Liquid lunch – vampire bats feed on invasive feral pigs and other ungulates

Vampire bats have long captivated the imagination of humans worldwide. Although often associated with myths about Dracula-like creatures (Mayen 2003), only three of about 1200 known bat species – *Desmodus rotundus, Diaemus youngi*, and *Diphylla ecaudata*, all restricted to the New World – feed exclusively on blood (Turner 1975). Of these, the common vampire bat (*D rotundus*) has the widest distribution, extending from Mexico to Argentina. This species feeds mostly on livestock and poultry (Greenhall *et al.* 1983) but has also been documented preying on native mammals (Catenazzi and Donnelly 2008; Sánchez-Cordero *et al.* 2011).

We have used camera traps to monitor mammals in the Brazilian Pantanal and Atlantic Forest for the past 12 years. After checking 10,529 photos and videos of several terrestrial mammals, we saw several examples of *D* rotundus feeding on invasive wild feral pigs (*Sus scrofa*; six instances), free-ranging cattle (two instances), and native ungulates (four instances) including lowland tapirs (*Tapirus terrestris*) and red brocket deer (*Mazama americana*). See WebVideos 1–5 for examples of bat feeding behavior and a thwarted attack on native and non-native mammals.

Because vampire bats feed nocturnally, we also analyzed a subset of the 10,529 records that included only nighttime photos and videos (from 18:00 pm to 6:00 am) showing tapirs, brocket deer, and feral pigs. To estimate the frequency of encounters between bats and these three ungulates, we considered each night (12-hour period) as an independent event. From the 4629 night records available, we logged 158 independent events in the Pantanal (101 for feral pigs, 38 for deer, and 19 for tapirs) and 87 independent events in the Atlantic Forest (35 for feral pigs, 29 for deer, and 23 for tapirs). Based on these encounters between vampire bats and each of the prey species, we estimated that the chances of an ungulate being attacked by a vampire bat in the Pantanal were 2% for feral pigs, 11% for tapirs, and 3% for brocket deer. In the Atlantic Forest, we found only feral pigs and brocket deer being attacked by bats, with a probability of 11% and 7%, respectively.

Feral pigs and brocket deer were the only ungulates recorded with vampire bats in both the Pantanal and Atlantic Forest. The frequency of encounters between bats and feral pigs is fivefold higher in the Atlantic Forest than in the Pantanal. However, our sample does not capture vampire bat–prey interactions when the prey is not foraging or moving. Consequently, the actual encounter frequency between bats and ungulates is probably higher than our estimates.

About 1.4% of vampire bats are infected with rabies virus in the Atlantic Forest (Scheffer *et al.* 2007), but this

 Figure 1. A common vampire bat (Desmodus rotundus) rides a female invasive feral pig (Sus scrofa) in the Brazilian Pantanal.

may reach up to 10% in the Peruvian Amazon (Streicker *et al.* 2012). Based on a vampire bat–rabies prevalence of 0.014 (Scheffer *et al.* 2007), the probability of rabies transfer to tapirs and deer by bats in the Pantanal is 0.15% and 0.04%, respectively, and is 0.09% for deer in the Atlantic Forest. Based on the same data, rabies transmission to feral pigs is 5.3 times as high in the Atlantic Forest (0.16%) as in the Pantanal (0.03%). Vampire bat-transmission of rabies is a major concern for livestock owners in Brazil, even in areas where cattle are routinely vaccinated (Ito *et al.* 2001; Kobayashi *et al.* 2006), but wild animals – including feral pigs – are not vaccinated and may therefore pose a serious threat by spreading the disease.

Besides attaching themselves to feral pigs' bodies to feed (Figure 1), the vampire bats were also seen hopping along on the ground in an attempt to catch the pigs and take blood from their feet when they stopped to root through or dig into the forest floor (WebVideos 1 and 2). On one occasion, two vampire bats fed on a feral pig while another bat hovered nearby (WebVideo 3). Vampire bats are able to dodge branches and other obstacles while riding the pigs or chasing after them on the forest floor. Similar behavior was recorded for a vampire bat feeding on a lowland tapir in the Pantanal, as the bat skillfully avoided being trampled while feeding from the tapir's foot (WebVideo 4). Vampire bats have also been seen chasing capybaras (*Hydrochoerus hydrochaeris*) at





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Figure 2. A common vampire bat (Desmodus rotundus) takes blood from the ear of a resting domestic pig (Sus scrofa) on a subsistence farm.

Anchieta Island, Atlantic Forest (VB Zipparro, unpublished data).

We recorded unsuccessful attacks on an adult female brocket deer in the Atlantic Forest (WebVideo 5). In response to the approaching bats, the brocket deer kicked out with its hind legs, charging at bats near or on the ground and snapping its jaw at one flying close-by. In most of the videos, more than one bat attacked the prey, but the vigorous avoidance behavior of the brocket deer successfully kept the bats at bay.

The population density of *D* rotundus is usually high in areas with domestic animals, especially cattle (Turner 1975). Land-use change converted the area's natural ecosystems into pasture for livestock, which may have boosted vampire bat populations due to food abundance (Turner 1975). However, conversion of pasture into sugar cane agriculture in most of southeastern Brazil during the past few decades (Rudorff *et al.* 2010) and the severe defaunation of the Atlantic Forest (Jorge *et al.* 2013) may have forced the bats to switch from the formerly abundant cattle to an alternative food source – feral pigs.

In the Pantanal, where cattle density can reach 1.4 head per hectare, *D* rotundus is the seventh most abundant bat, with a 4% capture frequency (Alho *et al.* 2011), whereas in the Atlantic Forest they represent <1% of the captures (Gorresen and Willig 2004). The growing population of feral pigs in the Atlantic Forest (Pedrosa *et al.* 2015) makes them ideal prey substitutes for the bats

(Figure 2), as pigs are among the preferred prey of this species (Mialhe 2014; Bobrowiec *et al.* 2015). Under the human-induced environmental changes described above, vampire bat populations may increase due to the wide-spread invasion of feral pigs, mostly in Brazil's southern regions (Pedrosa *et al.* 2015), and our findings on the encounter frequency between vampire bats and feral pigs support this suggestion.

The common vampire bat is a major reservoir of rabies virus and is well known for spreading this deadly disease to several mammals upon which it feeds (Turner 1975; Anderson *et al.* 2014). The rabies virus is transmitted through the saliva of infected bats (Aguilar-Setien *et al.* 2005), and exposure to saliva through small wounds or scratches may occasionally result in rabies infection (Rupprecht *et al.* 2002). Bushmeat hunters are exposed to saliva and other bodily fluids from their kills when they cut up the carcasses (Desbiez *et al.* 2011). Rabies-infected feral pigs may also occasionally bite hunters, their dogs, or even other predators of pigs (Jorge *et al.* 2010). There is therefore a danger of the virus being transmitted to hunters and dogs via feral pigs (Nociti *et al.* 2009; Pessoa *et al.* 2011).

D rotundus is also a reservoir for other viruses, including hantavirus, coronavirus, and adenovirus (Brandão et al. 2008; Lima et al. 2013; Sabino-Santos et al. 2015). Human-induced changes in the environment are linked to an increasing occurrence of emerging infectious diseases (Kuzmin et al. 2011), including spillover of viruses from bats to humans and other mammals (Plowright et al. 2015). Vampire bats feeding on the constantly spreading feral pigs may therefore be viewed as a potential risk to wildlife, livestock, and humans.

Supporting Information

References and additional web-only material may be found in the online version of this article at http:// onlinelibrary.wiley.com/doi/10.1002/fee.1431/suppinfo

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