

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

³
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⁹ **Abstract**

¹⁰ Aggressive resource defence is frequently observed throughout the animal kingdom and although it is a
¹¹ widespread phenomenon in nectar-feeding birds, reports of interference competition in nectarivorous bats
¹² are extremely rare. *Glossophaga soricina* has been observed to defend flowers of *Agave desmettiana* but not
¹³ much is known about the social structure during resource defence and how interference competition leads to
¹⁴ resource monopolization and affects nectar intake. Here, we investigated the resource defence behaviour of
¹⁵ *G. soricina* in a laboratory setting. By using an experimental set-up consisting of two patches of computer-
¹⁶ controlled artificial flowers we tracked the nectar intake of every group member. Furthermore, we established
¹⁷ an automated method for flagging potentially aggressive interactions at proximity to the artificial flowers.
¹⁸ Theoretical models of interference competition predict that aggressive interactions increase when resources
¹⁹ are spatially more clumped. We varied resource distribution across two patches from clumped to distributed
²⁰ to assess how resource density influences aggressive interactions. Resource defence behaviour was assessed in
²¹ 36 individuals divided into one male and one female group, as well as four mixed-sex groups. Males engaged
²² in potentially aggressive interactions significantly more often than females and in each group some individuals
²³ were successful in defending artificial flowers. Subordinate males experienced a substantial decrease in nectar
²⁴ intake. However, females were only marginally affected by male aggression and maintained nectar intake.
²⁵ These results suggest that aggressive interactions and their effect on nectar intake are sex-dependent in *G.*
²⁶ *soricina*. Furthermore, as expected, aggressive interactions were more frequent and resource defence was only
²⁷ successful in the mixed groups when resources were clumped. Our novel experimental set-up allowed us to
²⁸ perform a mostly automated experimental test of models of interference competition and resource defence
²⁹ with a mammal under the controlled conditions of the laboratory. This new approach may pave the way for
³⁰ further such studies with other animals.

³¹ **Keywords:**

³² resource defence, 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 defence 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 behaviour towards it (chasing, threatening, biting, etc.) while receiving
40 little or no aggression from the other (Chase et al. 2002). In the extreme, dominance behaviour 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 defence of an area as exclusive
43 territory. The rules of economic defendability (Brown 1964) determine the adaptive compromise to which a
44 species' dominance behaviour 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 defence, 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 defence 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 defence 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 defence 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 defence 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. Thus, glossophagine bats can show
68 aggressive resource defence.

69 In this study, we investigated for a nocturnal, nectar-feeding mammal, the flower-visiting bat *Glossophaga*
70 *soricina*, the role of aggressive interactions for gaining access to nectar food. We tested the predictions of
71 models of resource defence (Grant et al. 2002) and interference competition (Grant 1993) during a naturalistic
72 foraging paradigm in the laboratory. The occurrence of resource defence is predicted to be highest at
73 intermediate levels of food abundance (Grant et al. 2002). In line with this prediction, the transient nature of
74 nightly defence behaviour observed in the field suggests that changes in food-abundance or food-requirements
75 that occur within the night affected the strength of the observed behaviour. To mimic the natural situation
76 of flowers that replenish their nectar more or less continuously (e.g. Tschapka and Helversen 2007) we
77 programmed artificial flowers to provide nectar with a fixed interval reward schedule. Once a nectar reward
78 had been taken by any bat, the fixed interval had to pass before the next reward was available at this flower.
79 Furthermore, theoretical models of interference competition predict that clumped resources lead to more
80 agonistic behaviour and resource defence than evenly distributed resources (Grant 1993). To include a test
81 of these predictions in our experimental design, we spatially subdivided our flower field into two patches
82 and programmed them to automatically change during the night the spatial distribution of available nectar
83 resources. We performed our study with 36 individuals of male and female *G. soricina*. By using artificial
84 flowers in a closed environment, we could track all flower visits and total nectar consumption of every
85 individual in the group. Each individual carried an electronic ID tag and flowers were equipped with ID
86 sensors. This also enabled us to detect and quantify a typical class of aggressive interactions between pairs of
87 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 defence 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 *Glossophaga soricina* (Pallas's long-tongued bat). Bats came from a captive colony (founders originating
95 from Mexico, 1988) and were older than one year as judged by finger joint ossification (Brunet-Rossini and
96 Wilkinson 2009). Bats carried Radio Frequency Identification (RFID) tags attached to cable tie collars (total
97 weight of collar and RFID tag = 0.2g, max. 2.4% of the body weight) that were removed after the experiment.
98 Additionally, bats had numbered plastic split rings (A C Hughes Ltd., Middlesex, UK) around the forearm
99 for visual identification. Temperature in the experimental and colony room was kept at 20-25°C, air humidity
100 at 65-75%, and light conditions were 12:12 LD (light off at 16h).

