



## When bats are boxing: aggressive behaviour and communication in male Seba's short-tailed fruit bat



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Aggressive behaviours have an important impact on the social organization of animals and on the social status of individuals, especially in gregarious species. Agonistic interactions between territory holders are essential to set and reinforce territorial borders. Additionally, agonistic displays are used to demonstrate ownership of a territorial site and may indicate social status of the signaller. Between neighbouring territory owners, dynamic borders require frequent interactions. In daily repeated aggressive encounters, ritualization can help to avoid the need for serious fights and their costly consequences. In the bat *Carollia perspicillata*, a gregarious frugivore with resource defence polygyny, males defend territories at valuable roosting sites for females. Working with a captive bat colony of about 400 individuals, housed under seminatural conditions in a tropical zoo, we found that males defended territories aggressively by the use of a succession of displays forming a ritualized structure. Simultaneously, males used three different vocalization types during aggressive displays, namely down-sweeps, warbles and aggressive trills. A statistical analysis of 58 aggressive trills from five adult males showed that they contained sufficient variation to encode an individual signature. Using a habituation–dishabituation paradigm playback experiment, we found that males could discriminate between vocalizing males based on aggressive calls alone. Such discrimination is probably useful for distinguishing between neighbouring territory owners and more unfamiliar intruders, and thus allows for an economical response.

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Individuals attempting to gain ownership over the same finite resource may meet as contestants in an aggressive encounter (Bradbury & Vehrencamp, 2011; Hardy & Briffa, 2013). Animal contests can range from gentle agonistic displays of butterflies to deadly encounters among ants. They can be costly, require energy and entail risk of injury or even death (Clutton-Brock, Albon, Gibson, & Guinness, 1979; Mercier, Lenoir, & Dejean, 1997; Neat, Taylor, & Huntingford, 1998; Piper, Walcott, Mager, & Spilker, 2008). Thus, contestants usually have an interest in resolving conflicts before escalating to costly physical fights (Bradbury & Vehrencamp, 2011). Game theory approaches seek to explain how and why intraspecific contests are resolved (Smith & Price, 1973). The motivation to fight (hawk or dove) is a key factor in these theoretical models, but can be adjusted to avoid serious injuries with the so-called 'limited war type', in which individuals in a

conflict use inefficient weapons or ritualized tactics (Smith & Price, 1973). Ritualized encounters are composed of successive stages, each offering information about the contestants' motivation or resource-holding potential (i.e. showing fighting ability, sensu Bradbury & Vehrencamp, 2011). A continuous update during an interaction allows each contestant to decide at each successive stage whether to retreat or to engage further in the conflict. The resolution of a conflict at an earlier stage can be facilitated when both contestants use signals to provide information about their willingness to engage further in the conflict (Burmeister, Ophir, Ryan, & Wilczynski, 2002; Hofman & Schildberger, 2001; Logue et al., 2010), or reveal asymmetries between contestants (Davies & Halliday, 1978; Ladich, 1998; Mager, Walcott, & Piper, 2007). In the presence of a third party, the bystander can be influenced by the outcome of the conflict and adjust its own strategy: the winner and loser effect (Earley & Dugatkin, 2002; Hsu & Wolf, 1999). As the third party may be less willing to engage in a conflict with the winner, the latter has an interest in communicating its victory (Field & Rind, 1992; Grafe & Bitz, 2004). Such behaviours can be performed visually, but are mostly acoustically displayed to reach potential rivals further away (Bower, 2005).

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Bats are successful in their nocturnal environment because they are capable of using echolocation calls for orientation. Undoubtedly, echolocation calls serve bats to orient themselves in their environment and for foraging (Balcombe & Fenton, 1988; Barclay, 1982). But echolocation calls are not only limited to these functions. Several studies have demonstrated that sonar calls have a communicative function as well and can facilitate behavioural interactions (Fenton, 2003; Knörnschild, Jung, Nagy, Metz, & Kalko, 2012; Voigt-Heucke, Taborsky, & Dechmann, 2010). Aside from echolocation calls, bats possess a repertoire of social signals for purely communicative reasons.

The social function of communication signals in general is defined as transformation of information about the current motivational state of an individual or a certain social situation, directed to the receivers (Simmons, 2003). Acoustic signals produced during social interactions can influence the behaviour of both the signaller and the receiver, and also of individuals not directly involved (e.g. Otter et al., 1999). Social vocalizations can encode vocal or acoustic characteristics allowing for discrimination between frequently interacting individuals (McComb, Moss, Sayialel, & Baker, 2000; Rendall, Rodman, & Emond, 1996) and may also provide information about colony, group and/or individual identity (Arnold & Wilkinson, 2011; Boughman, 1997; Eckenweber & Knörnschild, 2013; Holekamp et al., 1999; Janik, Sayigh, & Wells, 2006; Kastein, Winter, Kumar, Kandula, & Schmidt, 2013; Semple, 2001).

