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Comments/Reflections

Place your bets: small prey faces large predators

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Abstract
Interspecific aggression is common between species that live together. We describe such behaviour in a mixed-species bat roost. A single small-bodied (approx. 15 g) frugivorous bat, *Carollia perspicillata*, aggressively antagonized a group of much larger (approx. 34 g) bats, *Trachops cirrhosus*, in defence of a roosting site, resulting in the larger *T. cirrhosus* relinquishing the site. This interaction was striking as *T. cirrhosus* are known to consume *C. perspicillata*. The small 'prey' individual caused the group of larger 'predators' to leave the roosting area by intensely vocalizing, rapidly flapping its wings, hitting the faces of the other bats with its wings, and flinging its body at the other bats. To our knowledge, this type of interspecies agonistic behaviour has never been observed before in bats and highlights the importance of intensively studying behavioural interactions in nature.

Keywords
antagonism, roosting dynamics, Chiroptera, interspecific interaction, predation.

1. Introduction

Interspecific aggression is common and is found across taxonomic groups (Peiman & Robinson, 2010). Agonistic interspecific interactions can occur as an antipredator response or when individuals from different species compete for the same resource (Grether et al., 2013). Such encounters often involve

ritualized displays that allow opponents a brief mutual assessment, which is often sufficient to anticipate the outcome of a physical interaction, allowing opponents to avoid physical confrontation (Grether et al., 2013).

As some of the most social mammals on the planet, bats are an excellent model to study intra- and interspecific interactions. Bats are gregarious and can congregate in groups of hundreds of thousands, exhibiting a wide variety of social interactions (Kunz & Lumsden, 2003). Moreover, roosts may house several different bat species often with roost competition, especially when roosts are limited. In many forest ecosystems, the most permanent and stable roosts are scarce, and species may compete for the same refuge (Kunz & Lumsden, 2003).

Seba's short-tailed bat, *Carollia perspicillata* (a small-bodied (approx. 15 g) frugivorous bat), and the fringe-lipped bat, *Trachops cirrhosus* (a large (approx. 34 g) animalivorous bat), are known to share roosts (e.g., Ibañez, 1981; Arias et al., 1999; Kalko et al., 1999; Jones et al., 2017; Medina-Fitoria et al., 2020), and tolerate one another in close proximity (unpublished data; Gamboa Bat Lab, www.noseleaf.org). This is surprising given that *T. cirrhosus* is known to feed on smaller bats (e.g., *Artibeus jamaicensis*, *Furipterus horrens*, *Glossophaga soricina*, *Micronycteris microtis*, *Myotis nigricans*), including *C. perspicillata* (Arias et al., 1999; Bonato & Facure, 2000; Bonato et al., 2004; Rodrigues et al., 2004; Jones et al., 2020; reviewed in Leal et al., 2018).

While video recording roosts in the rainforest understory in Panama, we observed *C. perspicillata* (most often one to two but occasionally up to seven) sharing a roost with a group of four adult and two juvenile *T. cirrhosus*. Most of our recordings show no interaction between heterospecifics, with species in opposite corners of the roost. Occasionally, however, we observed an individual *C. perspicillata* intensely vocalizing towards the group of *T. cirrhosus*. On a few occasions, the agonistic behaviour escalated, one of the longest incidences of which we describe below.

Here, we report for the first-time interference competition between a small-bodied frugivorous bat and a group of large-bodied animalivorous bats. We describe the behaviour of a male *C. perspicillata* confronting a group of *T. cirrhosus* over a contested resource: a specific corner of a shared roost. The escalating agonistic behaviour consisted of four components: (1) intense vocalizations, (2) wing shaking, (3) hitting the individuals' faces with the wing, and (4) flinging its body on the group.