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

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

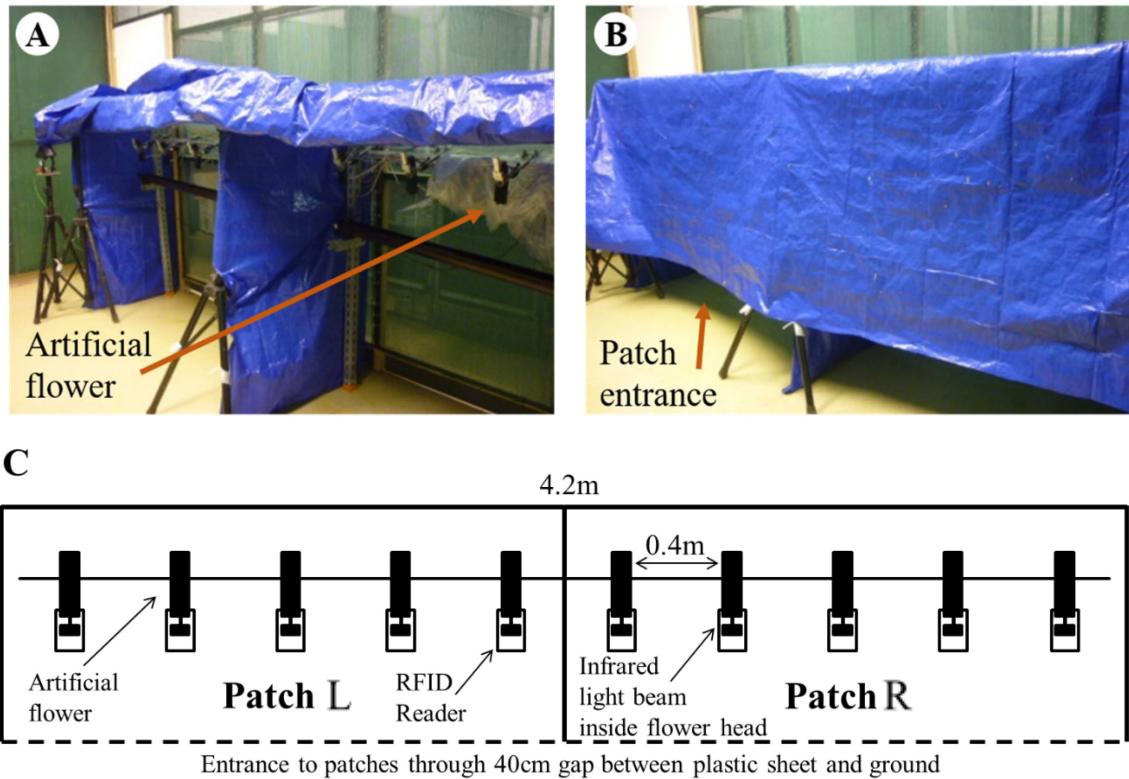


Figure 1: Experimental set-up consisting of two spatially separated flower patches. (A) The flowers were mounted 1.2m above ground. These ten flowers were divided into two patches (L and R) with five flowers each. (B) The patches were spatially separated by using a wooden frame covered with plastic sheet. 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 0.4m 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.

115 (c) Experimental procedure

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

119 During the nightly experiments, in addition to the nectar provided by artificial flowers, bats had access to
 120 pollen and water and to 6mL of additional food containing 200mg NektarPlus (Nekton, Keltern, Germany)
 121 and 300mg milk powder (Milasan Folgemilch 2, Sunval Baby Food GmbH, Mannheim, Germany) dissolved in
 122 water. Rewards at flowers consisted always of 30 μ L nectar (15% w/w sugar concentration, sucrose: fructose
 123 1:2). Before the experimental schedule started, individuals were allowed to familiarize themselves with the
 124 set-up and the artificial flowers. Since during this training phase the plastic cover was removed, the two
 125 flower patches were not spatially separated and every flower visit was rewarded. This phase lasted for one to
 126 four nights until each bat visited the flowers regularly. One female of the first mixed group did not visit any
 127 artificial flower during the first night and was replaced by another female.

128 During the main experiment, the two flower patches were covered and spatially separated. Experimental
 129 nights were divided into two phases. During the first phase of the night only one of the two flower patches was
 130 rewarding, and therefore the resources were spatially clumped. The fixed time interval between rewards was
 131 60s. During the second phase of the night both patches gave rewards, resources were evenly distributed across
 132 the patches, and the fixed time interval between two rewards at a flower was increased to 120s. Therefore, the
 133 amount of food available per unit time did not change during the whole night; only the spatial distribution of

134 food changed from the clumped resource condition with one patch rewarding (five flowers) during the first
135 phase of the night to the distributed resource condition with two patches rewarding (ten flowers) during the
136 second phase of the night. With this experimental schedule, the maximal amount of nectar the bats could
137 collect was 108mL, which corresponds to 18mL nectar per individual per night. The rewarding patch during
138 the first phase of the night was chosen pseudo-randomly and the same patch was never chosen in more than
139 two consecutive nights. For the mixed groups, the duration of the clumped resource condition was six hours
140 and the main experiment lasted nine nights (seven nights for the first mixed group). For the same-sex groups,
141 the duration of the first part of the night was variable (range = 4-8h, mean = 6h) and the main experiment
142 lasted eight nights for the male group and seven nights for the female group.

143 (d) Chasing behaviour

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

169 (e) Statistical analysis

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

males and females of each group. In order to assess the influence of resource defence on the individual differences in nectar consumption (standard deviation of nectar intake) we fit a `MCMCglmm` model with a Gaussian error structure and the following fixed effects: sex, experimental night (centered), and resource condition (clumped or distributed), as well as all two-way interactions. Again, we included group and individual as random effects.

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

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

3. Results

(a) Example of nectar intake in one experimental group

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

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

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

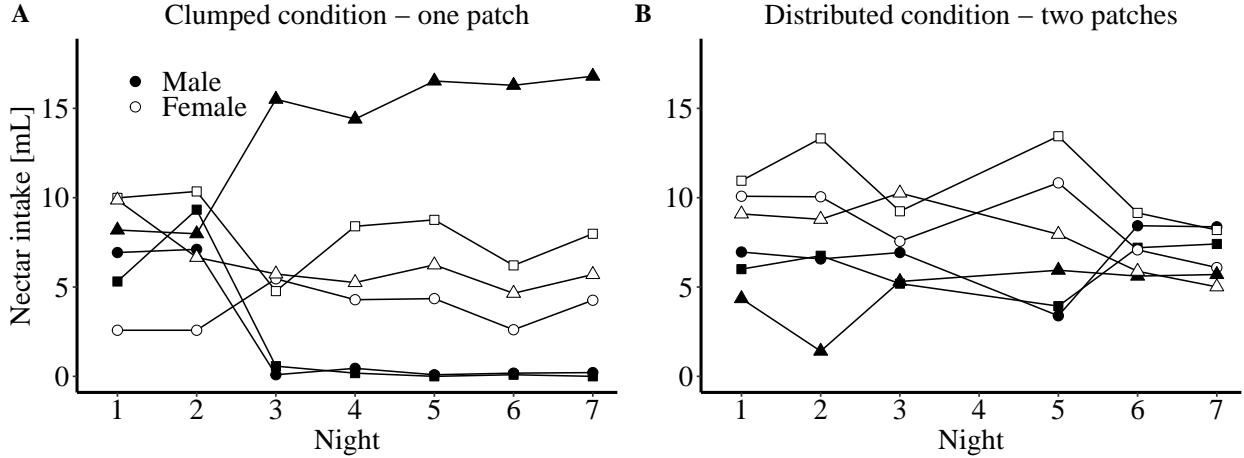


Figure 2: Exemplary change of individual daily nectar consumption during the experiment of one mixed experimental group consisting of three males and three females (symbols show different individuals). **(A)**. During the clumped resource condition (first part of the experimental night) rewards were 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.

