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Does Mouth-Licking In Vampire Bats Serve Other Functions Besides Food Sharing?

Tatyana Sopka[1], Elizabeth M. George[1], and Gerald G. Carter[2,3,4,*]

[1]Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus OH, USA
[2]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA
[3]Howard Hughes Medical Institute, Chevy Chase, MD, USA
[4]Smithsonian Tropical Research Institute, Balboa Ancon, Panama, Republic of Panama

*Corresponding author (Email: gc1511@princeton.edu)

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Abstract – Regurgitated food sharing in vampire bats is a cooperative behavior that has garnered scientific interest as an example of reciprocal helping among kin and non-kin. The amount of food given is estimated via the duration of mouth-licking. However, a growing body of evidence across other animal taxa, especially social insects, shows that mouth-to-mouth material transfer can serve many functions besides food sharing. In this review, we asked whether and to what extent mouth-licking in the common vampire bat (*Desmodus rotundus*) could be explained by functions other than regurgitated food sharing. We first review the evidence, including new analyses of published data, that food sharing occurs during mouth-licking bouts in vampire bats. We then review interpretations of mouth-licking in other mammal species and assess the likelihood that various hypothetical functions suggested in other species could occur in vampire bats. We conclude that the *primary* function of prolonged bouts of mouth-licking in vampire bats is sharing of ingested blood, but that microbial sharing is another likely benefit, and that short bouts of mouth-licking also function as social signals of begging or offering of food. Future work on this behavior should keep alternative explanations in mind when interpreting observations.

Keywords – Food sharing, Mouth-to-mouth, Regurgitation, Trophallaxis, Vampire bats

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The food-sharing relationships of common vampire bats (*Desmodus rotundus*) have garnered scientific interest as a possible example of reciprocal cooperation in nonhuman animals (Wilkinson 1984, reviewed by Carter, 2021). Adult vampire bats feed exclusively on the blood of other vertebrates, for which they forage each night. If repeatedly unsuccessful at obtaining a meal, the bats will die after 70 hours (Wilkinson, 1984), but unfed bats can obtain regurgitations of ingested blood from roost mates. Most observed regurgitations (~70%) are from mother to offspring (Wilkinson, 1984) but reciprocal food sharing also occurs among adult kin and non-kin (Carter & Wilkinson, 2013; Wilkinson, 1984). Maternal regurgitations to offspring occur in several other bat species and other mammals, and regurgitated food sharing in vampire bats is likely to have evolutionary origins in maternal care (reviewed by Carter, 2021).

To study food sharing among adult bats, experimenters can selectively fast individual bats, simulating a failed hunt. After fasting an individual for 24 hours, the experimenter then exposes the bat to conspecifics that have been allowed to feed, creating a scenario where the unfed bat is a potential recipient and all fed bats are potential donors (e.g. Carter & Wilkinson, 2013, 2015; Razik et al., 2021; Stockmaier et al., 2020; Wilkinson, 1984). Either a donor or a recipient can initiate a bout of food sharing by licking on or near the other bat's mouth (Carter & Wilkinson, 2013; Mills 1980; Schmidt et al., 1980). In our lab, we assume that food sharing has occurred once an unfed bat has licked on or inside the mouth of a donor for at least 5 seconds, and the duration of mouth-licking is used to estimate the relative amount of food given (e.g. Carter et al., 2020; Carter & Wilkinson, 2013).

The assumption of this method is that the primary motivation and result of mouth-licking by vampire bats is to transfer food, but there is widespread evidence from many other animal species that mouth-licking can serve additional functions. In many social insects, regurgitations called "trophallaxis" transfer not only food, but also microbes, growth hormones, and chemical cues that can communicate food preference or quality (Hakala et al., 2023; LeBoeuf, 2017; LeBoeuf et al., 2016; Meurville & LeBoeuf, 2021). For instance, the vast majority of trophallaxis events in honeybees (*Apis mellifera*) appear to function in communication, with less than 5% resulting in the measurable transfer of food (Korst & Velthuis, 1982). Across mammals, mouth-to-mouth contact appears to function in social interactions, such as greetings and reconciliations (e.g., De Waal, 2000; Sanchez-Hernandez et al. 2019; Cafazzo et al. 2016). Given these observations, it is reasonable to wonder to what extent mouth-licking in vampire bats also serves functions beyond food transfer.

