

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, *Glossophaga*

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 barrier 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.

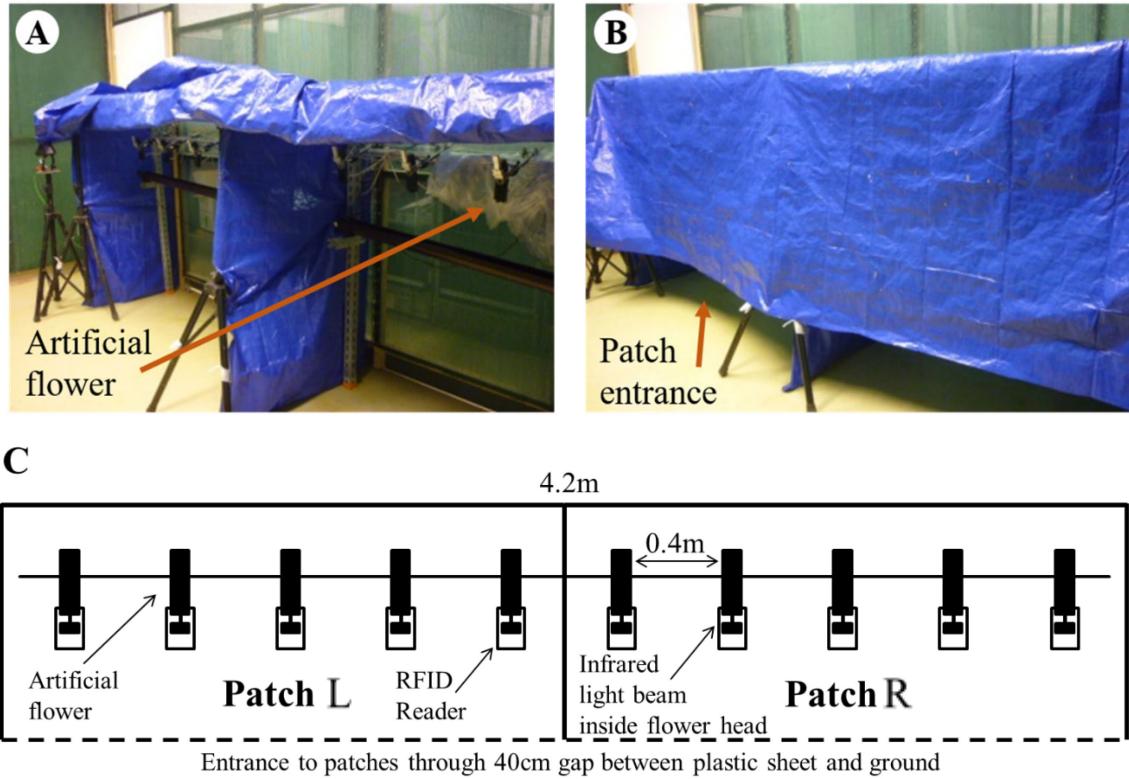


Figure 1: Experimental set-up consisting of two spatially separated flower patches. (A) The flowers were mounted 1.2m above ground. These ten flowers were divided into two patches (L and R) with five flowers each. (B) The patches were spatially separated by using a wooden frame covered with plastic sheet.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

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 training phase the plastic cover was removed, the two
 120 flower patches were not spatially separated and every flower visit was rewarded. This phase lasted for one to
 121 four nights until each bat visited the flowers regularly. One female of the first mixed group did not visit any
 122 artificial flower 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 was
 125 rewarding, and therefore the resources were spatially clumped. The fixed time interval between rewards was
 126 60s. During the second phase of the night both patches gave rewards, resources were evenly distributed across
 127 the patches, and the fixed time interval between two rewards at a flower was increased to 120s. Therefore, the
 128 amount of food available per unit time did not change during the whole night; only the spatial distribution of

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

138 (d) Chasing behaviour

139 We took the chasing frequency of individuals at the artificial flowers as an indicator of the intensity of
140 aggressive interactions between group members. We developed a method to automatically detect and score
141 chasing events using the computer-collected animal identification data from the RFID sensors and flower
142 sensors. In a previous pilot study (Wintergerst 2018), three mixed groups of bats were video recorded for 24h
143 over 14 nights, and the video data were synchronized to the computer-collected data. From the analysis of
144 the combined data we were able to identify the following pattern of visitation events that reliably indicated a
145 chasing event between two identified individuals: (i) an identified bat collected a reward at a flower, (ii) its
146 visit ended and (iii) was immediately followed by a very brief (<200ms) RFID detection of a second bat, the
147 chaser. Importantly, this second bat never attempted to drink and therefore did not insert its nose into
148 the artificial flower and interrupt the light barrier inside the flower head. This distinguished such a chase
149 from the occasional quick succession of two drinking visits by two bats at the same flower. The automated
150 detection of chasing events not only offers a considerable time profit for the experimenter, but also avoids the
151 human observer bias, a common drawback in video analysis. For the 24 hours of combined video data and
152 automatically logged data, all 89 chasing events detected in the computer-logged data were confirmed by
153 video. Therefore, we consider the algorithm for detecting chasing events in the logged data to be highly
154 reliable. Of course, chases did not only occur at the artificial flowers. Thus, our chase numbers are only
155 an indicator of chasing intensity between pairs of bats. For example, in one hour of video we observed 61
156 chasing events, but only five of those occurred during flower visits and were also automatically detected.
157 However, since with our algorithm (see below) we detected a total of 1811 chasing events (35.5 ± 12.3 events
158 per night during the main experiment and only 4.8 ± 3 during the training nights, mean \pm SD) for the
159 36 participating bats, we considered the automated approach adequate for quantifying the within-group
160 dominance relationships. The total number of individual detections per night constrains the number of
161 chasing opportunities. Therefore, we corrected our counts of chasing events by dividing the number of
162 observed chases by the total number of detections 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 labelled dominant
186 and subdominant males, respectively. Such a clear pattern was not observed in females. The identification of
187 dominant individuals was also supported by calculating the individual Glicko ratings from all chasing events
188 over the last two experimental nights in each group. Therefore, each mixed group contained individuals
189 belonging to one of three different types of social status: female, dominant male, and subdominant male. To
190 address the question whether nectar consumption varied depending on social status during the early and late
191 stages of the experiment we used Welch tests and adjusted the p values using the Holms method for multiple
192 comparisons.

