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Maternal mouth-to-mouth feeding behaviour in flower-visiting bats, but no experimental evidence for transmitted dietary preferences

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ABSTRACT

In addition to breast milk, several mammals feed their offspring with primary food items. This provisioning can offer both energetic and informational benefits: young might use parentally provided food as a source of nutrients, but also as a valuable option to socially learn about adults' food. For bats, there are only very few and partially anecdotal reports of adults feeding their pups with primary food, and there is also a lack of information about social learning processes during ontogeny. In the present study, we provide experimental evidence that lactating flower-visiting bats (*Glossophaga soricina*) provide regurgitated nectar via mouth-to-mouth feeding behaviour to their pups. After licking at their mothers' slightly opened mouth, pups defecated a marker substance that was exclusively available in the mothers' nectar diet. We additionally investigated associated informational benefits by testing for a social transmission of dietary preferences. We experimentally induced a dietary preference for specifically flavoured nectars to mothers with non-volant pups. Subsequently, after pups became volant, we tested their dietary preferences in a choice experiment. However, we found no experimental evidence that pups adopted the preferences of their mothers.

1. Introduction

In addition to breastfeeding, several mammals exhibit behavioural capabilities to additionally feed their young with primary food items (e.g. Brown et al., 1983; Holekamp and Smale, 1990; Jaeggi et al., 2008). While the provisioning using maternal nutrient reserves via breast milk enables mothers to provision young even when food supplies are unreliable, a provisioning with primary food items is argued to be more energy efficient at delivering nutrients to the offspring (Dall and Boyd, 2004).

Moreover, parental provisioning with primary food items might carry additional benefits, such as facilitated development of food-handling skills or even a transmission of foraging related information from parents to offspring. Juveniles might socially learn about their parents' dietary preferences or the characteristics of adults' food in general, for example helping them to discriminate palatable from toxic food when foraging alone (informational hypotheses, Brown et al., 2004; Jaeggi et al., 2008; Thornton, 2008).

There is only very little knowledge about parental provisioning of primary food in bats. Even though all bats exhibit a distinct parental care (Kunz and Hood, 2000), sharing of primary food items has only been observed in very few animal-eating and frugivorous species, and most of these observations remained anecdotal (e.g. Brown et al., 1983; Pierson and Rainey, 1992; Altringham, 1996; Wilkinson and Boughman, 1999). Food items are provided mouth-to-mouth in these species; predatory bats deliver solid prey items like small vertebrates or insects to their pups (e.g. Raghuram and Marimuhtu 2007; Geipel et al., 2013), while pups of vampire bats (*Desmodus rotundus, Diphylla ecaudata*) lick regurgitated blood out of the adults' mouth (Schmidt, 1978; Delpietro and Russo, 2002). Potential informational benefits of mouth-to-mouth feeding behaviour in bats were discussed, but have not been tested yet (Geipel et al., 2013).

While adult individuals in many bat species use social information when making foraging decisions (horizontal social learning; Hoppitt and Laland, 2013; bats: e.g., Ratcliffe and ter Hofstede, 2005; Wright et al., 2011; O'Mara et al., 2014; Rose et al., 2016), we know very little

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about social learning processes during juvenile development (vertical social learning; Ganesh et al., 2016; Wright, 2016). Comparable to other mammals, an early contact with food cues via mouth-licking (cf. McFadyen-Ketchum and Porter, 1989) or even via direct provisioning (cf. Thornton, 2008) should be a valuable option for bat pups to gain information about adults' food and enable them to adopt their parents' dietary preferences.