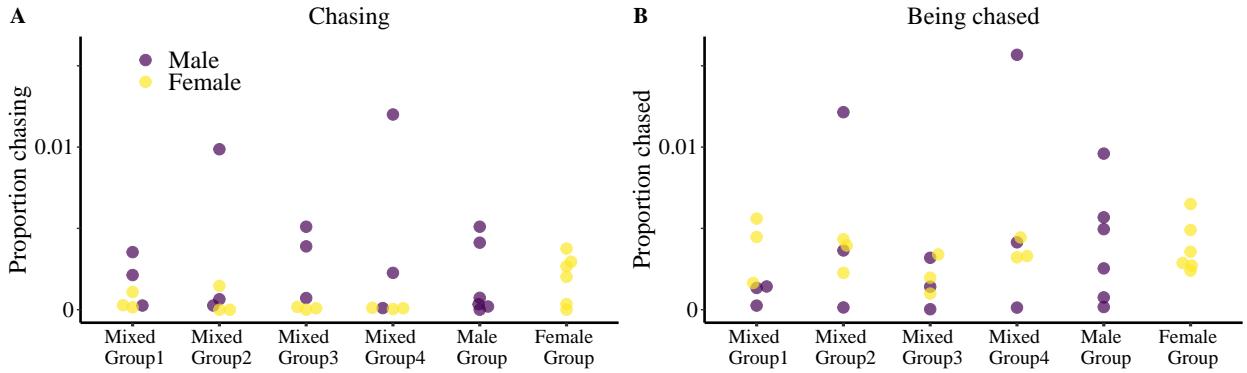


Figure 3: Sexes differed in the frequency of chasing other individuals. **(A)** Males (dark symbols) chased others significantly more than females did (light symbols, Table 1). Shown are the individual proportions of chasing events over the whole experiment. Notably, in the females-only group some females 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

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

226 Resource defence should lead to a larger between-individual difference in nectar consumption (Brown 1964).
 227 Differences in nectar consumption were quantified as the standard deviation of nectar intake in each group,
 228 separately for males and females. During the clumped resource condition, the standard deviation increased
 229 significantly over time for males (Table 2, Fig. S1) and was generally higher for males than for females (Table
 230 2, Fig. S1). For females in the clumped resource condition the increase in standard deviation was significantly
 231 smaller than in males (significant interaction between sex and night, Table 2), and was not itself significant
 232 (estimate = 0.03, 95% CI = -0.02, 0.07). Compared to the clumped resource condition, in the distributed
 233 resource condition the effect of experimental night was significantly lower for males (interaction between
 234 condition and night, Table 2), but not for females (estimate = 0, 95% CI = -0.03, 0.02). Moreover, in the
 235 distributed resource condition there was no significant change over the course of the experiment in males
 236 (estimate = 0.01, 95% CI = -0.03, 0.05) nor in females (estimate = 0.03, 95% CI = -0.02, 0.06). Overall,
 237 for both males (significant effect of condition) and females (estimate = -0.07, 95% CI = -0.14, -0.02) the
 238 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

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

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

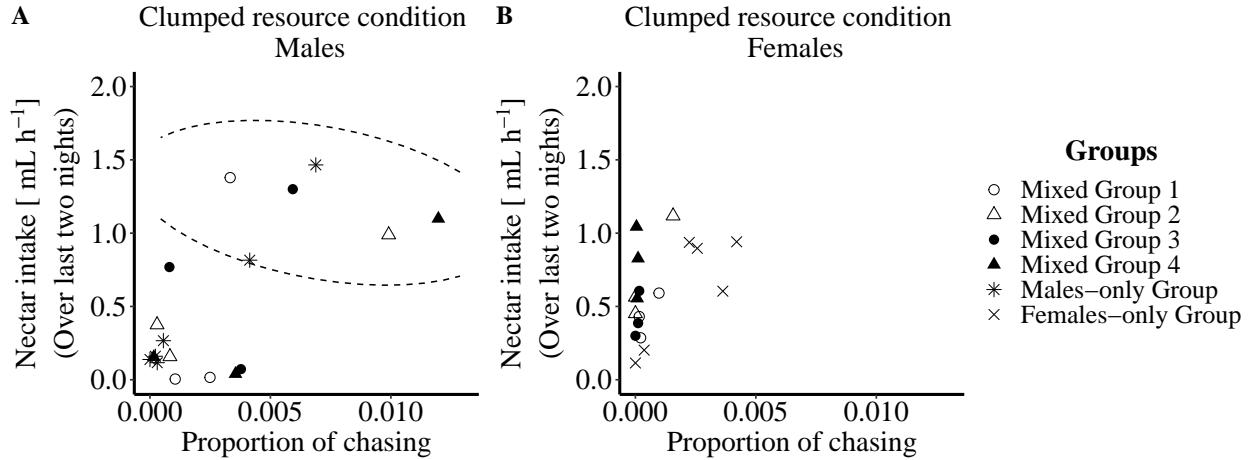


Figure 4: Influence of chasing frequency on nectar intake in the clumped resource condition during the last two nights of the experiment. **(A)** Males that more often chased other males also consumed more nectar. Males were divided into two non-overlapping groups by considering the chasing frequency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