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

195 3. Results

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

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

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

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

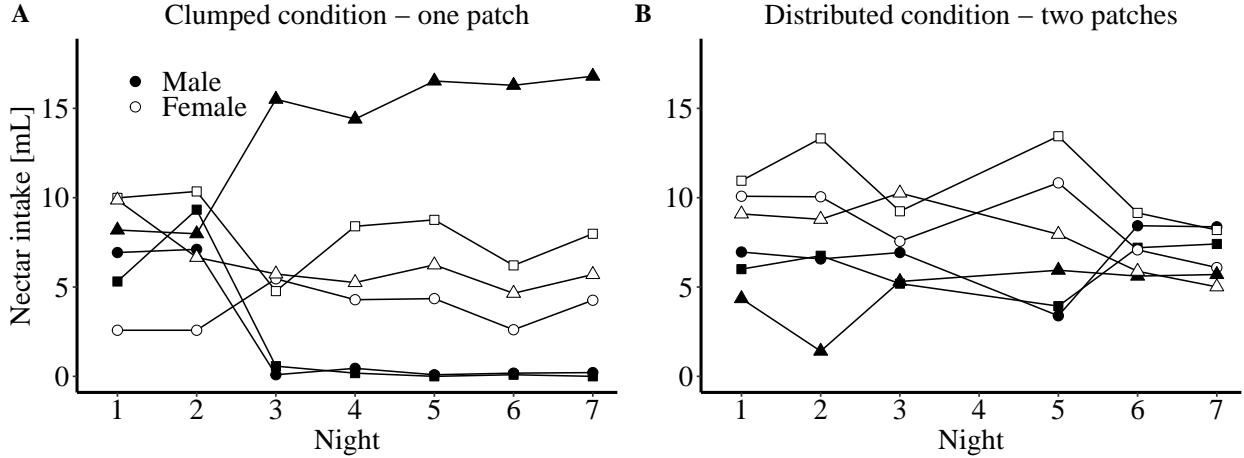


Figure 2: Exemplary change of individual daily nectar consumption during the experiment of one mixed experimental group consisting of three males and three females (symbols show different individuals). **(A)**. During the clumped resource condition (first part of the experimental night) rewards were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

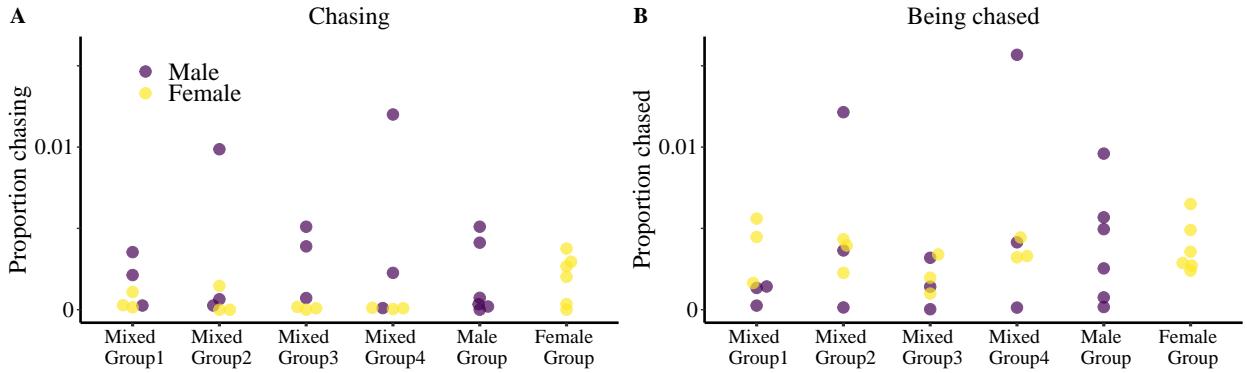


Figure 3: Sexes differed in the frequency of chasing other individuals. **(A)** Males (dark symbols) chased others significantly more than females did (light symbols, Table 1). Single sex groups for comparison. Shown are the individual proportions of chasing events over the whole experiment. Notably, 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 (dis- tributed)	-0.49	(-0.76, -0.23)	0.001
	weight	-0.01	(-1.34, 1.1)	0.962
	sex (fe- male):condition (dis- tributed)	-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 (dis- tributed)	-0.98	(-1.24, -0.74)	0.001
	weight	-0.40	(-1.26, 0.44)	0.326
	sex (fe- male):condition (dis- tributed)	-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

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

217 Resource defence should lead to a larger between-individual difference in nectar consumption. Differences in
 218 nectar consumption were quantified as the standard deviation of nectar intake in each group, separately for
 219 males and females. During the clumped resource condition, the standard deviation increased significantly for
 220 both sexes and males had higher standard deviations of nectar intake (Fig. A1, Table 2). However, during
 221 the distributed resource condition the standard deviation of mean nectar consumption was significantly lower
 222 (Fig. A1, Table 2), there was no difference between the sexes (estimate = 0.01, 95% CI = -0.07, 0.14) and
 223 there was no significant change over the course of the experiment (estimate = 0.02, 95% CI = -0.02, 0.07).