Here, we explore the form and function of mouth-licking in vampire bats in two ways. First, by reviewing previous findings and presenting new analyses of published data, we revisit the evidence that food sharing is occurring during mouth-licking bouts in vampire bats. Second, we review observations and interpretations of mouth-licking in other mammal species and assess the likelihood that its purported functions in other species could occur in vampire bats. Our aim is in this short review is to highlight potential lines of inquiry involving this social behavior.

Evidence that the Primary Function of Mouth-Licking in Vampire Bats is Food Transfer

The primary evidence that mouth-licking does transfer food comes from studies using the previously described fasting protocol. Several studies using this method have found that the observed duration of mouth-licking by a fasted (unfed) bat strongly predicts its weight gain during the observation period (Carter et al., 2020; Carter & Wilkinson, 2013; Schmidt et al., 1980; Wilkinson, 1984). Although this correlation has been found repeatedly, the most accurate sampling of both mass and mouth-licking times occurred during 121 fasting trials among familiar bats (Carter & Wilkinson 2015). Compared to other published studies, these bats were the most closely observed and had the highest rates of mouth-licking. A linear mixed effect model predicting mass change with mouth-licking seconds as a fixed effect, and bat as a random intercept, estimated that 37 milligrams of food [95% CI: 31-43 mg] is transferred per minute of mouth-licking. Thus, over an observation period of 1-2 hours, a bat can gain over 2.5 grams of mass (roughly 6-7% of their body weight). Notably, mouth-licking time explains 63% of the variance in weight change, with 75% of the variance explained by mouth-licking duration, day, and recipient (Carter & Wilkinson 2015). The remaining unexplained variance in mass gain could be caused by errors in measurements of mouth-licking duration, by changes in body mass for other reasons (e.g., mass loss due to urination), by differences in rate of regurgitation across individual donors, or by mouth-licking that occurs without food transfer for other functions (explored below).

We also find support for food-sharing as the primary function of mouth-licking when we compare the licking behavior of bats in fasted and non-fasted contexts. This comparison can best be made using data from a study in which experimenters induced and measured food sharing by fasting individuals in a captive colony of vampire bats that varied in familiarity (Razik et al. 2021). Each bat (n = 24) was observed during a 1 hr trial after being fasted for 24 hr (mean trials per bat = 12), and the same individuals were also observed for 576 hr over 114 days when they were non-fasted (Razik et al., 2021). In a new analysis of this published data set, we find that unfed vampire bats lick the mouths of groupmates far more than sated bats do. Within one hour of being returned to the cage, 22 of 24 bats licked the mouths of other bats. In contrast, despite daily observations over multiple months, only 10 of the 24 bats were ever observed mouth-licking without being fasted, and most were never seen mouth-licking when sated. Comparing the rates of mouth-licking among fasted and non-fasted individuals, we find that fasted bats engage in mouth-licking with a probability of 31% within that hour (bootstrapped 95% confidence interval (CI): 22–42%), whereas the per-hour probability of mouth-licking for non-fasted bats is only 5.4% (95% CI: 3.6–7.5%). When comparing the duration of mouth-licking bouts within the same daytime hour and bat, we find that bats spent 26 times longer mouth-licking when fasted (mean = 59 s/hr, 95% CI: 30–94 s/hr) than when non-fasted (mean = 2.3 s/hr, 95% CI: 0.3–4.7 s/hr; mean difference = 57 s/hr, 95% CI: 30–94 s/hr). The observation that non-fasted bats still occasionally engage in mouth-licking could suggest that some non-fasted bats occasionally did engage in food sharing, perhaps because they did not obtain sufficient food that night (due to illness or food competition); or it could suggest an alternative function besides food sharing (discussed below).

These results show that if prolonged mouth-licking in the absence of food sharing does occur in this species, its occurrence must be rare. However, it is still possible that mouth-licking could serve secondary functions, either in brief periods of mouth-licking without food sharing or while food is being transferred. Below, we explore three categories of potential secondary functions: communication, social grooming, and transfer of other beneficial materials.