2. Methods

Recordings started in June 2020 and lasted a year (approximately 292 hours and 37 min of roost video recordings). We observed the interaction while video recording roosts (0.8 × 0.8 × 2 m high rectangular concrete structures) we had erected in the forest adjacent to Soberanía National Park (9°07′N, 79°65′W), near the town of Gamboa, Panama. Following the standard recording procedure, a video camera (Sony HD HDRCX560) with two 60 LED infrared lights was left recording from 09:42 h to 17:53 h on June 19 2020 in the monitored roost.

3. Results

On 19 June at 09:55 h we observed a 6.5 min agonistic interaction between a *C. perspicillata* and a group of *T. cirrhosus*. One of the two *C. perspicillata* (presumably the male based on previous captures and a visible penis in the video recordings) started vocalizing (Figure 1A) towards a group of four adult (three females and one male) and two juvenile (one female and one male) *T. cirrhosus*, while the other *C. perspicillata* individual remained motionless throughout the interaction. The male *C. perspicillata* continued to vocalize, then flapped and rapidly shook his wings (Figure 1B). He next hit the *T. cirrhosus* individuals with one of his wings (Figure 1C). During the first 3 min of repeatedly vocalizing, wing shaking, and hitting, the male *T. cirrhosus* (identifiable by his prominent chest gland) displayed defensive behaviours that included vocalizing (Figure 2A), displaying wings (Figure 2B), biting attempts (Figure 2C) and actual biting (Figure 2D). Immediately after the male *T. cirrhosus* bit the *C. perspicillata*'s wing (Figure 2D; at 3:23 in the supplementary video at 10.6084/m9.figshare.19139717), the male *C. perspicillata* threw himself on the group of *T. cirrhosus* (Figure 1D), flapping his wings repeatedly over the group. The *T. cirrhosus* individuals remained together in their corner. The male *C. perspicillata* returned to his original position (at 3:26 in the supplementary video at 10.6084/m9.figshare.19139717) in front of the *T. cirrhosus* group and continued vocalizing, shaking wings, and hitting mostly the face of the male *T. cirrhosus* who finally flew away (at 4:20 in the supplementary video at 10.6084/m9.figshare.19139717) from the contested corner, almost one minute after the male *C. perspicillata* threw himself on the group. Vocalizations continued throughout the interaction.