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	(0.19, 0.42)	0.002
sex (female)	-0.14	(-0.26, -0.04)	0.010
condition (distributed)	-0.12	(-0.21, -0.01)	0.022
night	0.05	(0.01, 0.09)	0.036
sex (female):condition (distributed)	0.15	(0.06, 0.23)	0.001
condition (distributed):night	-0.02	(-0.04, 0)	0.012
sex (female):night	-0.01	(-0.03, 0)	0.160

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

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

225 When plotting chasing events against nectar consumption the data for males fall into two non-overlapping
 226 groups. The males of one cluster (Fig. 4A, inside dashed oval) chased other individuals and consumed more
 227 nectar than the other males. This cluster included only one male from the mixed groups but two males from
 228 the males-only group. These males were categorized as “dominant.” The second cluster of males (Fig. 4A,
 229 outside and below dashed oval) was characterized by a low frequency of chasing and low nectar consumption.
 230 These males were categorized as “subdominant.” In females such a pattern did not emerge (Fig. 4B). This
 231 classification was also supported by the Glicko ratings in each group (Fig. A2) and the obersvation that
 232 there was generally an inverse relationship between the frequency of chasing and the frequency of being
 233 chased, especially in males (Fig. A3). While in the females-only group four females chased other females
 234 more frequently, only one of these females would be classified as dominant using the same cut-off criteria we
 235 used for the males (Fig. 4B), but it was not the female with the best Glicko rating (Fig. A2). During the
 236 first two nights of the experiment in the clumped resource condition, there was a difference in nectar intake
 237 between dominant and subdominant males and between subdominant males and females (Fig. 5). During
 238 the last two nights of the experiment in the clumped resource dondition, the three groups clearly differed,
 239 with the highest nectar intake in dominant males, an intermediate intake in females, and lowest nectar intake
 240 in subdominant males (Fig. 5). In contrast, in the distributed resource condition there were no differences
 241 between the nectar intake of dominant and subdominant males in any stage of the experiment (Fig. 5). The
 242 subdominant males had a significantly lower nectar intake than females in the first two, but not in the last
 243 two experimental nights (Fig. 5).

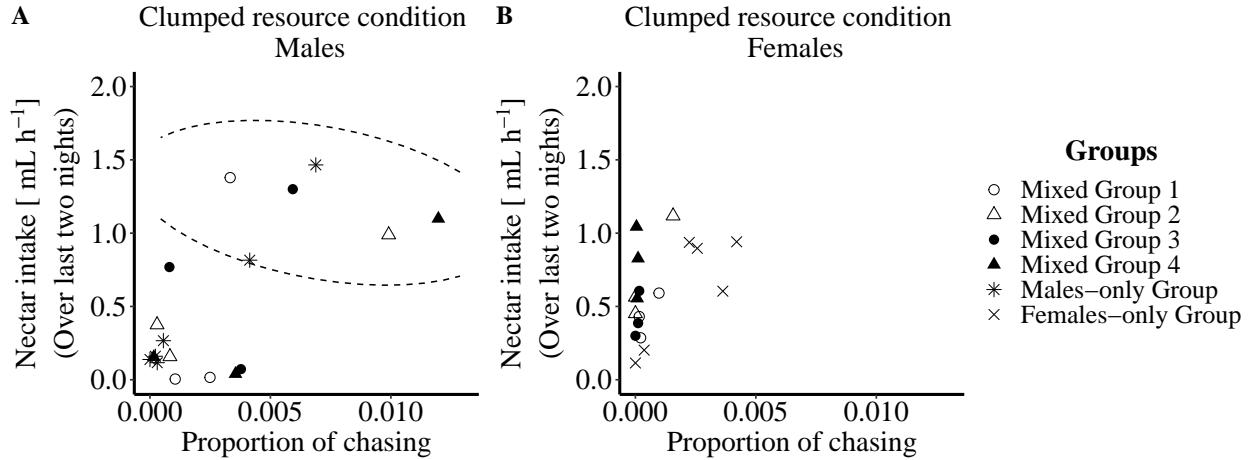


Figure 4: Influence of chasing frequency on nectar intake in the clumped resource condition during the last two nights of the experiment. (A) Males that more often chased other males also consumed more nectar. Males were divided into two non-overlapping groups by considering the chasing frequency and the amount of nectar an individual received during the clumped resource condition at the end of the experiment. Dominant males (inside dashed line oval) met two criteria: they chased other individuals at flowers more frequently (> 0.003) and received more nectar ($> 0.75 \text{ mL h}^{-1}$) during the clumped resource condition. Individuals outside the dashed line oval were categorized as 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.

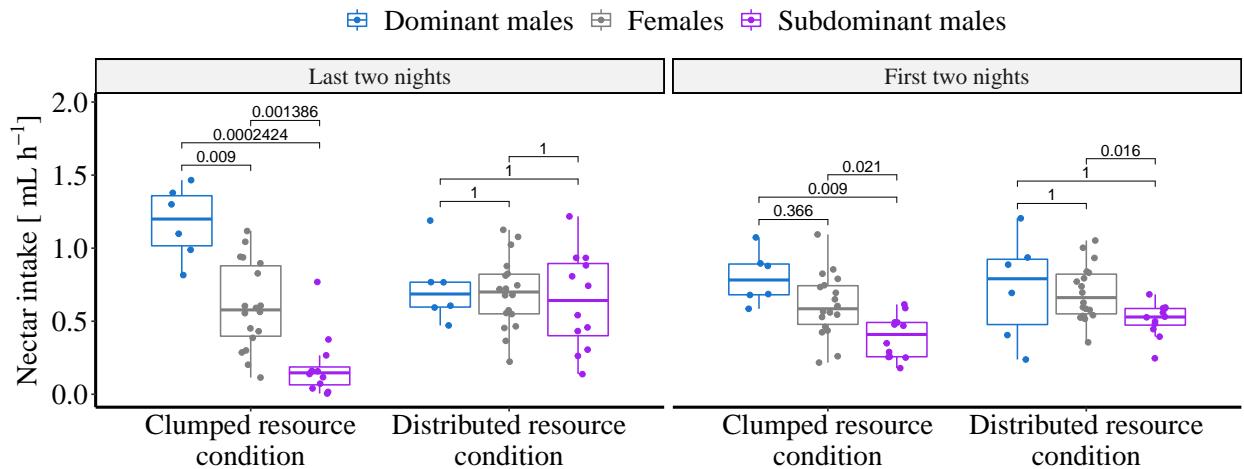


Figure 5: Comparison of nectar consumption during the first and last two nights of the experiment depending on sex and social status. During the clumped resource distribution (left panel), already at the beginning of the experiment subdominant males collected significantly less nectar than dominant males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

244 (e) Behavioural observations

245 Qualitative behavioural observations of four hours of video recordings revealed several behaviours that seem
246 to be characteristic for dominant males. Instead of just visiting the flowers and leaving the patch as the other
247 individuals did, dominant males remained hanging between the flowers within the patch for a significant
248 amount of time (Fig. A4). When other individuals came close due to visits of directly adjacent flowers,
249 dominant males often spread one wing in the direction of the other individual which could be interpreted as
250 a threatening posture. Some individuals were attacked and chased away by dominant males while visiting
251 artificial flowers. In this case, dominant males mostly attacked from above with their mouth wide open, and
252 followed the intruder for a short distance. Sometimes the chasing escalated into fighting with both bats
253 tumbling towards the ground and resuming their flight only shortly above the floor. In rare cases, these fights
254 might have led to small injuries. One subdominant male had several fresh scratches on its wing that were not
255 present before the experiment and that were possibly caused by teeth or claws (Fig. A5). After a successful
256 flower defence, the dominant male normally visited most of the five flowers within the patch before returning
257 to its position between the flowers.

