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Authors: Breviglieri, Crasso Paulo Bosco, and Kuhnen, Vanessa Villanova

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Resource-defense behaviour: first report of an agonistic interaction between the opossum *Didelphis aurita* and the bat *Artibeus lituratus*

Crasso Paulo Bosco BREVIGLIERI and Vanessa Villanova KUHNEN

Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP), CEP 13083-970, CP 6109, Campinas-SP, Brazil; e-mail: crassopaulo@gmail.com

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Abstract. Species coexistence depends mainly on the spatiotemporal distribution of resources, and, in extreme cases, results in direct competition (interference). In the present study, we report for the first time an agonistic interaction between marsupials and bats, and food defense behaviour in the black-eared opossum *Didelphis aurita*. We describe the agonistic interaction between the opossum and a bat of the species *Artibeus lituratus* while they foraged on the same infructescences of *Cecropia glaziovii* and *C. hololeuca* in an Atlantic Forest area. While competing for food, the bats foraged in group (of approximately six individuals) and apparently showed a synchronized and coordinated behaviour to pick the infructescences. Then, a male *D. aurita* showed an aggressive behaviour toward the bats, moving on branches and leaf petioles and vocalizing to the bats, apparently trying to scare them away. We conclude that *D. aurita* defends food in a way consistent with the concept of economic defendability. We know little about how Neotropical mammals share resources in time and space, so future studies on the foraging behaviour of the black-eared opossum should focus on agonistic interaction with competitive species.

Key words: interference competition, vocalization, great fruit-eating bat, didelphids, marsupial, *Cecropia*, southeastern Brazil

Introduction

The genus *Didelphis* (Didelphimorphia: Didelphidae) comprises the largest living American marsupials. The black-eared opossum *Didelphis aurita* (Wied-Neuwied, 1826) is one of the largest marsupials in Brazil (Gardner 2007). It is a nocturnal, solitary species that uses all forest strata (Leite et al. 1996, Cunha & Vieira 2002). This species is generalistic and opportunistic: it consumes small vertebrates, fruits, and flowers (Vieira et al. 1991, Cáceres & Monteiro-Filho 2001). Seasonal variations in resource availability seem to influence the diet of *D. aurita* (Ceotto et al. 2009). However, records of *D. aurita* defending food in periods of low availability are scarce, and little is know about the interspecific interactions made by this species.

The great fruit-eating bat *Artibeus lituratus* (Olfers, 1818) (Chiroptera: Phyllostomidae) feeds mainly on fruits (Urticaceae and Moraceae; see Passos et al. 2003, Bredt et al. 2012). However, it can also consume nectar, insects, and leaves, depending on resource availability over the year (Gardner 1977, Emmons & Feer 1997, Bredt et al. 2012). This bat species forages in groups that vary from a few to tens of individuals (Oprea et al. 2007, Breviglieri et al. 2013), but its foraging behaviour is poorly known.

Although *D. aurita* and *A. lituratus* are phylogenetically distant species, they can feed on similar fruits. When their diets overlap considerably, their coexistence will depend on resource partitioning in time and space. Alternatively, there might be direct competition for food, when the benefits provided by defending a given food exceed the costs of repelling intruders (Brown 1964, Stamps 1994). In general, encounters between individuals with similar ecological requirements can lead to competition, if the resources are scarce (e.g. Righetti et al. 2000, Harris & McDonald 2007). Species can exhibit several defensive behaviours, such as direct aggression (Isbell 1991), vocalization (Kinnaird 1992), or frequent visits to the resource (Lara et al. 2011).

According to Brown's (1964) concept of economic defendability, the advantage of resource defense depends on the amount of resource available, the number of competitors, and the spatiotemporal distribution of the resource. Therefore, plants that

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produce fruits throughout the year play an important role as a keystone species for frugivorous animals. For example, fruits of Neotropical pioneer trees of the genus *Cecropia* Loefl. (Urticaceae) are part of the diet of several vertebrates throughout the year (Berg & Franco 2005), including Neotropical bats (Bredt et al. 2012). Therefore, the defense of *Cecropia* fruits in a period of food scarcity should be profitable.

Here, we describe the aggressive behaviour of the black-eared opossum *D. aurita* towards bats of the species *A. lituratus* while defending infructescences of *Cecropia glaziovii* Snethl. and *C. hololeuca* Miq. in winter. We report for the first time an interference competition between marsupials and bats and a food-defense behaviour in *D. aurita*.