Pallas' long-tongued bat (*Glossophaga soricina*) is a medium sized flower-visiting bat of ca. 10 g, inhabiting tropical habitats from Mexico to Argentina (Alvarez et al., 1991). Its diet mainly consists of nectar and pollen from flowers of a variety of different bat-pollinated plants, which partially share distinct chiropterophilous characteristics, including an unpleasant, garlic-like scent based on sulphur-containing compounds (Heithaus et al., 1975; Knudsen and Tollsten, 1995; Tschapka and Dressler, 2002), which are also flavouring the nectar of some species (Raguso, 2004). While feeding, bats perform hovering flights in front of these flowers and lick up nectar using their elongated tongue (e.g. Harper et al., 2013). Females give birth to a single pup that is nursed with breast milk for about two months (Alvarez et al., 1991; Pink, 1996; Engler et al., 2017). Pups start becoming volant at an age of about 20 to 25 days, but like in other bat species, first flights are short and performed clumsily for at least another week (Pink, 1996). Flower-visiting bats (Phyllostomidae: Glossophaginae) have not been reported to incorporate sharing of primary food into parental care so far, but nursing pups of *G. soricina* were observed to perform a licking behaviour at their mothers' mouth. This behaviour, which was observed to start at a pup age of 9 to 12 days and interpreted as feeding behaviour by Pink (1996), appears comparable to the behaviour of vampire bat pups when fed by adults with regurgitated blood (Wilkinson, 1990).

In the present study, we tested the hypothesis that the pups' licking behaviour at their mothers' mouth represents a mouth-to-mouth feeding behaviour and thus maternal provisioning of floral nectar. We further investigated the possibility that this behaviour might not only provide nutrients to *G. soricina* pups, but also information about food sources and their mothers' dietary preferences. We hypothesized that pups would adopt the dietary preferences of their mothers. Such a vertical social transmission of dietary preferences could help pups to learn about the characteristics of palatable food, for example by getting familiarized with the scent and taste of bat-pollinated flowers.

2. Materials and methods

2.1. Verification of nectar transfer via mouth-to-mouth feeding behaviour

The potential mouth-to-mouth feeding behaviour was experimentally investigated in captive *G. soricina* at the University of Erlangen-Nuremberg. Once pups' licking behaviour at their mothers' mouth was observed for the first time during ontogeny (Fig. 1), we started a verification experiment by adding pollen grains as marker substance to the mothers' nectar diet. In the experiment, mothers had *ad libitum* access to the marked nectar for up to five hours and were allowed to share the marked nectar with their respective pup via mouth-to-mouth feeding behaviour. Since pups were not proficient in flying at the time, maternal mouth-to-mouth feeding was the only available nectar source for pups. Additionally, behaviour of bats was monitored throughout the experiment. To verify the transfer of marked nectar from mothers to pups, we screened faecal samples of pups and counted the number of excreted pollen grain exines. The experiment was performed with 2 mother-pup-pairs and was repeated multiple times during the following days (pair 1: three repetitions / pair 2: four repetitions). A detailed description of the experimental procedures is provided in the online supplementary material (Supporting Information S1).

2.2. Potential implications for vertical social learning

The potential importance of mouth-to-mouth feeding behaviour for

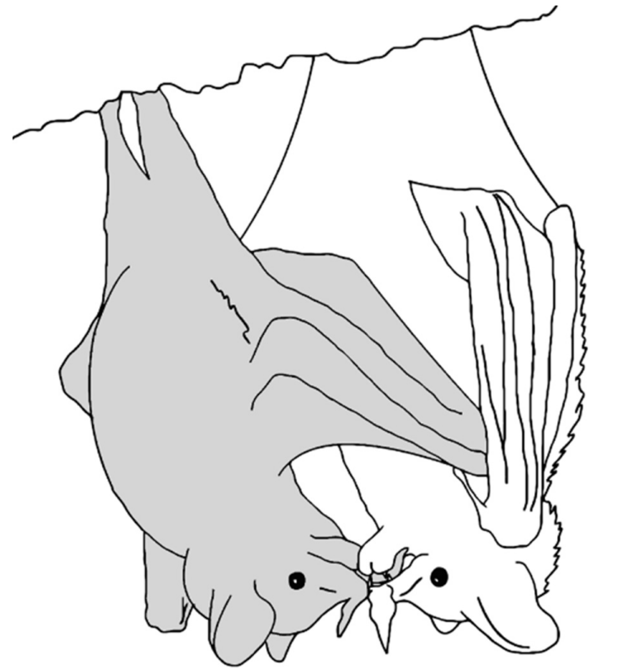

Fig. 1. Mouth-to-mouth feeding behaviour. Pup (left) feeds on regurgitated nectar out of the slightly opened mouth of its mother (right).

vertical social learning of dietary preferences was investigated in free living *G. soricina* in the Santa Rosa National Park, Costa Rica (UTM: 16 P 651,137 1,198,498). Over two reproductive periods, we caught 16 mother-pup-pairs that were split into two experimental groups and kept separated in flight cages.