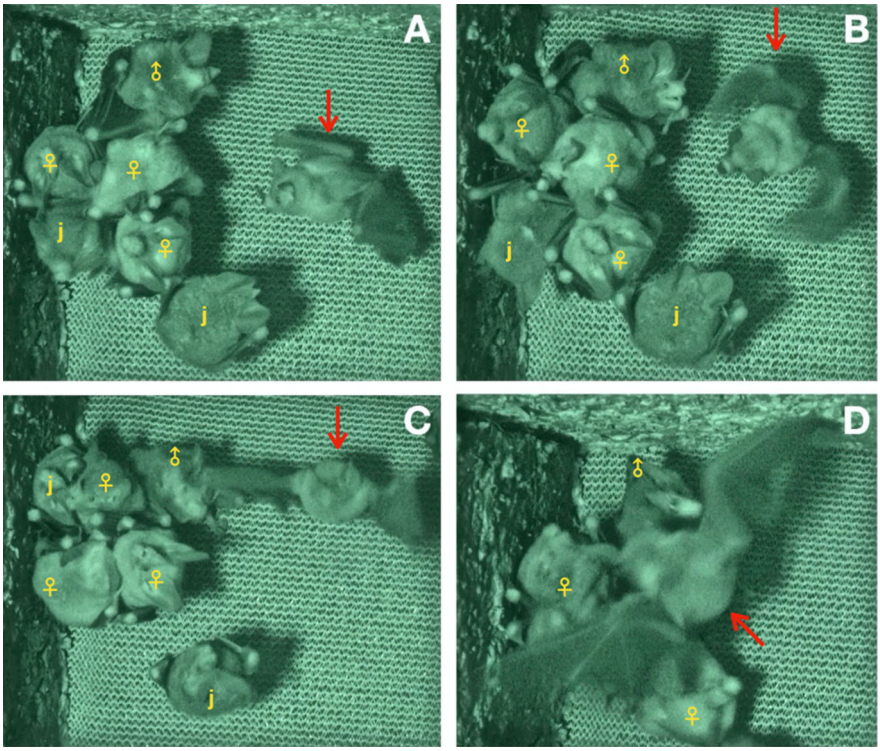

Figure 1. Male *C. perspicillata* (red arrow) vocalizing towards a group of four adult (♂ and ♀♀) and two juvenile (j) *T. cirrhosus* (A), flapping and shaking his wings (B), hitting the adult male *T. cirrhosus* with the wing (C), and throwing himself on the group of *T. cirrhosus* (D).

After the male *T. cirrhosus* left, the remaining *T. cirrhosus* continued to be antagonized by the male *C. perspicillata* through vocalizations, wing shaking displays and hitting, until they also left (4:40–5:29 in the supplementary video at 10.6084/m9.figshare.19139717), except for a single *T. cirrhosus* female that held her position in the corner. The male *C. perspicillata* vocalized and shook his wings towards the isolated female (Figure 3A). She initially remained motionless (5:29–5:48 in the supplementary video at 10.6084/m9.figshare.19139717); then attempted to bite the male *C. perspicillata* (Figure 3B; at 5:49 in the supplementary video at 10.6084/m9.figshare.19139717), approaching him with her mouth opened (Figure 3C; at 6:18 in the supplementary video at 10.6084/m9.figshare.19139717t). The female *T. cirrhosus* kept her mouth opened, and finally faced the male *C. perspicillata*, making chest to chest contact (at 6:18 in the supplementary video at 10.6084/

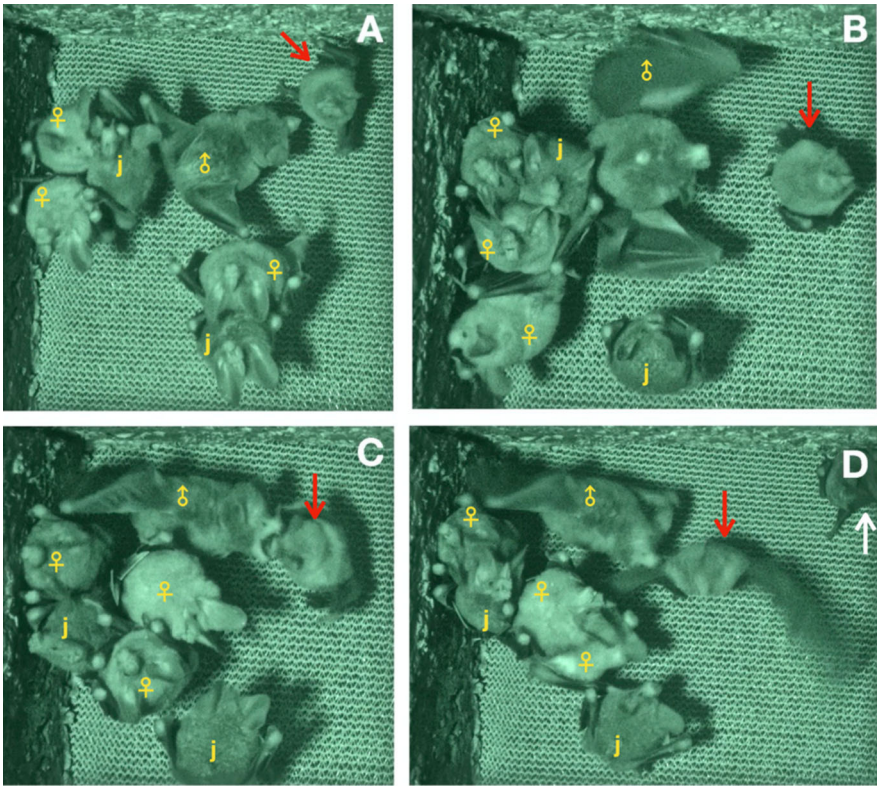

Figure 2. Male *T. cirrhosus* defensive behaviour included vocalizing (A), displaying open wings (B), biting attempts (C), and actual biting (D). Aggressive *C. perspicillata* (red arrow); motionless *C. perspicillata* (white arrow); adult (♂ and ♀♀) and juvenile (j) *T. cirrhosus*.