258 4. Discussion

259 Similar to observations in free-living populations, in this experiment *Glossophaga soricina* competed for
260 nectar not only by exploitation but also by interference competition. However, the results show that the
261 predisposition to defend resources and the influence of interference competition on individual nectar intake
262 differed significantly between the sexes. Only a subset of males successfully defended flower patches. These
263 dominant males were characterized by the highest frequency of chasing other individuals away from profitable
264 flowers and by a substantial increase in nectar intake by the end of the experimental run. Although these
265 dominant males chased females and other males equally often, only the nectar intake of subdominant males but
266 not of the females was affected by this behaviour. Thus, male-initiated interference competition increased the
267 difference in nectar intake between males but did not affect females. The frequency of aggressive interactions
268 was higher and males only defended resources successfully when the available nectar was concentrated at
269 only one flower patch. This supports the hypothesis that clumped resources favour an increase in aggressive
270 interactions (Grant 1993).

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

273 To the best of our knowledge, this study is the first report of sex-dependent differences in the resource
274 defence behaviour of neotropical nectar-feeding bats. In mixed sex groups, females seemed to be unaffected
275 by the behaviour of dominant males whereas subdominant males were excluded at least partially from the
276 defended flower patch. This finding is consistent with observations of free-flying *G. commissarisi*, in which
277 males visited on average a smaller number of artificial flowers than females did (Nachev and Winter 2019),
278 presumably because of interactions with other males. There are two possible explanations for this differential
279 effect on subdominant males and females. On the one hand, dominant males might just not be capable of
280 excluding females. On the other hand, dominant males could tolerate females in their defended patch because
281 they might receive additional benefits, for example tolerating females could lead to an increase in (future)
282 mating opportunities. Similar social dynamics have been described in the insectivorous bat species *Myotis*
283 *daubentonii* (Senior, Butlin, and Altringham 2005). Dominant males of this species temporarily exclude
284 other males from profitable habitats whereas females are tolerated and in addition to securing access to
285 resources, the successful exclusion of other males has been shown to increase the reproductive success of
286 dominant males (Senior, Butlin, and Altringham 2005). Similarly, it has been observed that male *Eulampis*
287 *jugularis* hummingbirds, which successfully defend highly profitable feeding-territories against other males
288 while sharing the available resources with females, experienced an increase in their mating success (Temeles
289 and Kress 2010).

290 However, in our experiment dominant males chased females about as often as they chased subdominant males
291 (Table 1). If females were able to feed in the defended patch because dominant males tolerated them due
292 to potential additional benefits, it could be that the detected chasing events by dominant males differed

293 in quality depending on the sex of the intruder. This was not further quantified in the current study, but
294 could potentially be investigated using audio recordings (Knörnschild, Glöckner, and Helversen 2010). We
295 extracted the frequency of chasing events from data automatically recorded at artificial flowers (successive
296 detection of two different IDs while the first was feeding at the flower). Therefore, it was not possible to
297 determine if males showed behavioural differences when chasing other males in comparison to chasing females.
298 However, the recorded video revealed that individuals chased each other not only directly at the artificial
299 flowers but also in other areas of the flower patch. Since individuals could only be identified by their RFID
300 tag directly at the RFID reader attached to artificial flowers the sex of individuals chasing each other in
301 other areas of the experimental room remains unknown. However, some subdominant individuals showed
302 marks from small injuries at their wings after the experiment (see example in Fig. A5) and such marks were
303 only observed in males. This could be an indication that dominant males directed more aggression (biting)
304 towards subdominant males than towards females. Such sexual dimorphism in aggressive resource defence is
305 also known from other nectar-feeding vertebrates, like hummingbirds. It is thought that the beaks of the
306 males of some territorial species are specifically adapted as intrasexually selected weapons (Rico-Guevara et
307 al. 2019).

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

309 Generally, females showed lower chasing frequencies, but, surprisingly, some females in the females-only
310 group showed an increased nectar consumption and chasing frequency, compared to the females in the mixed
311 groups (Fig. 4B). Thus it appears that in the absence of male individuals, some females begin to exert
312 dominant behaviour over the other females. These findings are similar to the social structure of resource
313 defence found in some nectar-feeding bird species. For example, in free-living ruby-throated hummingbirds
314 females also have lower levels of defence (Rousseau, Charette, and Bélisle 2014). Moreover, although both
315 male and female *Eulampis jugularis* hummingbirds defend feeding territories during the non-breeding season,
316 males are always dominant over females (Wolf and Hainsworth 1971; Temeles, Goldman, and Kudla 2005). It
317 would be interesting to better understand why females are less affected by the aggressive resource defence
318 behaviour of dominant males compared to subdominant males and also why females themselves were not
319 able to consistently monopolize the profitable patch against other females. Of course, as the sample size of
320 single-sex groups was only one of each, these patterns need to be confirmed with more data. One possibility
321 is that females do not need to defend flowers when a dominant male is already reducing the number of flower
322 visitors and thus increasing the amount of food available.
323 In all mixed sex groups, only one male per group became dominant and successfully defended flowers, whereas
324 in the males-only group two males exhibited dominant behaviour (Fig. 4A). A closer look at the nectar
325 consumption at each flower revealed that on the last night of the experiment these two males had nearly
326 monopolized different flowers within the same patch rather than sharing access to the same flowers (Fig.
327 A6). Such flower partitioning was also observed in the females-only group (Fig. A7), but rarely seen in the
328 mixed groups (Figs. A8-A11). The successful resource defence by two individuals in the male-only group
329 showed that resource defence can occur independent of the presence of females, but was only based on a
330 single observation.