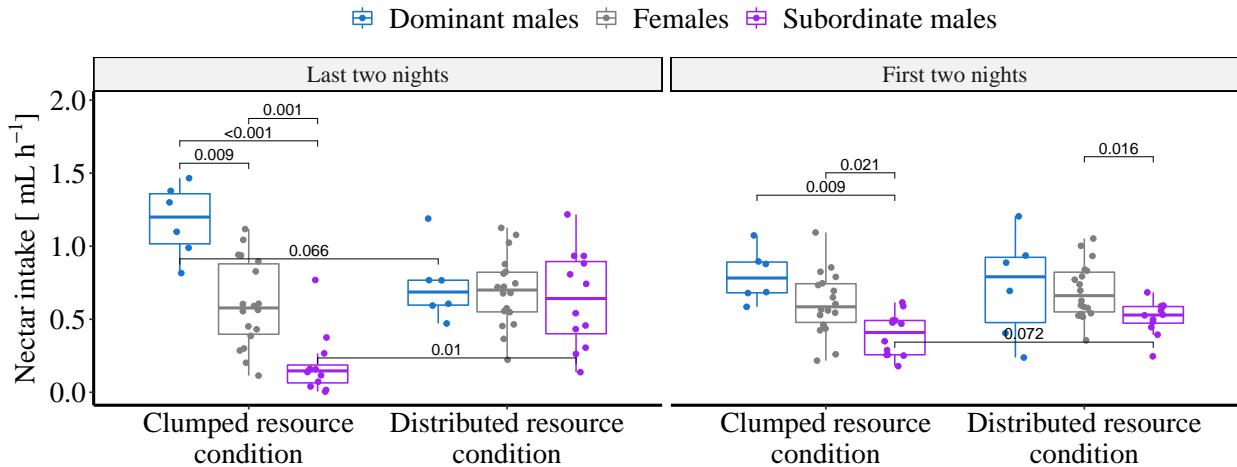


Figure 5: Comparison of nectar consumption during the first and last two nights of the experiment depending on sex and social status. During the clumped resource distribution (left panel), already at the beginning of the experiment subordinate males collected significantly less nectar than dominant males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

261 (e) Behavioural observations

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

275 4. Discussion

276 Similar to observations in free-living populations, in this experiment *Glossophaga soricina* competed for
 277 nectar not only by exploitation but also by interference competition. However, the results show that the
 278 predisposition to defend resources and the influence of interference competition on individual nectar intake
 279 differed significantly between the sexes. Only a subset of individuals, exclusively male in the mixed-sex groups,
 280 successfully defended flower patches. Dominant individuals were characterized by the highest frequency of
 281 chasing other individuals away from profitable flowers, by the highest Glicko ratings, and by a substantial
 282 increase in nectar intake by the end of the experimental run. Although the dominant males in the mixed

283 groups chased females and other males equally often, only the nectar intake of subordinate males but not
284 of the females was affected by this behaviour. Thus, male-initiated interference competition increased the
285 difference in nectar intake between males but did not affect females. The frequency of aggressive interactions
286 was higher and males only defended resources successfully when the available nectar was concentrated at
287 only one flower patch. This supports the hypothesis that clumped resources favour an increase in aggressive
288 interactions (Grant 1993).

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

291 To the best of our knowledge, this study is the first report of sex-dependent differences in the resource defence
292 behaviour of neotropical nectar-feeding bats. In mixed sex groups, females seemed to be much less affected
293 by the behaviour of dominant males whereas subordinate males were excluded at least partially from the
294 defended flower patch. This finding is consistent with observations of free-flying *G. commissarisi*, in which
295 males visited on average a smaller number of artificial flowers than females did (Nachev and Winter 2019),
296 presumably because of interactions with other males. There are two possible explanations for this differential
297 effect on subordinate males and females. On the one hand, dominant males might just not be capable of
298 excluding females. On the other hand, dominant males could tolerate females in their defended patch because
299 they might receive additional benefits, for example tolerating females could lead to an increase in (future)
300 mating opportunities. Similar social dynamics have been described in the insectivorous bat species *Myotis*
301 *daubentonii* (Senior, Butlin, and Altringham 2005). Dominant males of this species temporarily exclude other
302 males from profitable habitats whereas females are tolerated and in addition to securing access to resources,
303 the successful exclusion of other males has been shown to increase the reproductive success of dominant males
304 (Senior, Butlin, and Altringham 2005). Similarly, it has been observed that male purple-throated caribs
305 (*Eulampis jugularis*), which successfully defend highly profitable feeding-territories against other males while
306 sharing the available resources with females, experienced an increase in their mating success (Temeles and
307 Kress 2010).

308 However, in our experiment dominant males chased females about as often as they chased subordinate males
309 (Table 1). If females were able to feed in the defended patch because dominant males tolerated them due
310 to potential additional benefits, it could be that the detected chasing events by dominant males differed in
311 quality depending on the sex of the intruder. This was not further quantified in the current study, but could
312 potentially be investigated using audio recordings (Knörnschild, Glöckner, and Helversen 2010). We extracted
313 the frequency of chasing events from data automatically recorded at artificial flowers (successive detection
314 of two different IDs while the first was feeding at the flower). Therefore, it was not possible to determine
315 if males showed behavioural differences when chasing other males in comparison to chasing females. The
316 recorded video revealed that individuals chased each other not only directly at the artificial flowers but also
317 in other areas of the flower patch. Since individuals could only be identified by their RFID tag directly at
318 the RFID reader attached to artificial flowers the sex of individuals chasing each other in other areas of the
319 experimental room remains unknown. However, after the experiment some subordinate individuals showed
320 marks from small injuries at their wings (see example in Fig. S5) and such marks were only observed in males.
321 This could be an indication that dominant males directed more aggression (biting) towards subordinate
322 males than towards females. Such sexual dimorphism in aggressive resource defence is also known from other
323 nectar-feeding vertebrates, like hummingbirds. It is thought that the beaks of the males of some territorial
324 species are specifically adapted as intrasexually selected weapons (Rico-Guevara et al. 2019).

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

326 Generally, females showed lower chasing frequencies, but, surprisingly, some females in the females-only group
327 showed an increased nectar consumption and chasing frequency, compared to the females in the mixed groups
328 (Fig. 4B). Thus it appears that in the absence of male individuals, some females exerted dominant behaviour
329 over the other females, similar to males. These findings are similar to the social structure of resource defence
330 found in some nectar-feeding bird species. For example, in free-living ruby-throated hummingbirds females
331 also have lower levels of defence (Rousseau, Charette, and Bélisle 2014). Moreover, although both male and
332 female *Eulampis jugularis* hummingbirds defend feeding territories during the non-breeding season, males are

333 always dominant over females (Wolf and Hainsworth 1971; Temeles, Goldman, and Kudla 2005). It would be
334 interesting to better understand why females were less affected by the aggressive resource defence behaviour of
335 dominant males compared to subordinate males and why females themselves did not consistently monopolize
336 the profitable patch against other females, not even in the females-only group. Of course, as there was but a
337 single females-only group, the latter observation needs to be confirmed with more data. One possibility is
338 that females do not need to defend flowers when a dominant male is already reducing the number of flower
339 visitors and thus increasing the amount of food available.