Material and Methods

We recorded agonistic interactions between *D. aurita* and *A. lituratus* in June 2015, during winter in a remnant of Atlantic Forest in Guarujá, state of São Paulo, southeastern Brazil (approx. 23°54′ S 46°17′ W). The interaction between the two species lasted only 30 min in a single night. We recorded the interaction in photograph (DSC-HX200V Sony Cyber-shot®) and video, using a directional microphone (HT-81Yoga®) connected to a digital recorder (Digital mini-recorder, ICD-PX240 4GBSony®). We recorded the vocalizations of both species for 15 min with the microphone positioned approximately 8 m away from the animals. We analyzed the acoustic parameters of the recordings in the program RAVEN Pro 1.5, Beta

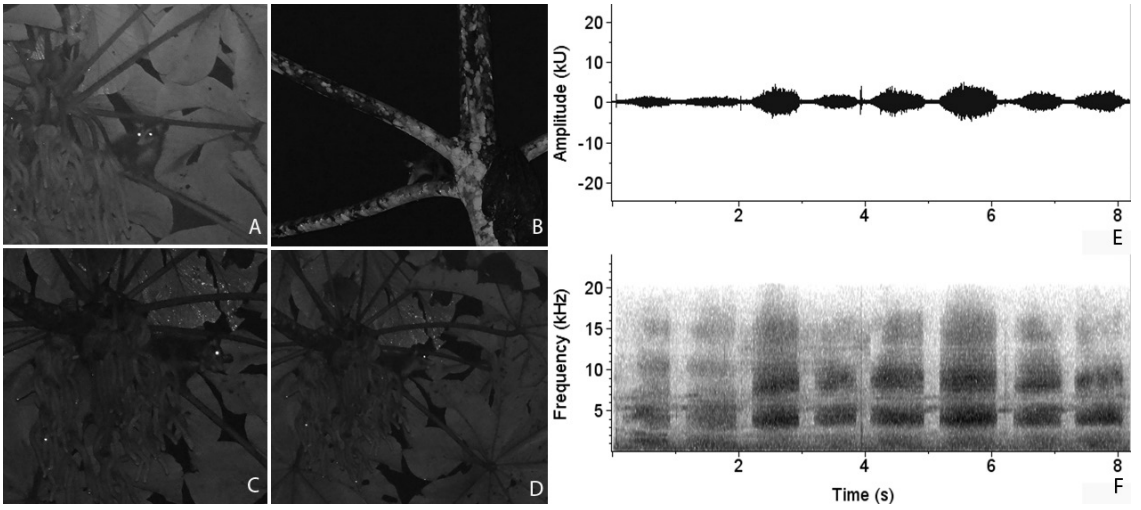


Fig. 1. A male *Didelphis aurita* moving on leaf petioles (A) and the branches (B) of a *Cecropia hololeuca*, apparently vocalizing to defend some infructescences (C and D). (Photo credits: Breviglieri C.P.B.). In E, the amplitude (kU) and in F, frequency (KHz) of the calls produced by *D. aurita*.