331 (c) Social status and social hierarchy

332 Although the position of the rewarding patch during the clumped resource condition changed between the
333 nights between the left and right, usually the same male continued to successfully defend the patch, especially
334 in the mixed-sex groups (Figs. A6-A11). This means that males defended the resources themselves and not a
335 particular location. Furthermore, this shows that even after changing the location of the defended patch
336 the same individuals were usually able to succeed in re-establishing their dominance against other males,
337 indicating a stable hierarchy at least for the duration of the experiment.
338 The ability of an individual to successfully defend and monopolize resources is often correlated with distinct
339 physical characteristics for example body size (Searcy 1979). However, our results show that weight as an
340 approximation of size did not correlate significantly with the chasing frequency of individuals (Table 1) and
341 therefore did not predict which male succeeded to defend a flower patch during this study. Another factor that
342 could influence the success in defending flowers is age and therefore experience (Arcese 1987; Yasukawa 1979).

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

363 (d) Conclusion

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

373 **Supplementary material**

374 **Video analysis**

375 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).
 376 Every time the algorithm marked an event as a chase event, there were two individuals following each other.
 377 Some chase sequences did not get detected. The individual that chased never drank immediately after the
 378 chase at the same flower location where the chase occurred. There were 16 incidences that were difficult to
 379 classify by observation or did not appear to be aggressive interactions.

380

381 $f \rightarrow f$ appear to be less aggressive

382 $f \rightarrow m$ appear aggressive

383 $m \rightarrow f$ appear aggressive

384 $m \rightarrow m$ appear aggressive

385

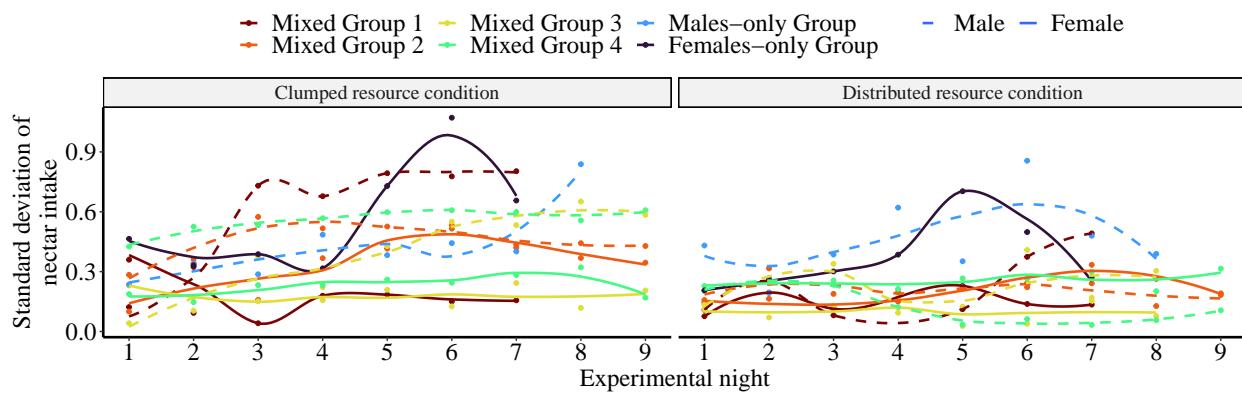


Figure A1: The standard deviation of group nectar consumption was used to measure the between individual differences in nectar intake. It was calculated for the clumped (left panel) and the distributed (right panel) resource conditions, separately for males (dashed lines) and females (continuous lines) 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).

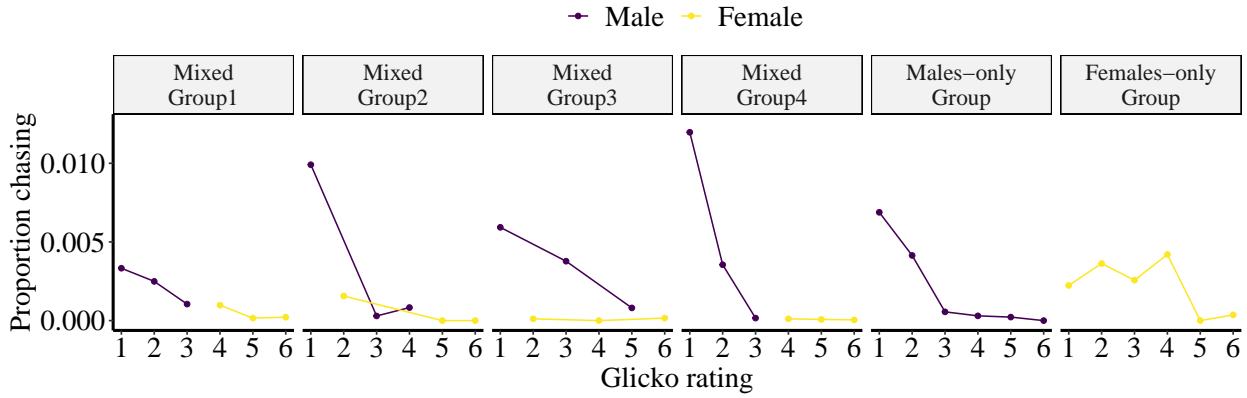


Figure A2: Over the last two experimental nights, the males (dark lines and symbols) with the highest proportion of chasing events were also the individuals with the Glicko rating of 1 in each group (panels) during the clumped resource condition. There was no such correspondence for females in the female-only group (right panel).