For a period of 18.2 (± 6.4 SD) days during which pups were still non-volant, we artificially induced different dietary preferences to mothers of each group by allowing them to feed *ad libitum* on only one of two different-flavoured artificial nectars from an artificial flower (flavoured period; group 1: strawberry flavour; group 2: chocolate flavour). Both flavoured nectar types were easily distinguishable by the human nose and mouth. Pups were unable to fly during the whole flavoured period and solely fed by their mothers with breast milk, and with nectar during mouth-to-mouth feeding behaviour.

Once pups became volant (indicated by the onset of first, clumsy flights) and thus had potentially access to nectar on their own, we stopped flavouring the nectar to prevent them from becoming acquainted with our experimentally flavoured nectar without being fed with it by their mothers. During this unflavoured period of 12.3 (± 4.8) days, pups learned to perform hovering flights and to feed from the artificial flower by themselves (Table 1). Even though this inevitable break of flavour presentation was rather long, it should have not affected the experimental outcome, as bats are adapted to feed on several seasonally available resources and show long memory-retention of food stimuli (Ruczynski and Siemers, 2011; Clarin et al., 2014; Rose et al., 2016). For additional information on capturing and husbandry see Supporting Information S2. Procedures of additional behavioural observations are provided in Supporting Information S3.

After pups were proficient in feeding by themselves, we conducted a choice experiment on their flavour preferences (familiar vs. unfamiliar flavour, *i.e.* strawberry vs. chocolate flavour) to test whether they adopted the experimentally induced dietary preference of their mothers. In the experiment, pups were allowed to feed on two artificial flowers with different-flavoured nectar: strawberry flavour vs. chocolate flavour. For pups of both groups, this design represented the option to choose between familiar flavoured nectar, which was previously maternally provided, and unfamiliar flavoured nectar. The two artificial flowers were mounted side by side with 40 cm space on an array in a

Table 1
Husbandry of pups prior to the choice experiment. Description of the two consecutive periods with flavoured and unflavoured nectar, as well as corresponding flight ability of pups (n = 16).

	flavoured period	unflavoured period	choice experiment
duration	18.2 ± 6.4 days	12.3 ± 4.8 days	
nectar	flavoured	unflavoured	flavoured
flight ability	non-volant	volant	volant
description	pups solely fed by mothers (breastfeeding, mouth-to-mouth feeding)	pups improving flight abilities and learning to feed from the artificial flower	pups proficient in flying and feeding from the artificial flower

height of 90 cm. Each pup was tested for an experimental time of three hours, and we switched the flower positions halfway through to balance potential side preferences. Flowers held enough nectar to not be depleted during the experiment. Subsequently, we additionally tested pups' mothers for potentially individually learned preferences with the same setup. However, in contrast to pups, we did not expect mothers to learn the flavour preference to the same extent, as they were experimentally forced to feed on the flavoured nectar during the flavoured period and did not undergo the social demonstration via maternal mouth-to-mouth feeding as their pups did. Additionally, mothers were already experienced to feed on a variety of different food types in the wild, making them possibly less susceptible for learning new food preferences. As adult bats evaluate experimental situations faster and start foraging more readily, we reduced experimental time to only one hour. By applying this shorter duration, we also reduced the total time mother-pup pairs were physically separated. For additional information on experimental procedures see Supporting Information S4.