Mouth-Licking as a Potential Signal

Mouth-licking can communicate information between the licker and receiver, independent of any material transfer or removal. Across several mammalian species, mouth-licking has been suggested to function in greetings, play, reconciliation, and general affiliation. In humans, mouth-to-mouth kissing in a romantic or sexual context has been reported in 46% of human cultures (Jankowiak et al., 2015), and recent evidence suggests this behavior has occurred since 2500 BCE (Arbøll & Rasmussen, 2023). It remains unclear whether the biological or cultural evolution of kissing is related to a food-sharing behavior found across human societies and other great apes—called ‘premasticated food transfer’, ‘prechewing’, or ‘kiss feeding’—in which the donor chews food before feeding it to another individual, often mouth to mouth (e.g. Bădescu et al. 2020). In many cultures, kissing or mouth-to-mouth contact also occurs between children and parents as part of a greeting after separations (Bowlby, 1973). In some other mammals, young also lick their mothers’ mouths upon reunion (e.g., chimpanzees [*Pan troglodytes*], Lawick-Goodall, 1971; two-toed sloths [*Choloepus didactylus*], Stine and Dryden 1977). Mouth-licking also occurs during greetings in African wild dogs (*Lycaon pictus*), arctic wolves (*Canis lupus arctos*), and domestic dogs (*Canis lupus familiaris*) (Rütten et al. 2004, Miklósi 2014, Cafazzo et al. 2016). Chimpanzees kiss mouth-to-mouth while reconciling after a fight (de Waal, 2000). Northern tree shrews (*Tupaia belangeri*) engage in mutual mouth-licking, chinning, and nape grooming with opposite-sex partners, which Martin (1968) suggested is a pair-bonding behavior. In toothed cetaceans, mouth-to-mouth contact has been described as a signal of affiliation (captive orcas [*Orcinus orca*]; Sánchez–Hernández et al., 2019), a sexual or aggressive signal (bottlenose dolphins [*Tursiops truncatus*]; Overstrom, 1983), or a form of play (young captive beluga whales [*Delphinapterus leucas*]; Hill et al, 2018).

Mouth-licking can also function as a food-begging signal, prior to any transfer of material. In Shiras moose (*Alces alces shirasi*), calves appear to use mouth-licking and face rubbing to request attention or food from their mother (Altmann, 1963). African wild dogs and other canids lick each other’s mouths to signal that they are begging for regurgitated food (Rütten et al., 2004, Carlson et al., 2010, Cafazzo et al. 2016). Coyote (*Canis latrans*) females were observed licking a male’s lower jaw and mouth, which appeared to trigger a regurgitation of food (Carlson et al., 2010). Finally, mouth-licking might function in the opposite direction, indicating an intention to share food, as seems to be the case in vampire bats, discussed below.

There are several ways that mouth-licking is likely to serve a communication function in vampire bats. First, potential recipients appear to use brief bouts of mouth-licking as a signal requesting a regurgitation, i.e., ‘begging’. In our observations, begging does not usually last for more than a few seconds, because it typically leads to the recipient either opening its mouth to regurgitate or turning and moving away. To avoid scoring begging as feeding, we do not count mouth-licking bouts less than 5 s in duration, but it is possible that some prolonged bouts of mouth-licking by recipients are extended periods of begging without any food transfer.

Second, donors often approach and briefly lick the mouths of potential recipients prior to sharing, which we interpret as a signal of intention to share (Carter & Wilkinson 2013). A similar behavior is seen in big brown bats (*Eptesicus fuscus*), where mothers have been observed licking the lips of their young prior to nursing (Davis et al. 1968). Big brown bats do not regurgitate food to pups, suggesting that mouth-licking behavior might predate the evolution of regurgitated food sharing. Finally, some amount of mouth-licking could function as a greeting, since fasted bats have always been separated from the group in our fasting observations. To investigate this last hypothesis, future work could compare the reintroduction of fasted versus fed bats that have also been isolated.