The ability to discriminate or even individually recognize individuals based on vocalizations can be a valuable social skill (e.g. Carter, Skowronski, Faure, & Fenton, 2008; Müller & Manser, 2008; Rendall et al., 1996; Semple, 2001), especially in repeated encounters (Godard, 1991). Individual signatures in aggressive vocalizations can facilitate interactions between opponents. Individuality encoded in vocalizations allows animals to discriminate between well-known individuals and strangers (Mackin, 2005), providing information that can facilitate decision making in different social circumstances, e.g. during aggressive encounters (Bradbury & Vehrencamp, 2011).

Research on aggressive behaviour, aggressive signalling and vocalizations has been conducted in a range of species, for example anurans (Reichert & Gerhardt, 2013) crickets (Hack, 1997; Hofman & Schildberger, 2001; Logue et al., 2010), chameleons (Stuart-Fox, 2006), birds (Searcy, Anderson, & Nowicki, 2006) and monkeys (Kitchen, 2004). In bats, however, studies on aggressive interactions and associated vocal signals are still scarce (i.e. Behr & von Helversen, 2004; Markus, 2002; Ortega & Arita, 2000; Porter, 1979a, 1979b).

Seba's short-tailed bat, *Carollia perspicillata*, is a highly social species occurring in the Neotropics from southern Mexico to southern Brazil (Cloutier & Thomas, 1992). The bats live in colonies, occupying hollows (e.g. trees, buildings, caves, bridges) for their day roost sites. There, they form groups composed of one male together with up to 18 females (Williams, 1986). Males occupy spots in the day roost, which they defend vigorously against other males (Porter, 1979a; Williams, 1986). Male territories are then selected by females for roosting. This selection is assumed to be based on territory quality, and the *C. perspicillata* mating system is consequently considered to be resource defence polygyny (Fleming, 1988). The harem males have privileged access to females (Porter, 1979a), but nevertheless may not father every young born in the respective harem (Porter & McCracken, 1983). Males not competitive enough to own a territory cluster together in bachelor groups during the day. To obtain mating opportunities, the bachelor males attempt to gain access to females in nearby territories. Males are thus daily involved in aggressive encounters, either between neighbouring territory holders or between sneaker males and the respective harem owner. Aside from bachelor groups and harems,

solitary bachelors and mixed-sex subadult groups can be found in day roosts (Porter, 1979a).

Here we studied aggressive interactions between resident males in a large captive colony of *C. perspicillata* to investigate the behavioural patterns during aggressive encounters between males and to document the vocalizations associated with these encounters. Because males are daily involved in agonistic encounters, we hypothesized that these encounters are ritualized. Ritualized encounters allow animals to minimize energy expenditure and costly fights. First, we predicted that during an aggressive encounter several distinct behavioural displays would be observed. Second, we predicted that the different behavioural displays would follow a sequential structure. Our second hypothesis proposed that males utter distinct aggressive vocalization types during agonistic encounters that are not produced in other contexts. Finally, we hypothesized that male aggressive vocalizations possess an individual signature to facilitate discrimination. As males are repeatedly involved in agonistic encounters they should benefit from being able to discriminate between different individuals. Following our hypothesis we predicted that males would be able to discriminate between two opponents based on aggressive vocalizations only, and that the aggressive vocalizations would encode a statistically detectable individual signature.

## METHODS

### Study Animals

The study was performed in a captive breeding colony of *C. perspicillata*, housed in a tropical zoo (Nocturama; in the Papiliorama Kerzers FR; Switzerland, [www.papiliorama.ch](http://www.papiliorama.ch)). All work was approved by the University of Bern, the veterinary office of Fribourg (permit number 2012-15E-FR), reviewed by the cantonal ethics committee and adhered to the ASAB/ABS Guidelines for the use of animals in research. In the Nocturama, a 40 m diameter dome, a colony of about 400 bats lives in a reversed light cycle tropical environment (night: 0930–2130 hours; day: 2130–0930 hours), which mimics the bats' original habitat in Central America. The bats fly freely under the dome, while their roosting sites are situated in an artificial cave. Bats are fed twice a night with a house-made fruit-based mixture. The dome is open to visitors during the day from 0900 to 1800 hours, and we thus worked outside of the visiting hours to avoid potential disturbance (between 0700 and 0900 hours and 1800–2100 hours). A unique combination of three different coloured plastic rings (AC Hughes Ltd., U.K., size XB), positioned on both forearms, allowed for visual individual identification.

Based on regular spatial and behavioural monitoring of the bats at their roosting site, and on the literature (Porter, 1979a; Williams, 1986), we differentiated between two categories of male social status (territorial versus nonterritorial). Territorial (or harem) males were individuals occupying a roosting site as their territory and defending it vigorously against any male intrusion. Moreover, during our social monitoring, these males were very faithful to their territory. Some males protected a group of females (harem males), but as we were interested in aggressive behaviours, we considered single territorial males with similar fidelity to their roosting site as having the same social status. The other status category comprised the nonterritorial bachelor males (or sneakers). These males were not territorial as they were observed in several places in the cave during the social monitoring and rarely initiated aggressive behaviours. They mainly roosted in large bachelor groups (groups composed of males only). As harem males do not sire all the young born in their harem, they share their reproductive success with bachelor males (Porter & McCracken, 1983). The costs of guarding females imposed on harem males may therefore offer the

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