m9.figshare.19139717). The female *T. cirrhosus* made bite attempts (Figure 3D), followed by both individuals aggressively hitting each other with both wings (Figure 3E; at 6:20 in the supplementary video at 10.6084/m9.figshare.19139717). The *C. perspicillata* flew away (at 6:21 in the supplementary video at 10.6084/m9.figshare.19139717), and immediately returned and continued vocalizing towards the female *T. cirrhosus*, who flew away a few seconds later, relinquishing the corner (at 6:25 in the supplementary video at 10.6084/m9.figshare.19139717; 10:12 h). The *C. perspicillata* settled in the contested corner and began grooming himself (at 6:49 in the supplementary video at 10.6084/m9.figshare.19139717). The other *C. perspicillata* then joined him (at 7:49 in the supplementary video at 10.6084/m9.figshare.19139717).

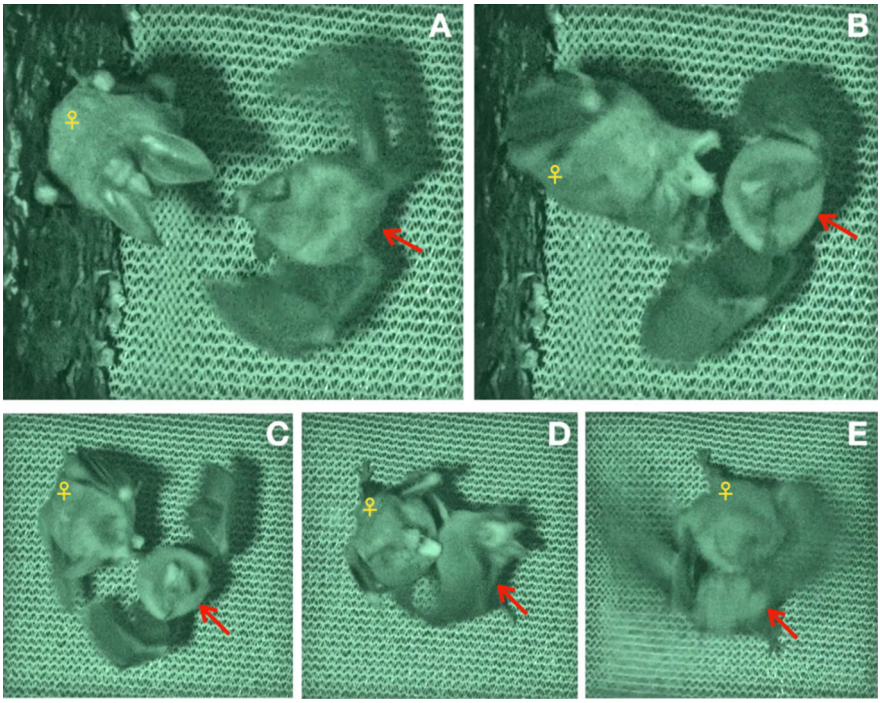

Figure 3. *C. perspicillata* (red arrow) vocalizing and shaking its wings towards a female *T. cirrhosus* (A) who made bite attempts (B) and faced the *C. perspicillata* with mouth opened (C). The two bats then physically contacted each other chest to chest (D) and hit each other with both wings (E).

While this was one of the longest, most intense interactions observed (and the only one in this roost), we video recorded two other similar antagonistic interactions between *C. perspicillata* and *T. cirrhosus* in other monitored roosts (7 and 23 December 2020).