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

347 (c) Social status and social hierarchy

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

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

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

379 (d) Conclusion

380 Although flower defence behaviour of *G. soricina* was investigated in a laboratory setting, we observed similar
381 behaviour as described in free-living populations. Our results revealed a sexual dimorphism in flower defence
382 behaviour in mixed-sex groups. Only males successfully defended flower patches and excluded other males

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

389 **Supplementary material**

390 **Video analysis**

391 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).
392 Every time the algorithm marked an event as a chase event, there were two individuals following each other.
393 Some chase sequences did not get detected. The individual that chased never drank immediately after the
394 chase at the same flower location where the chase occurred. There were 16 incidences that were difficult to
395 classify by observation or did not appear to be aggressive interactions.

396

397 $f \rightarrow f$ appear to be less aggressive

398 $f \rightarrow m$ appear aggressive

399 $m \rightarrow f$ appear aggressive

400 $m \rightarrow m$ appear aggressive

401

402 **Supplementary figures**

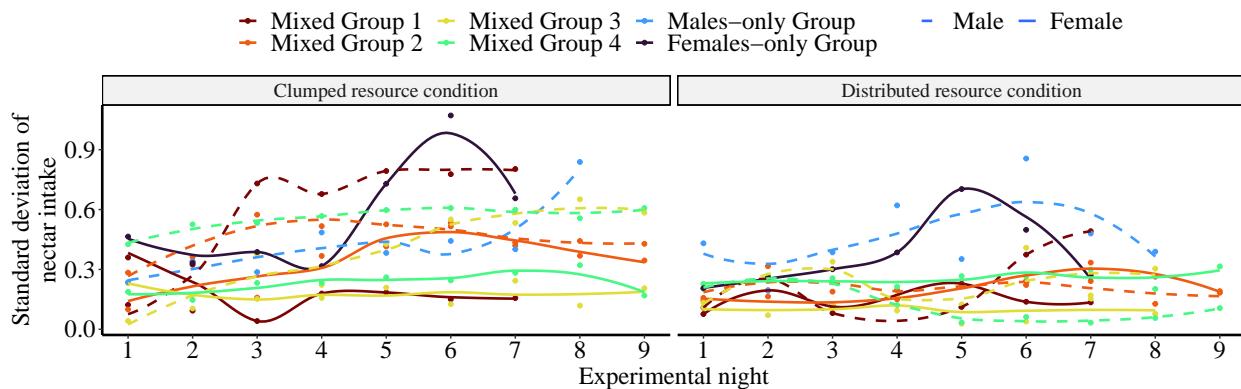


Figure S1: The standard deviation of group nectar consumption was used to measure the between individual differences in nectar intake. It was calculated for the clumped (left panel) and the distributed (right panel) resource conditions, separately for males (dashed lines) and females (continuous lines)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

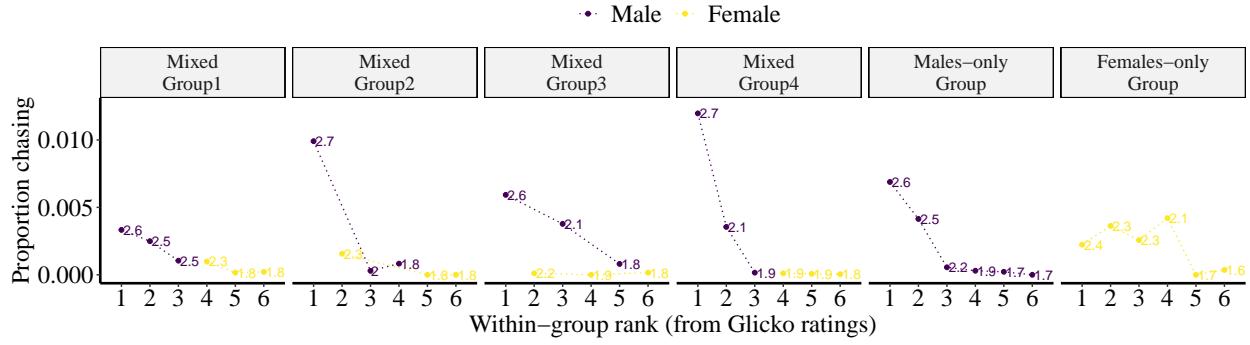


Figure S2: Over the last two experimental nights, the males (dark lines and symbols) with the highest proportion of chasing events were also the individuals with the highest Glicko rating (numbers, in thousands) in each group (panels) during the clumped resource condition. There was no such correspondence for females in the female-only group (right panel).

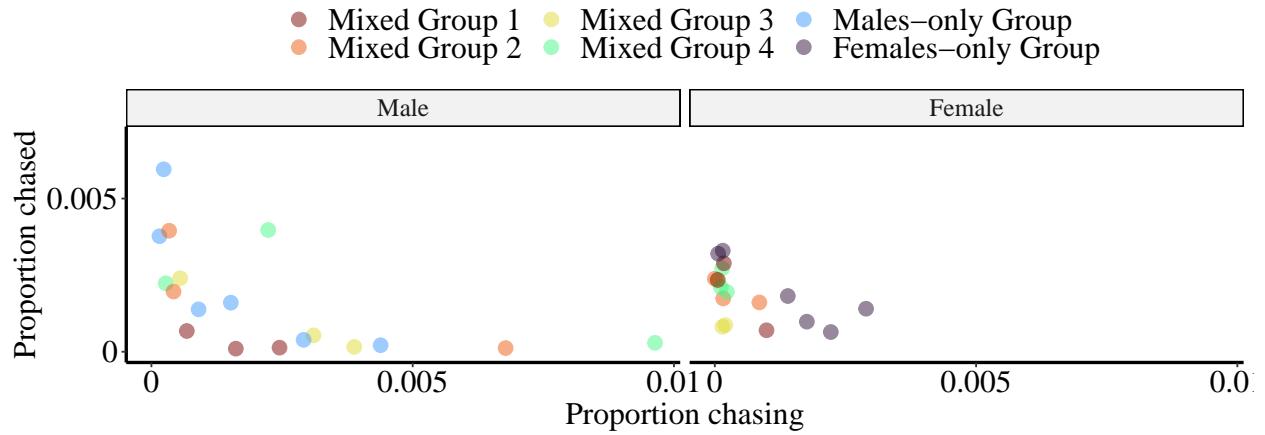


Figure S3: The relationship between proportion of chases versus the proportion of being chased out of all detections over the whole experiment for the female (right) and male (left) individuals in the six experimental groups (different colours).