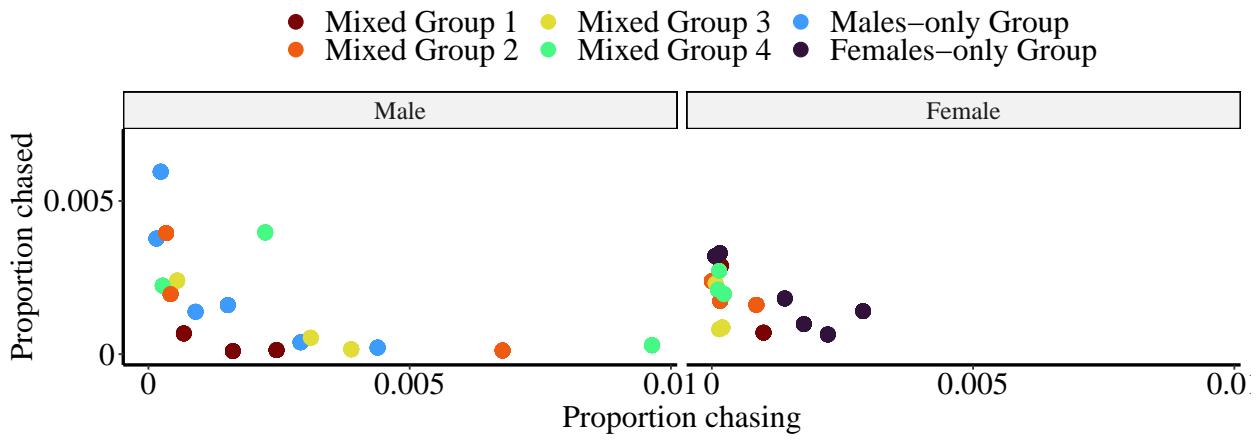


Figure A3: The relationship between proportion of chases versus the proportion of being chased out of all detections over the whole experiment for the female (left) and male (right) individuals in the six experimental groups (different colors).

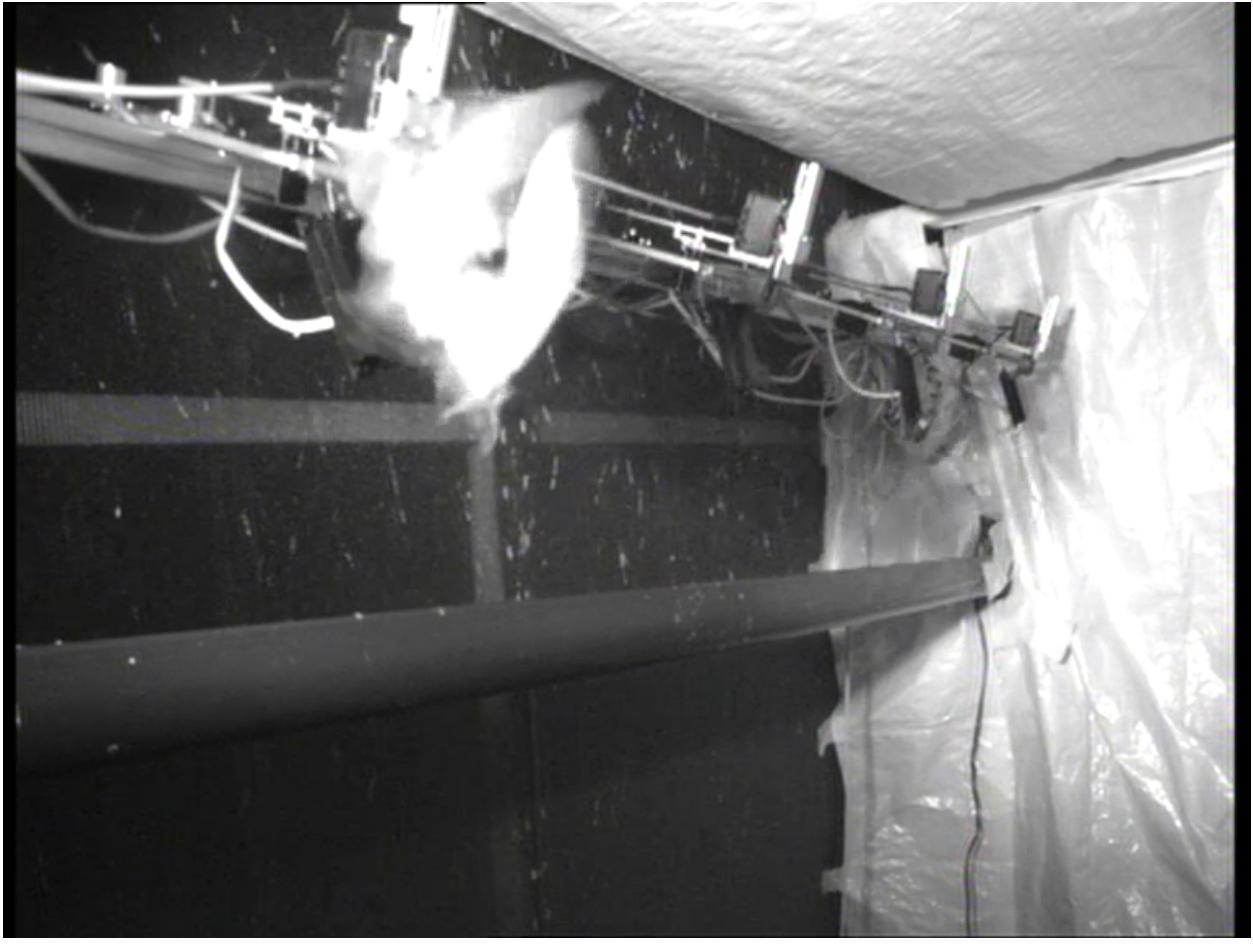


Figure A4: Video of the dominant male in mixed group 3 chasing all bats approaching the rewarding flowers in the rewarding patch during the clumped resource condition.



Figure A5: 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.