Mouth-Licking as Potential Byproduct of Social Grooming

There are many examples of mammals licking the body parts of conspecifics as a form of social grooming (i.e., allogrooming). Beyond its utilitarian function in removing ectoparasites and detritus from the fur and skin, allogrooming also functions in communication and in the formation and maintenance of social bonds, across several mammalian species. This behavior could also explain some amount of mouth-licking. There are some examples of a groomer targeting the mouth of the grooming recipient: mother cheetahs *(Acinonyx jubatus*) lick the faces of their cubs after they feed (Schaller, 1972) and tree shrews (*Tupaia chinensis*) often groom the nose, back, and the sides of the mouth of others (Hasler & Sorenson, 1974).

Female vampire bats spend 5% of their awake time social grooming or "allogrooming" (Carter & Leffer, 2015), which involves licking several body parts of the recipient, including the face. A recipient bat tends to receive more social grooming when it has wetted and disturbed fur and also after it grooms itself, suggesting that social groomers are sensitive to cues of the recipient's need (Narizano & Carter, 2020). Allogrooming appears to be an important part of social bond formation (Carter et al., 2020). When previously unfamiliar and unrelated females first meet, a period of escalating reciprocal allogrooming predicts the formation of a future food-sharing relationships, suggesting that vampire bats use allogrooming to 'test the waters' of new relationships (Carter et al., 2020). Given the importance of allogrooming, it is possible that some small amount of mouth-licking could be a mere byproduct of allogrooming. One hypothesis is that allogrooming may be targeted to body parts that are difficult for the recipient to reach by itself, such as the back. Areas of the body that a bat can lick itself would then receive less allogrooming. If so, the mouth might actually be avoided during allogrooming sessions. To explore this further, future work should compare the distribution of allogrooming across different parts of the body.

Mouth-Licking to Transfer Other Beneficial Materials

Several authors suggest water transfer as the likely function of mouth-licking in cases where young mammals lick saliva from the mouths of their mothers, as seen in a range of taxa including raccoons (*Procyon lotor*) (Sieber 1986), civets (*Civettictis civetta*) and genets (*Genetta genetta*) (Dücker 1957, Ewer & Wemmer, 1974), woodrats (*Neotoma cinerea*) (Alligood et al., 2008), mink (*Neovison vison*) (Brink et. al 2004), ringtail (*Bassariscus astutus*) (Poglayen-Neuwall, 1980), musk shrews (*Suncus murinus*) and allied rock-wallabies (*Petrogale xanthopus*) (Hornsby, 1981; Lapidge, 2001; Lim et al*.,* 1987; Stine & Dryden, 1977) and kangaroos (*Macropus rufus*) (Croft 1980).

In vampire bats, water and food transfer are entangled because ingested blood is their main, if not only, source of water. Vampire bats can drink water, but they do not require it. Regurgitations are likely to have less water than blood, because vampire bats rapidly remove water from ingested blood both during and after feeding (Busch 1988), resulting in regurgitated material that should be condensed (a kind of "blood honey"). The relative importance of calories vs. water in regurgitated food sharing is unclear and has never been studied. Future work could assess the relative effect of hunger versus thirst in the bats seeking regurgitations.

In social insects, a major function of trophallaxis is the sharing of symbiotic microbes (Meurville & LeBoeuf, 2021). Microbiota benefit their hosts in a variety of ways, including aiding in immune function and digestion (Clark & Walker, 2018), and some obligate sanguivorous invertebrates rely on their microbiota to be able to digest blood (Graf, 1999). Mouth-licking can also transmit beneficial microbes in mammals. Socially transmitted microbiota are abundant and functional throughout vertebrates, including in the mouth and gut, and have clearly shaped the evolution of dietary specializations (Ley et al., 2008). The vampire bat microbiome is distinct and adaptive for the unique dietary challenges of digesting blood (Zepeda Mendoza et al., 2018). The microbiomes of vampire bats that are experimentally introduced to one another become more similar over time, and this convergence is predicted by rates of social interaction, including mouth-licking (Yarlagadda et al., 2021). We have observed sick vampire bats in captivity to lick feces, suggesting possible regulation of gut microbiomes (Carter, pers. obs.). It therefore seems likely that microbial sharing is an additional benefit of mouth-licking, especially from mothers to newborn pups. Stine and Dryden (1977) and Croft (1980) suggest that there are digestive enzymes (e.g., lipase) in the saliva transferred from mother to young during lip-licking events in musk shrews and red kangaroos, respectively. The existence of such digestive enzymes in vampire bat regurgitations is unknown.