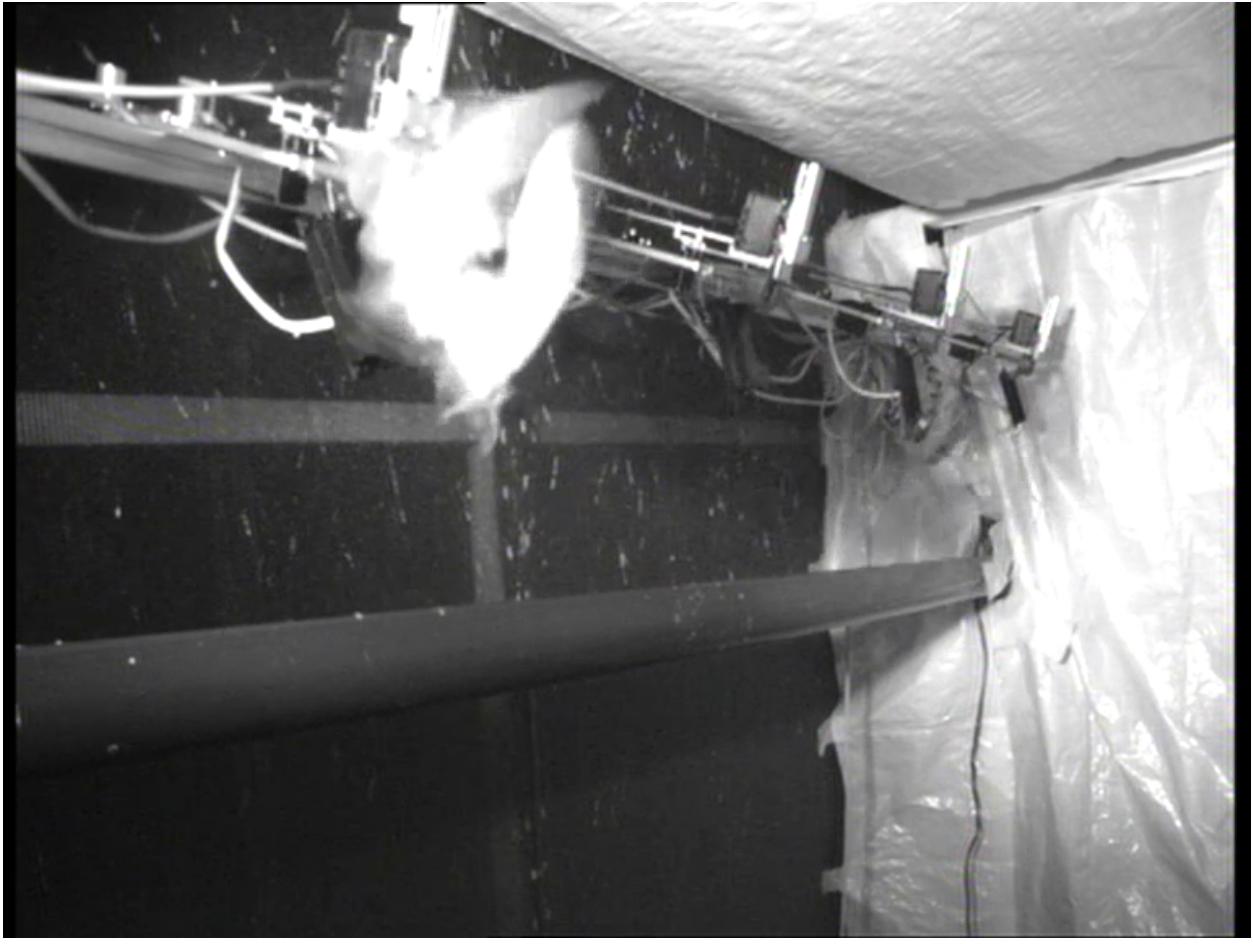


Figure S4: Video of the dominant male in mixed group 3 chasing all bats approaching the rewarding flowers in the rewarding patch during the clumped resource condition.

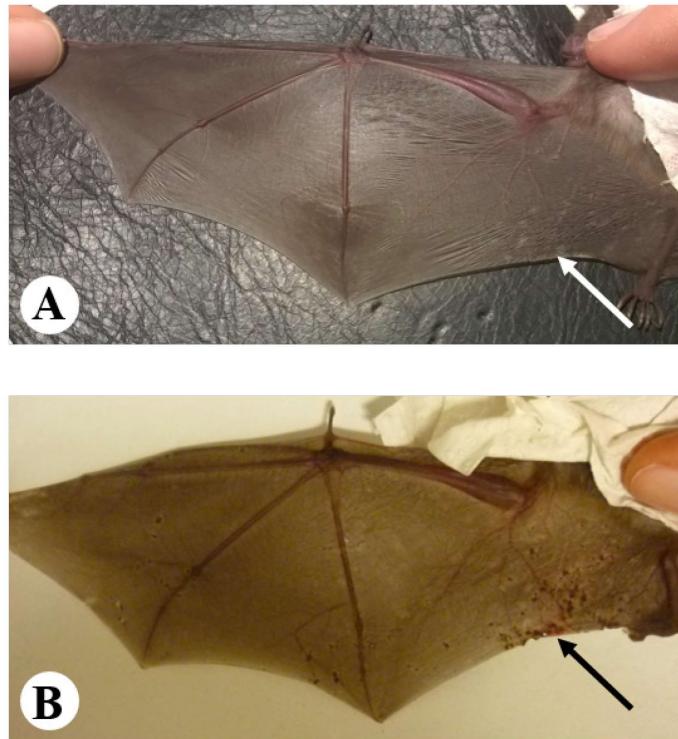


Figure S5: Wing images of a subordinate male from mixed group 4. The same individual was photographed before (**A**) and after the experiment (**B**). The black arrow points to the scarred location due to wing injuries, purportedly caused by the dominant male.

