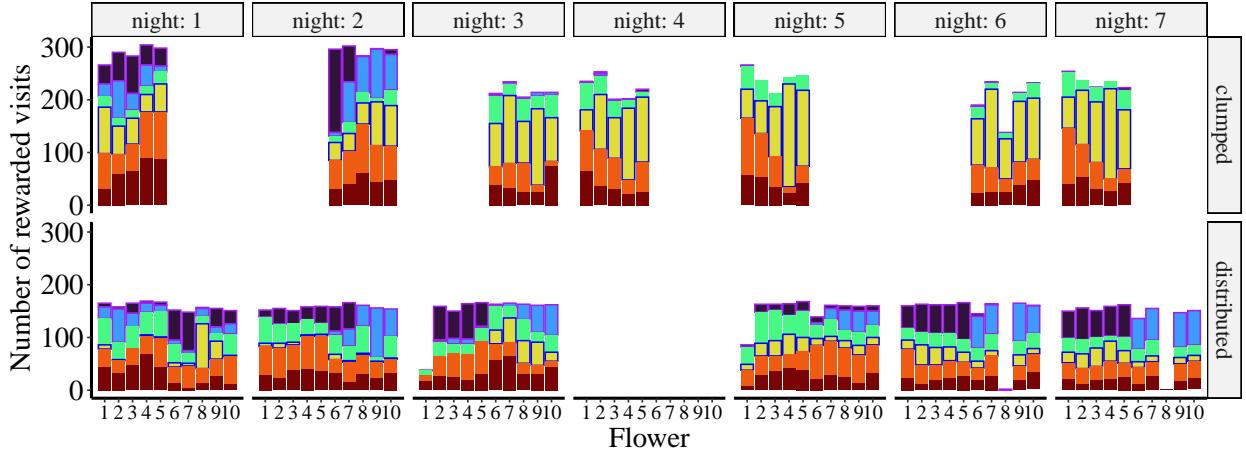


Figure A5: Distribution of visits across flowers for the six bats in mixed group 2. The colored bars give the number of visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns). The dominant male is shown with a blue border, the subdominant males are shown with a purple border, and the females are shown without a border. 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.

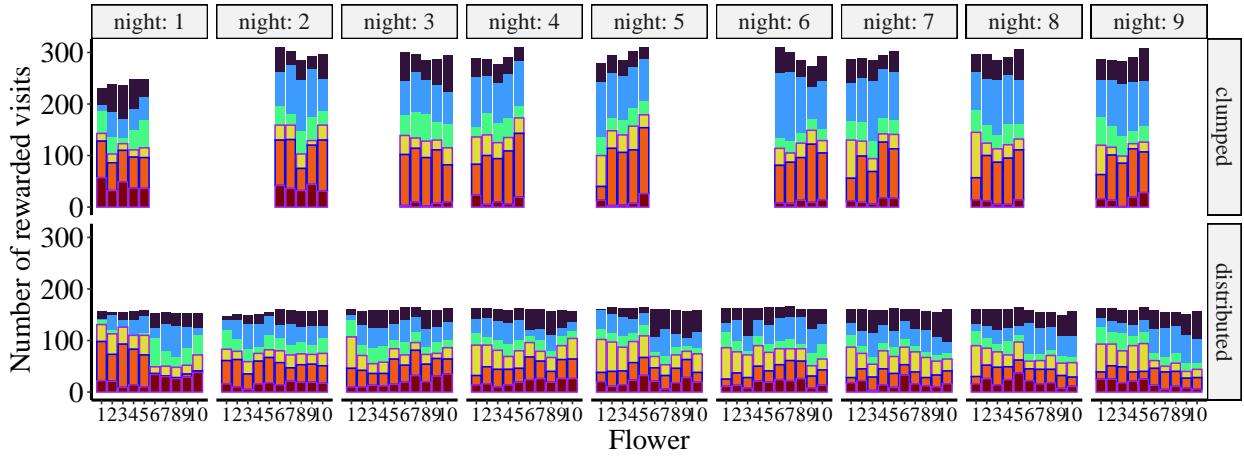


Figure A6: Distribution of visits across flowers for the six bats in mixed group 2. Same notation as in Fig. A5, but the colors correspond to different individuals.