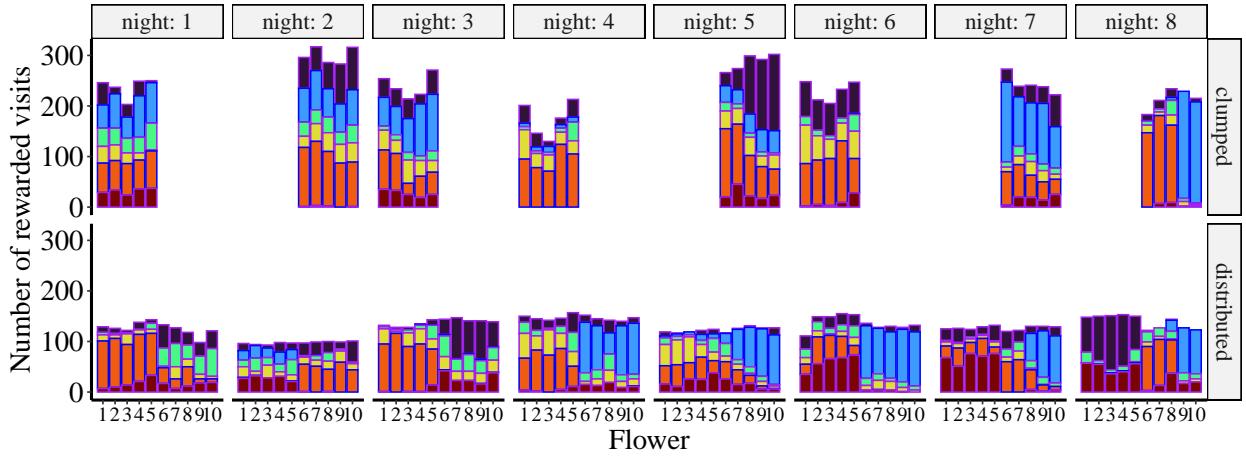


Figure A6: Distribution of visits across flowers for the six bats in the males-only group. The coloured bars give the number of visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns). The dominant males 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.

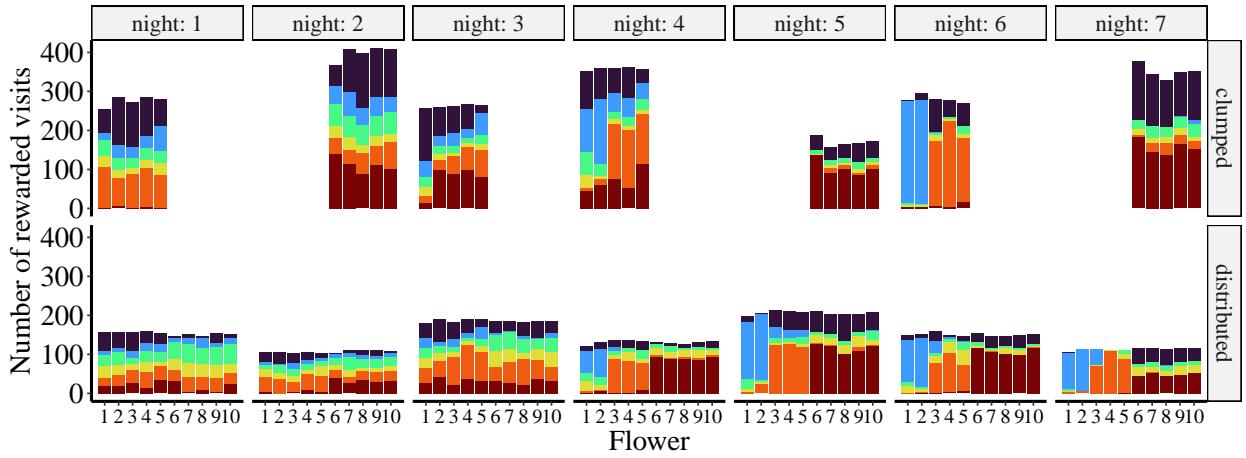


Figure A7: Distribution of visits across flowers for the six bats in the females-only group. The colored bars give the number of visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns). Females in this group 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.

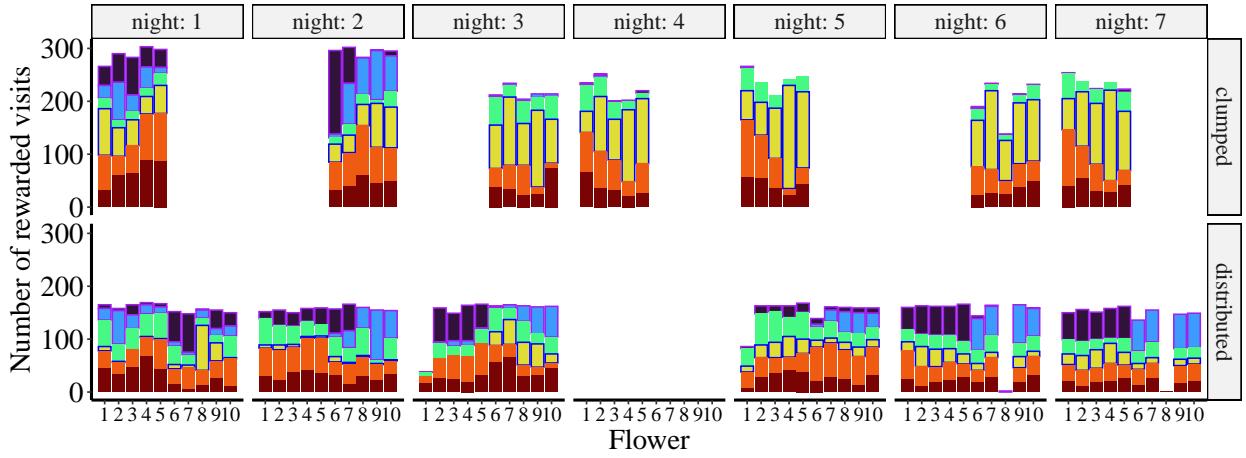


Figure A8: Distribution of visits across flowers for the six bats in mixed group 2. The colored bars give the number of visits of each individual at the ten flowers during the clumped (top) and distributed (bottom) resource conditions for each experimental night (columns). The dominant male is shown 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.