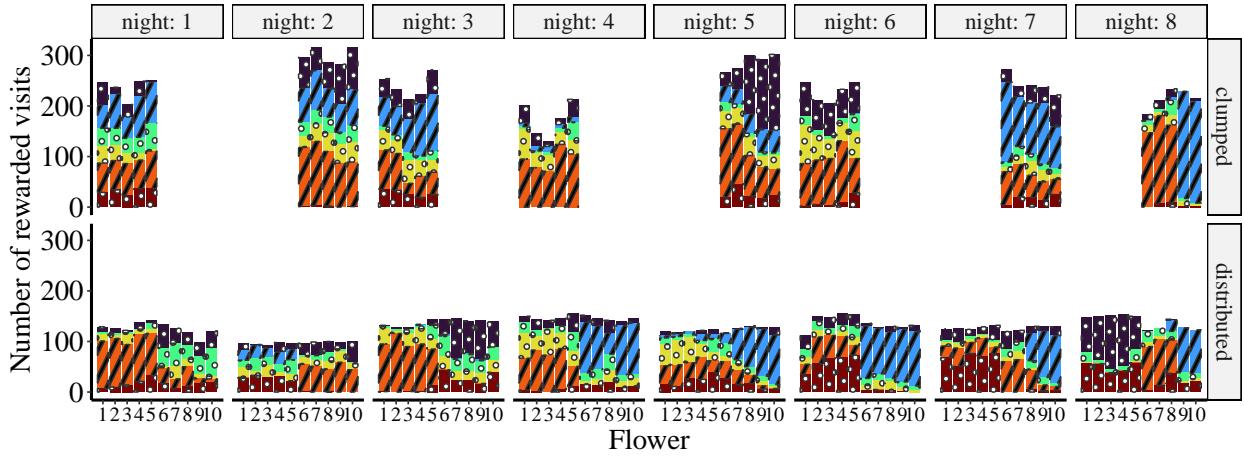


Figure S6: Distribution of rewarded visits across flowers for the six bats in the males-only group. The coloured bars give the number of rewarded visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns). The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

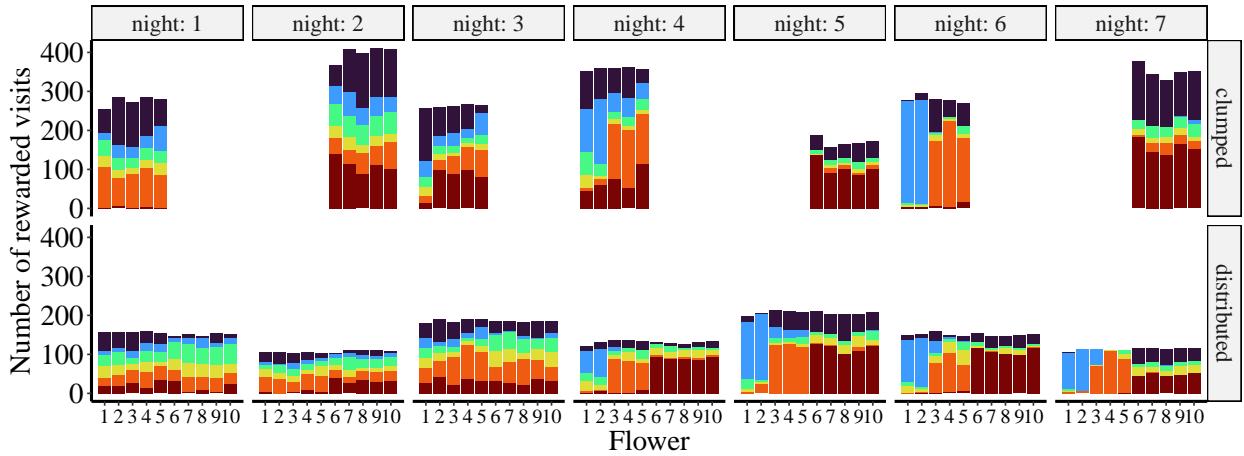


Figure S7: Distribution of rewarded visits across flowers for the six bats in the females-only group. The coloured bars give the number of rewarded visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns).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

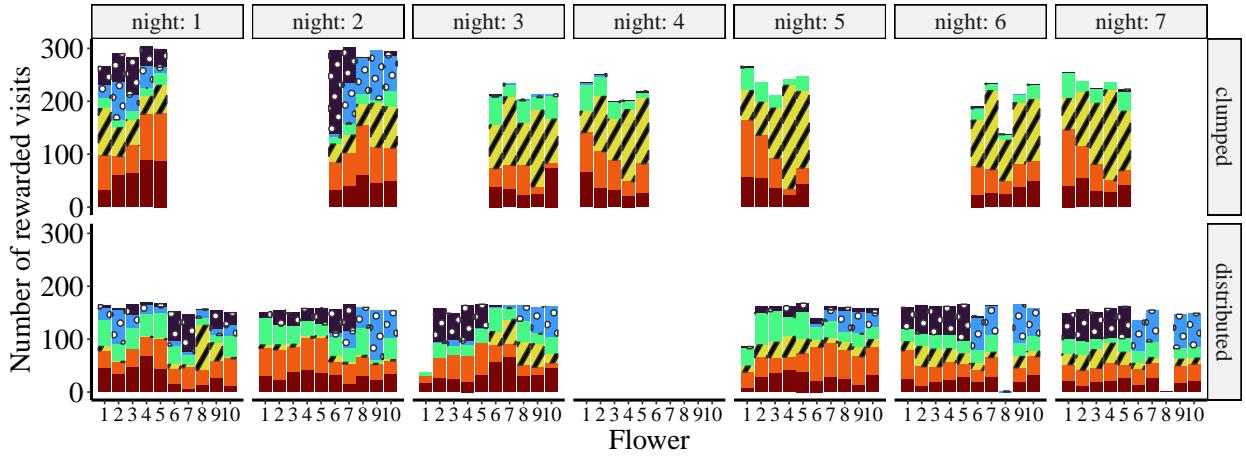


Figure S8: Distribution of rewarded visits across flowers for the six bats in mixed group 1. The coloured bars give the number of rewarded visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns). The dominant 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.