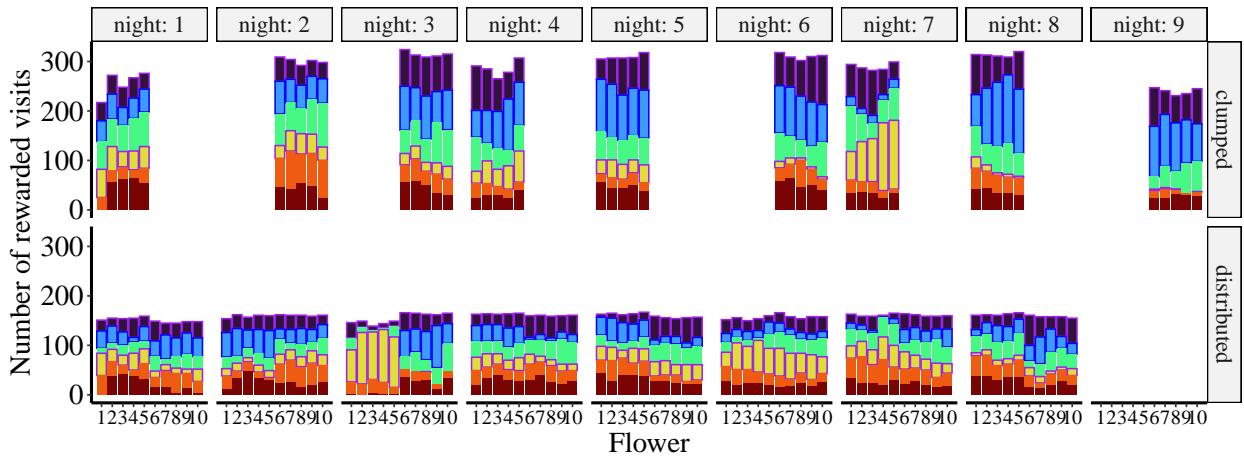


Figure A7: Distribution of visits across flowers for the six bats in mixed group 3. Same notation as in Fig. A5, but the colors correspond to different individuals. Due to a technical malfunction on night 9, there were no rewards delivered in the distributed resource condition and the data were excluded from analysis.

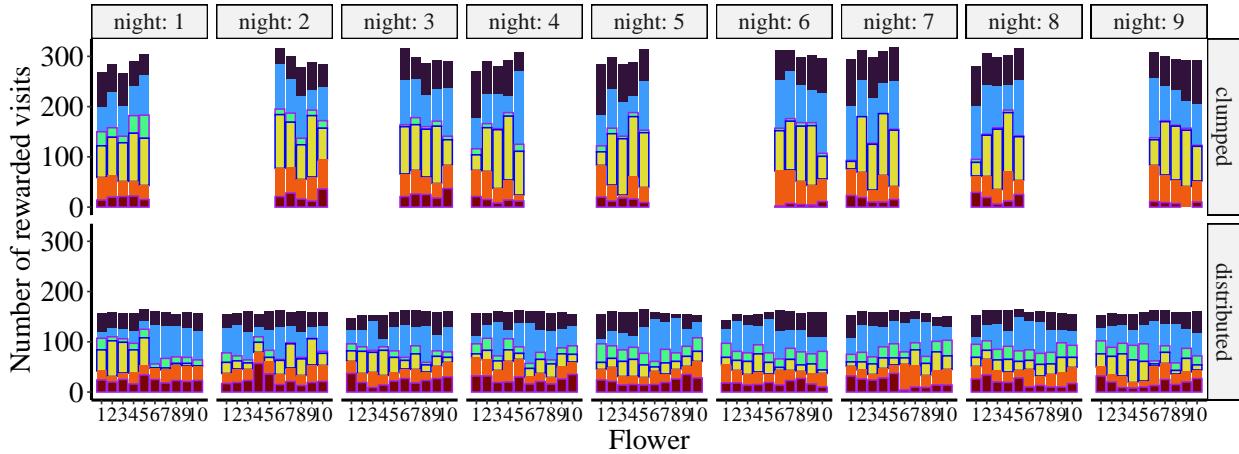


Figure A8: Distribution of visits across flowers for the six bats in mixed group 4. Same notation as in Fig. A5, but the colors correspond to different individuals.

365 Consent to participate

366 Not applicable.

367 Consent for publication

368 Not applicable.

369 Availability of data and material

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

371 Code availability

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

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376 We declare we have no competing interests.

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382 review and editing, Visualization, Supervision, Project Administration.

383 Y.W. Conceptualization, Resources, Methodology, Software (data acquisition), Writing—review and editing,
384 Supervision.

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