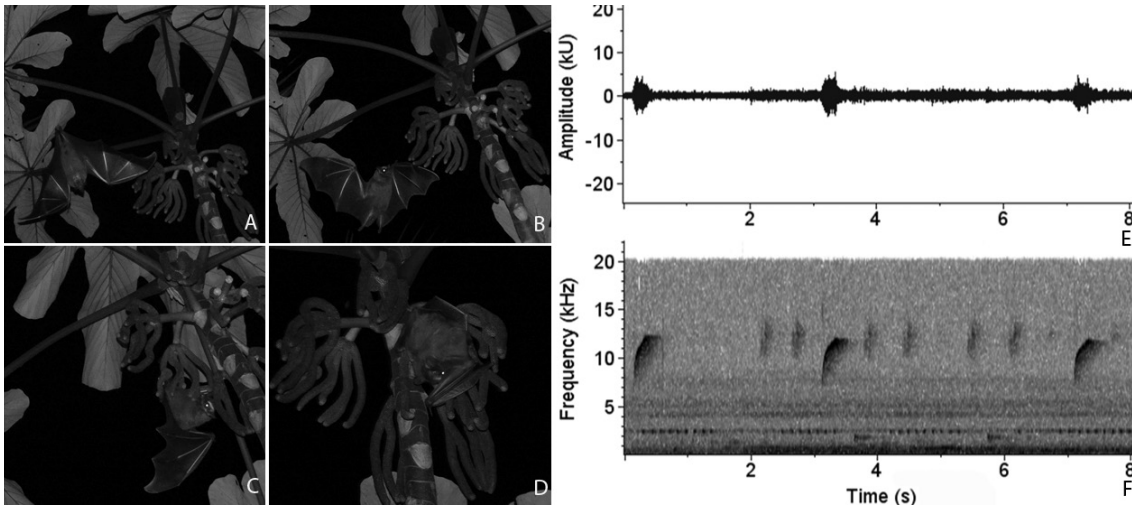


Fig. 2. Visiting behaviour of *Artibeus lituratus* on ripe infructescences of *Cecropia glaziovii*. Notice that the bat flies around the infructescences (A and B), lands upside down (C), takes a bite from the infructescence (D), and then flies away from the plant. (Photo credits: Breviglieri C.P.B.). In E, the amplitude (kU) and in F, frequency (KHz) of the calls produced by *A. lituratus*.

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Table 1. Average values of the acoustic parameters of the calls produced by *Didelphis aurita* (N = 450) and *Artibeus lituratus* (N = 5) during agonistic interactions near infructescences of two *Cecropia* species in southeastern Brazil. The values are presented as average and standard deviation (in parenthesis). Du: duration (milliseconds), IPI: Interval between pulses (milliseconds), SF: initial frequency (kHz), EF: final frequency (kHz), MaxF: maximum frequency (kHz), MinF: minimum frequency (kHz), PF: frequency peak (dB).

Species	Du	IPI	SF	EF	MaxF	MinF	PF
Didelphis aurita	0.75 (0.08)	0.27 (0.03)	3.87 (0.88)	4.20 (1.10)	18.77 (1.04)	1.77 (0.22)	16.50 (3.57)
Artibeus lituratus	0.50 (0.06)	4.84 (3.33)	9.91 (0.24)	11.74 (0.33)	12.01 (0.18)	7.37 (0.19)	65.40 (2.50)

Version®. Those parameters included call duration (seconds), interval between pulses (milliseconds), initial, final, maximal, and minimal frequencies (kHz), and frequency peak (dB).

Results

The interaction between *D. aurita* and *A. lituratus* occurred in the first minutes after sunset on the day of observation (between 18:30 and 19:30). It took place on the branches of one *Cecropia hololeuca* and one *C. glaziovii*, located side by side on the edge of an Atlantic Forest fragment. The two trees were approximately 8 m tall, and each of their branches had one or two developed infructescences. We observed one male *D. aurita* positioned on the branches above the infructescences, which was apparently inhibiting the landing of a foraging group of six *A. lituratus* (Fig. 1A). The opossum used the entwined branches of the two trees to move rapidly from one tree to the other (Fig. 1B) and vocalized relentlessly. While still on the infructescences (Fig. 1C and D), the opossum intensified its vocalization and seemed to scare away the foraging bats.

While flying without emitting audible vocalizations, the bats began to forage on infructescences that were more distant from the opossum (±2 m). Whenever the bats found those infructescences, they vocalized (Fig. 2A) and attracted other bats (Fig. 2B). Next, one of the bats landed upside down on an infructescence (Fig. 2C), and quickly took a bite from a ripe spike (Fig. 2D), removed part of it, and flew away. Then the bat flew towards the crown of an adjacent *Guarea macrophylla* Vahl (Meliaceae) carrying part of the spike on its mouth, probably to consume it. As soon as opossum noticed that bats were visiting infructescence, the marsupial was toward them vocalized, but before he could reach the bats, they flew away without fruit. Although the bats moved to infructescences farther from the opossum, the opossum rapidly moved towards them, and this pattern of behaviour continued. The animals repeated this behaviour approximately ten times during 30 min. The opossum just stopped vocalize and began to consume the spikes when the bats ceased to visit the *Cecropia* trees. After the bats dispersed, the male opossum remained foraging on the infructescences for about 12 min. Then, the marsupial also moved toward the crown of the adjacent *G. macrophylla* tree, which also had one branch contacting the *C. hololeuca*, and did not return in the next minutes. The audio recordings made during the interactions showed four sequences emitted by *A. lituratus*, each containing five calls (Table 1, Fig. 2E and F). *D. aurita* showed only intermittent calls (Table 1, Fig. 1E and F). However, it was possible to identify two periods of silence during the 15 min recorded: the first lasted 4 min and the second, 3 min. These pauses occurred when the bat activity on the tree canopy decreased. During the observation period, the opossum emitted approximately 450 calls.