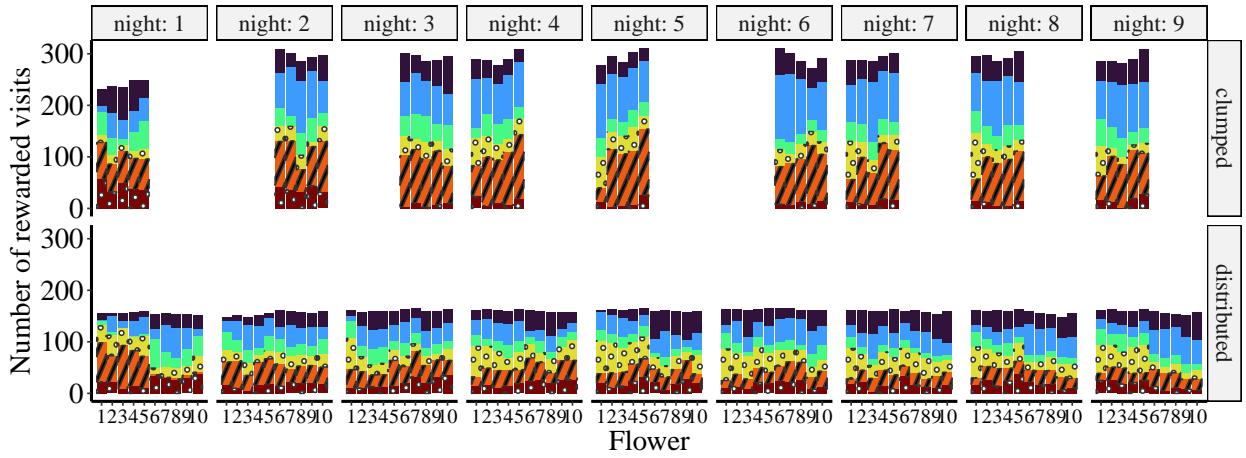


Figure S9: Distribution of rewarded visits across flowers for the six bats in mixed group 2. Same notation as in Fig. S8, but the colours correspond to different individuals.

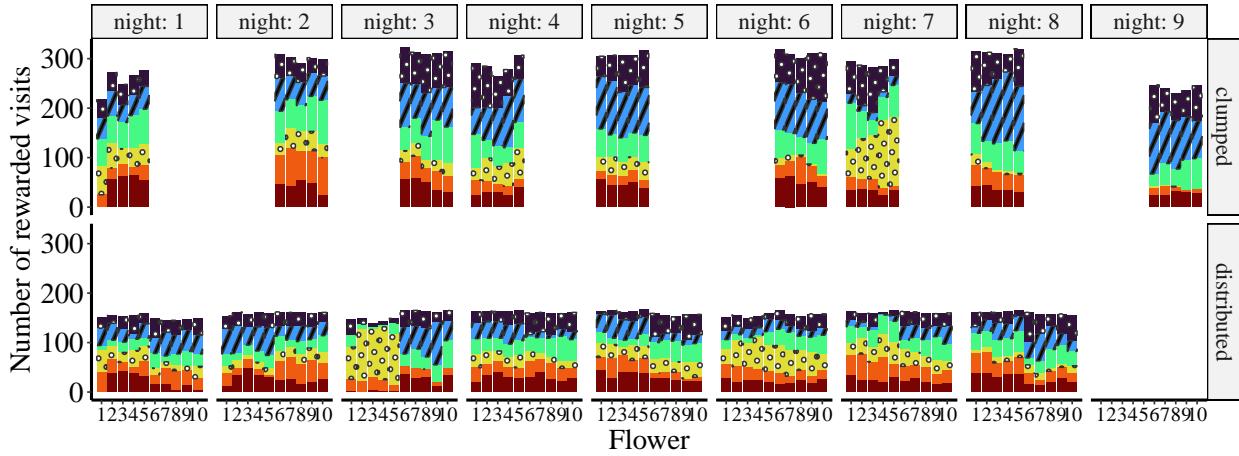


Figure S10: Distribution of rewarded visits across flowers for the six bats in mixed group 3. Same notation as in Fig. S8, but the colours correspond to different individuals. Due to a technical malfunction on night 9, there were no rewards delivered in the distributed resource condition and the data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

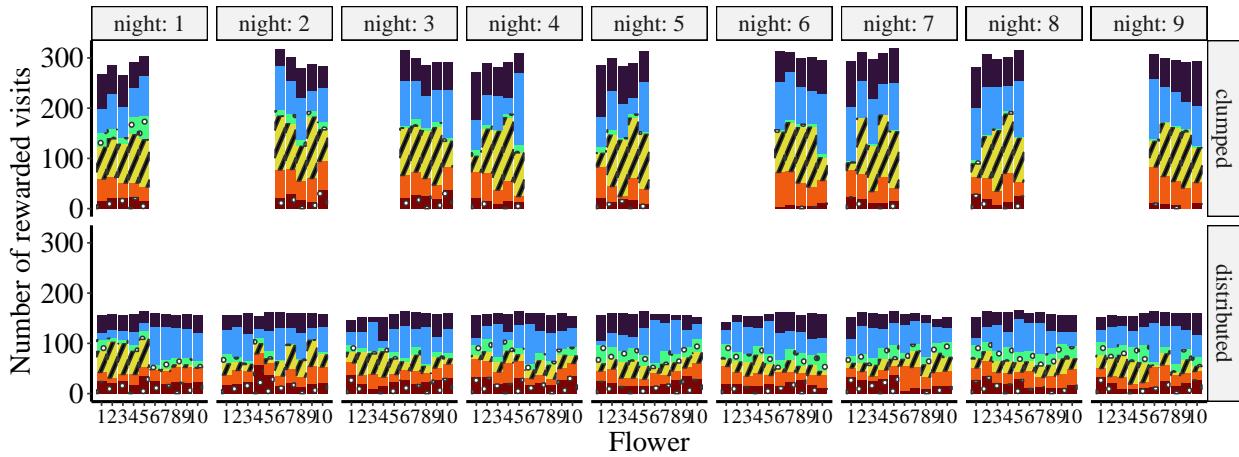


Figure S11: Distribution of rewarded visits across flowers for the six bats in mixed group 4. Same notation as in Fig. S8, but the colours correspond to different individuals.

403 Data accessibility

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

405 Authors' contributions

406 S.W. Conceptualization, Methodology, Software, Data collection, Formal Analysis, Video Analysis, Writing—
407 original draft. V.N. Conceptualization, Methodology, Software, Formal Analysis, Data curation, Writing—
408 review and editing, Visualization, Supervision, Project Administration.
409 Y.W. Conceptualization, Resources, Methodology, Software (data acquisition), Writing—review and editing,

⁴¹⁰ Supervision.

⁴¹¹ Competing interests

⁴¹² We declare we have no competing interests.

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