Mouth-Licking as Information Gathering

Mouth-licking can gather information about conspecifics, including identity, relatedness, and even reproductive status. Chemical cues may be prevalent in saliva and at or around the mouth. Von Holst (2009) suggested that young northern tree shrews begin mouth-licking with their mothers and then later with unfamiliar adults, because the saliva contained chemical cues. In both rodents and musk shrews, sebum glands are located in the mucocutaneous region of the mouth (Quay, 1965), and when shrews mouth-lick, they may ingest the sebum of the other animal (Stine & Dryden, 1977). In Mongolian gerbils (*Meriones unguiculatus*), young are preferentially attracted to the saliva of their mother, subadults prefer saliva of kin over nonkin, and sexually mature males prefer the saliva of estrous females over nonestrous females (Block et al., 1981). Like many bats, vampire bats have enlarged facial glands that could produce scents (Rehorek et al., 2010), but it is unclear what chemical social signals exist in saliva or around the mouth.

Mouth-licking can also gather information about food. Some authors suggest that in many mammals, mothers might help offspring develop preferences for food that they will consume after weaning by passing information to their young through the scent of food in their saliva (Ewer, 1968, 1973; Alligood et al., 2008). This hypothesis is consistent with observations that mouth-licking is often observed between a mother and young that are transitioning away from nursing and often initiated by the young, as seen in *Suncus* shrews (Stine & Dryden, 1977), the long-tailed weasel (*Mustela frenata*) (Hamilton, 1933), the genet (Ducker, 1957), and the African civet (Ewer, 1973). There is also experimental and observational evidence that young prefer novel foods they have smelled or licked in their mothers' mouths over other novel foods, in several species, including the spiny mouse (*Acomys cahirinus*), Azara's grass mice (*Akodon azarae*), and Lesser hedgehog tenrec (*Echinops telfairi*) (Eisenberg & Gould, 1966; McFadyen-Ketchum & Porter, 1989; Suárez & Kravetz, 1998). Well-controlled experiments with rats show that the co-occurrence of food remnants and sulfur dioxide in the mouths of conspecifics leads to changes in preference for novel food odors (Galef et al. 1988, Galef 1996; Munger et al. 2010). Socially acquired food preferences, likely from the breath of conspecifics or food around the mouth, have also been demonstrated in fruit-eating bats (O'Mara et al., 2014; Ratcliffe & ter Hofstede, 2005).

Relative to other bats, vampire bats have a poorly developed sense of taste (Thompson et al., 1982), and they do not acquire taste aversions from their own feeding behavior (Ratcliffe et al., 2003); however, the existence of social learning from breath cues has never been tested. Whether a preference for blood from a particular host species could be transmitted via saliva or shared blood meals is unknown, but such information is unlikely to explain the patterns of mouth-licking that we observe in vampire bats. It seems more likely that vampire bats could lick the mouths of group members to assess if they have recently fed, but this hypothesis has not been tested either.

Conclusion

In social insects, trophallaxis was originally assumed to be only food sharing, but oral contact is now understood to serve a wide variety of other functions (Hakala et al., 2023; LeBoeuf, 2017; LeBoeuf et al., 2016; Meurville & LeBoeuf, 2021). Across mammals, mouth-licking also serves a variety of functions beyond food sharing, including transmitting and gathering information, water, microbiota, and possibly enzymes. Although the primary function of long bouts of mouth-licking in vampire bats is food sharing, other secondary functions documented across other mammals could also occur among vampire bats. These non-feeding explanations of mouth-licking are worth considering in vampire bats for at least two reasons. First, if mouth-licking occurs without food sharing, then estimates of food-sharing measurements may be inflated. Second, if mouth-licking has important additional functions beyond food sharing, then interpretations of the behavior could be misattributed. Future work in this system will seek to tease apart some of the potential functions and keep these alternative explanations in mind when interpreting observations of mouth-licking.

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