4. Discussion

To our knowledge, this is the first report of a smaller frugivorous bat repeatedly antagonizing a group of larger predatory bats in the roost. Agonistic behaviour among roostmates may be more widespread than previously thought and may play a critical role in heterospecific roosting dynamics. This behaviour occurred infrequently, underlying the fundamental importance of intensive long-term observations of animal behaviour in nature. Infrequent/rare behaviours are likely to be missed with short-term studies

that often capture only brief snapshots of animals' social lives. Studying social interactions in the wild also confirms that the observed behaviours are indeed natural behaviours rather than artefacts of captivity.

Our observations beg the question, why would a small individual exhibit energetically costly, potentially risky behaviour to confront a group of potential predators? We identify three possible (non-mutually exclusive) hypotheses. First, the observed heterospecific aggressive interaction may be a byproduct of male-male intraspecific aggression (Grether et al., 2013) in defence of females or territory, common behaviours in bats (e.g., Markus, 2002; Ortega & Arita, 2000). Indeed, male *C. perspicillata* have been found to engage in frequent aggressive encounters with conspecifics, either between neighbouring territory holders or between sneaker males and the harem owner (Fernandez et al., 2014). The complex ritualized intraspecific agonistic interactions observed by Fernandez et al. (2014) share several similarities with our observations. In both, levels of aggression increased following what appears to be a defined succession of behavioural stages. It is possible that *C. perspicillata* evolved this stereotyped aggressive behaviour in the context of defending access to females from conspecific males, but with *T. cirrhosus* roosting in close physical proximity, this antagonism spilled into a heterospecific context.

A second hypothesis is that due to distinct microclimatic conditions, the contested corner may be advantageous to roosting bats. It may be less draughty, darker, or otherwise more protected from the elements or from potential predators. In our study, in addition to the three empty corners in the disputed roost structure, three additional roosts of identical dimensions were available in the nearby forest (i.e., about 50 m). When a resource is common, evenly distributed, or of low value, it is unlikely to induce agonistic interactions (Grether et al., 2013). Thus, it is possible that this specific roosting corner had microclimatic conditions promoting competition.

Third, because *T. cirrhosus* is known to prey on *C. perspicillata* (Rodrigues et al., 2004; Jones et al., 2020), and because the two species commonly share roosts (Ibañez, 1981; Arias et al., 1999; Kalko et al., 1999; Jones et al., 2017; Medina-Fitoria et al., 2020), it is possible that the agonistic behaviour displayed by *C. perspicillata* serves as a preemptive strike (e.g., Simunovic et al., 2013). *C. perspicillata* may be using aggressive interactions to communicate to *T. cirrhosus* that it is a formidable opponent and that attack would be costly. DNA metabarcoding analyses found evidence for *C. perspicillata*

in *T. cirrhosus* feces (Jones et al., 2020), and field observations identified the culled remains of *C. perspicillata* below a group of roosting *T. cirrhosus* (Rodrigues et al., 2004), but to date it is unclear whether the individuals consumed were juveniles or adults. *T. cirrhosus* has been observed feeding on the pup of another frugivorous bat species (*Artibeus jamaicensis*) when these species shared a roost (Arias et al., 1999). However, to date no one has observed *T. cirrhosus* preying on adult or juvenile *C. perspicillata* in shared roosts, even though the species commonly roost together. These observations indicate that more research is required to better understand the context of *T. cirrhosus* predation on *C. perspicillata*, which would help disentangle the three hypotheses proposed here.

Agonistic behaviours are widespread, occurring across animal taxa (Peiman & Robinson, 2010; Grether et al., 2013). Our report of an unexpected agonistic interaction among heterospecific roostmates highlights the importance of intensive long-term behavioural studies in the natural environment and sheds light on several fascinating topics for further research: (1) variation in microclimatic conditions of roosts, (2) interspecific tolerance, (3) costs and benefits of heterospecific roost sharing, (4) facultative prey items, and (5) the possibility of species-specific behavioural traits.

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Supplementary video. Interaction between *Carollia perspicillata* and *Trachops cirrhosus* in the roost. This video can be seen at 10.6084/m9.figshare.19139717.