Discussion

Fruits of several *Cecropia* species are important food sources for Neotropical bats of the genus *Artibeus* (Lobova et al. 2003, Bredt et al. 2012, Andrade et al. 2013). We noticed in our observation that, in spite of the aggression risk, the bats kept on flying over the tree and tried to pick ripe infructescences. This behaviour suggests that the fruits of *Cecropia* might be important for those bats, so that the potential energy gained was worth the cost of competing with the opossum (see Estrada et al. 1984). In addition, the infructescences of species of *Cecropia* are exploited by many different species of vertebrates: birds, bats, monkeys, fish, and others mammals (Lobova et al. 2003). Therefore, when available, this feature should be defended tooth and nail literally.

We believe that the behaviour of flying from one side to the other (i.e. through the canopy of trees) avoiding the approach of opossum has allowed bats to consume at least part of the fruit. On the other hand, we do not believe that the opossum attacked bats to prey on them. The behaviour described in the presented study differs from other situations in which marsupials hunt bats; in those other cases, the marsupials stalked bats in silence (see Breviglieri & Pedro 2010, Breviglieri & Uieda 2014).

The flight around *Cecropia* trees, followed by audible vocalizations made by one individual bat, and the

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attraction of other bats by those calls are evidence of a social foraging behaviour. In some cases, group foraging can bring more benefits than solitary foraging (Hunter & Skinner 1998). For example, bat foraging in groups reduces predation risk due to better patrolling, reduces aggression imposed by dominant males, optimizes prey finding and capture, favours social bonds among individuals of the same colony, and allows the defense of resources (Wilkinson & Boughman 1998). The habit of group foraging in *A. lituratus* has been already described by other authors (Breviglieri et al. 2013), and also in other bat species of the same family, in which screech calls appear to help recruit and coordinate the foraging activity (Wilkinson & Boughman 1998). In our observations, the call emitted by *A. lituratus* had apparently the objective of re-grouping individuals around a food source that showed lower predation risk. However, it is not possible to corroborate this hypothesis based only on direct and random observations. Hence, we highlight the need for further behavioural studies in the medium and long terms to shed light on the ecology of this species.

On the other hand, it was clear that the vocalization by the male *D. aurita* had the only objective of scaring away the bats from the infructescences. Opossums of the genus *Didelphis* emit different vocalizations, mainly hiss, growl, and screech, which are produced in agonistic encounters (McManus 1970). Interspecific agonistic behaviours have been described for captive *Didelphis* sp. (Reynolds 1952, McManus 1970). However, reports on agonistic behaviours in the field are rare, especially during interspecific interactions, and there are no such records for *D. aurita*. The sonogram presented here is the first description of an aggressive vocalization by *D. aurita* towards another species in its habitat (Fig. 2F).

D. aurita was successful in defending resource, although bats consumed some of the infructescence, opossum consumed most part of the resource. According to the concept of economic defendability (Brown 1964), defending *Cecropia* infructescences from bats would be advantageous to *D. aurita*. *Cecropia* fruits are consumed by a variety of animals (see Lobova et al. 2003) and the infructescences were ripening along period of ripe fruit scarcity (C.P.B.B., pers. observ.). It is known that during the winter, in the Atlantic forest, some species of *Cecropia* only have 1-4 ripe fruits along the day and that are consumed quickly by mammals (see Hirsch 2009). Therefore, we can consider that during this period, the scarcity of ripe fruit may have influenced the conflict between the bats and opossum. However, future studies should evaluate the relationship between resource availability and competition for interference among these species in the Atlantic forest. Studies show that although *D. aurita* is a generalistic, and opportunistic species, seasonal variations in resource availability seem to affect its diet (Lessa & Geise 2010). In a dense rainforest in southeastern Brazil, Kuhnen (pers. comm.) observed that 20 % of the captured *D. aurita* consumed *C. glaziovi*, especially in winter. This information suggests that *D. aurita* is an important disperser of *Cecropia* seeds, as evidenced by Grelle & Garcia (1999).

The present study sheds new light on the interactions between bats and marsupials, and on the defensive vocalizations of *D. aurita*. In conclusion, our description of the *D. aurita* food defense behaviour gives support to Brown's (1964) concept of economic defendability. Hence, we suggest that exploitation and interference competition influence the relationship between *D. aurita* and *A. lituratus*. However, additional behavioural studies are necessary, to better understand the ecology of those species in the medium and long terms, and their behaviour should be monitored throughout different seasons of the year.

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