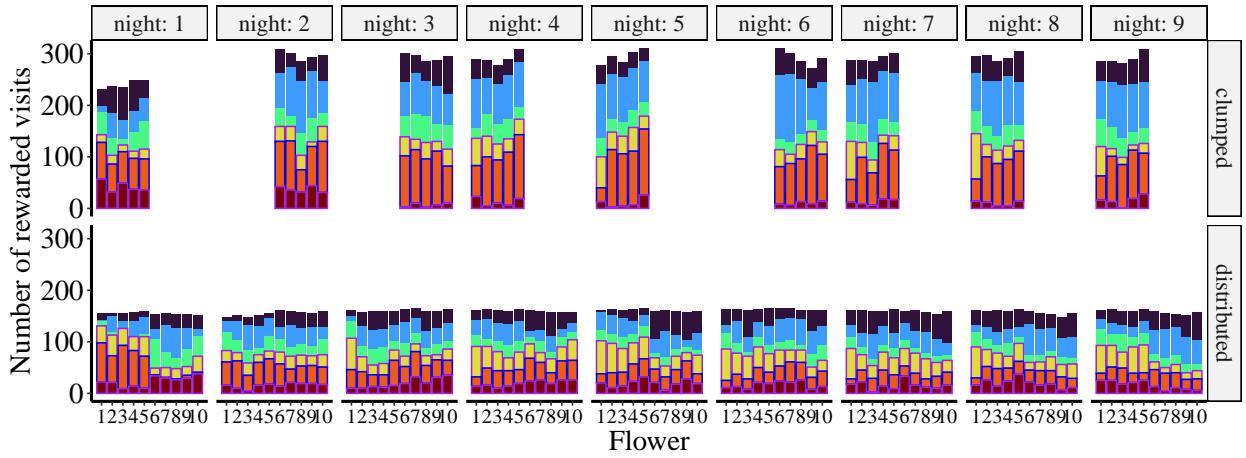


Figure A9: Distribution of visits across flowers for the six bats in mixed group 2. Same notation as in Fig. A8, but the colors correspond to different individuals.

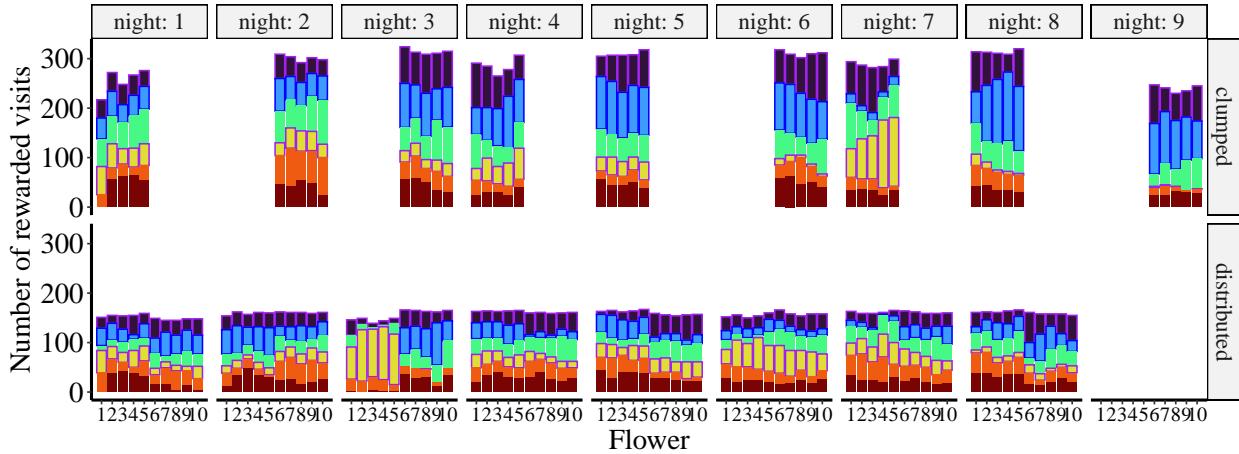


Figure A10: Distribution of visits across flowers for the six bats in mixed group 3. Same notation as in Fig. A8, but the colors correspond to different individuals. Due to a technical malfunction on night 9, there were no rewards delivered in the distributed resource condition and the data were excluded from analysis.

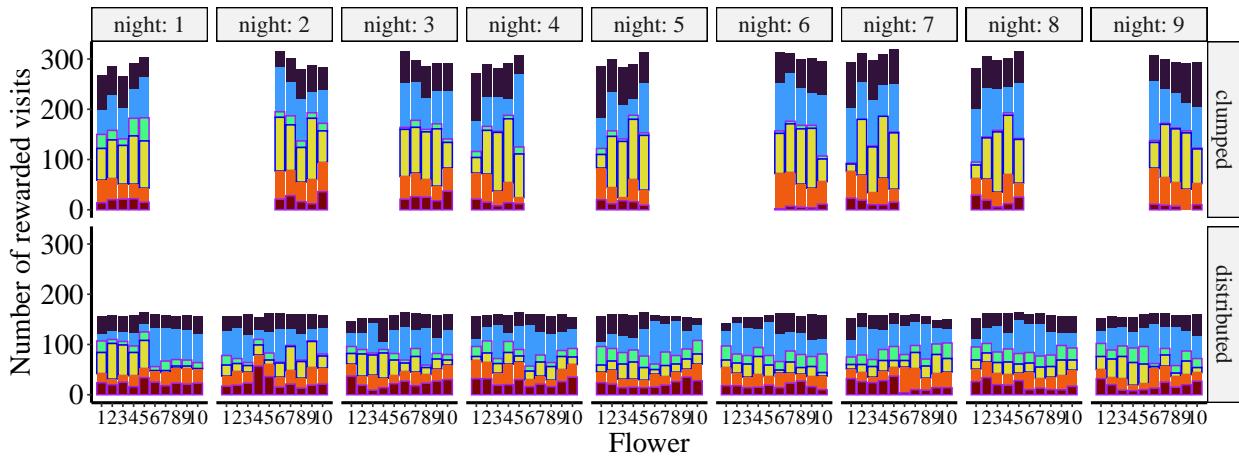


Figure A11: Distribution of visits across flowers for the six bats in mixed group 4. Same notation as in Fig. A8, but the colors correspond to different individuals.

386 Data accessibility

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

388 Authors' contributions

389 S.W. Conceptualization, Methodology, Software, Data collection, Formal Analysis, Video Analysis, Writing—
 390 original draft. V.N. Conceptualization, Methodology, Software, Formal Analysis, Data curation, Writing—
 391 review and editing, Visualization, Supervision, Project Administration.
 392 Y.W. Conceptualization, Resources, Methodology, Software (data acquisition), Writing—review and editing,
 393 Supervision.

394 **Competing interests**

395 We declare we have no competing interests.

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