We scored the bats' foraging behaviour from the video footage which was recorded using an IR sensitive Camcorder (DCR-SR, Sony) under infrared illumination (2 HV L-IRC, Sony). Dietary preferences were approximated by measuring the total time bats fed in hovering flight in front of the two different-flavoured artificial flowers. For one pup that occasionally landed on the flowers for feeding, we additionally counted the time it entered its snout to the flower opening. The hovering time was measured frame by frame using the video analyser Kinovea (v.0.8.15, Kinovea Association). We additionally counted the number of flower visits from the video footage and calculated the amount of nectar that was removed from each flower with a pocket scale (in 2015 only for pups; LS2000H, G&G GmbH, Neuss, Germany). However, nectar occasionally spilled out due to heavy wind gusts, resulting in only limited reliability for the latter measurement. Foraging behaviour was scored throughout the complete experimental time. However, to exclude habituation effects on a potential initial preference in the choice experiment, we performed an additional analysis of the first 15 min of foraging, starting from the first flower visit.

2.3. Statistical analyses

Statistical analysis of dietary preferences was conducted in R (v. 3.4.3, R Core Team, 2017) using the Rcmdr package by Fox and Bouchet-Valat (2017). As pups of both groups were tested on the same flavours in the choice experiment, we combined the results of both groups and compared respective preferential differences between familiar flavour, which was previously maternally provided, and unfamiliar flavour. Data were analysed pairwise by either applying parametric paired t-tests, if pair differences were normally distributed, or non-parametric Wilcoxon signed-rank tests in case of not normally distributed pair differences. All tests were two-sided. Testing for normal distribution was performed with Shapiro-Wilk normality test. Data preparation and calculation of basic statistical parameters (mean; standard deviation; median) was performed in Microsoft Excel. Graphs were generated using an Excel template from Weissgerber et al. (2015).

3. Results

3.1. Verification of nectar transfer from mothers to pups via mouth-to-mouth feeding behaviour

Prior to our verification experiments, mouth-to-mouth feeding behaviour was first observed at an approximate pup age of 20 days (pair 2) and 29 days (pair 1), respectively. During seven experiments, we observed a total number of 34 mouth-to-mouth feeding events (mean ± SD per verification experiment: 4.9 ± 2.1; median: 5). Pup faecal samples of each experiment contained a substantial number of pollen grains that were used as marker substance (104,275 ± 107,635; median: 87,800; per experiment), indicating that mothers transferred previously consumed nectar to their respective pups. Mean pollen grain concentration of the marked nectar that was previously provided to mothers was 1854 ± 498 μl^{-1} (median: 2068; Table 2).

3.2. Potential implications for vertical social learning - choice experiment

Our choice experiment showed no significant differences in the pups' preference between the familiar flavoured nectar, which was previously maternally provided, and the unfamiliar flavoured nectar. Significant differences were neither detected in the total hovering time, nor in the number of flower visits and amount of removed nectar. Per choice experiment, pups hovered in front of the flowers while feeding for a total of 41.2 ± 25.3 s and showed a non-significant trend to hover longer in front of the familiar flavoured flower (paired t-test: $t = 1.55$, $df = 15$, $p = 0.14$) (Fig. 2a). Meanwhile, they performed 54.6 ± 31.8 flower visits (paired t-test: $t = -0.48$, $df = 15$, $p = 0.64$) (Fig. 2b). The

Table 2
Verification experiment. After licking at their mothers slightly opened mouth (mouth-to-mouth feeding events), pups defecated a substantial number of pollen grains that were previously added as a marker substance to the mothers nectar diet (marked nectar).

verification experiment	pup	age [d]	experimental time [h]	pollen grain concentration in marked nectar [μl^{-1}]	pup faecal samples obtained	aggregate number of pollen grains in pup faecal samples per experiment	mouth-to-mouth feeding events
1	pup_pair1	29	5.0	1262	1	10022	2
2	pup_pair1	30	2.2	1010	2	154800	7
3	pup_pair1	32	3.2	2357	2	100350	8
4	pup_pair2	ca. 20	2.5	2415	3	338100	6
5	pup_pair2	ca. 24	2.5	2091	2	87800	5
6	pup_pair2	ca. 27	1.5	1777	2	7150	3
7	pup_pair2	ca. 31	2.5	2068	3	31700	3

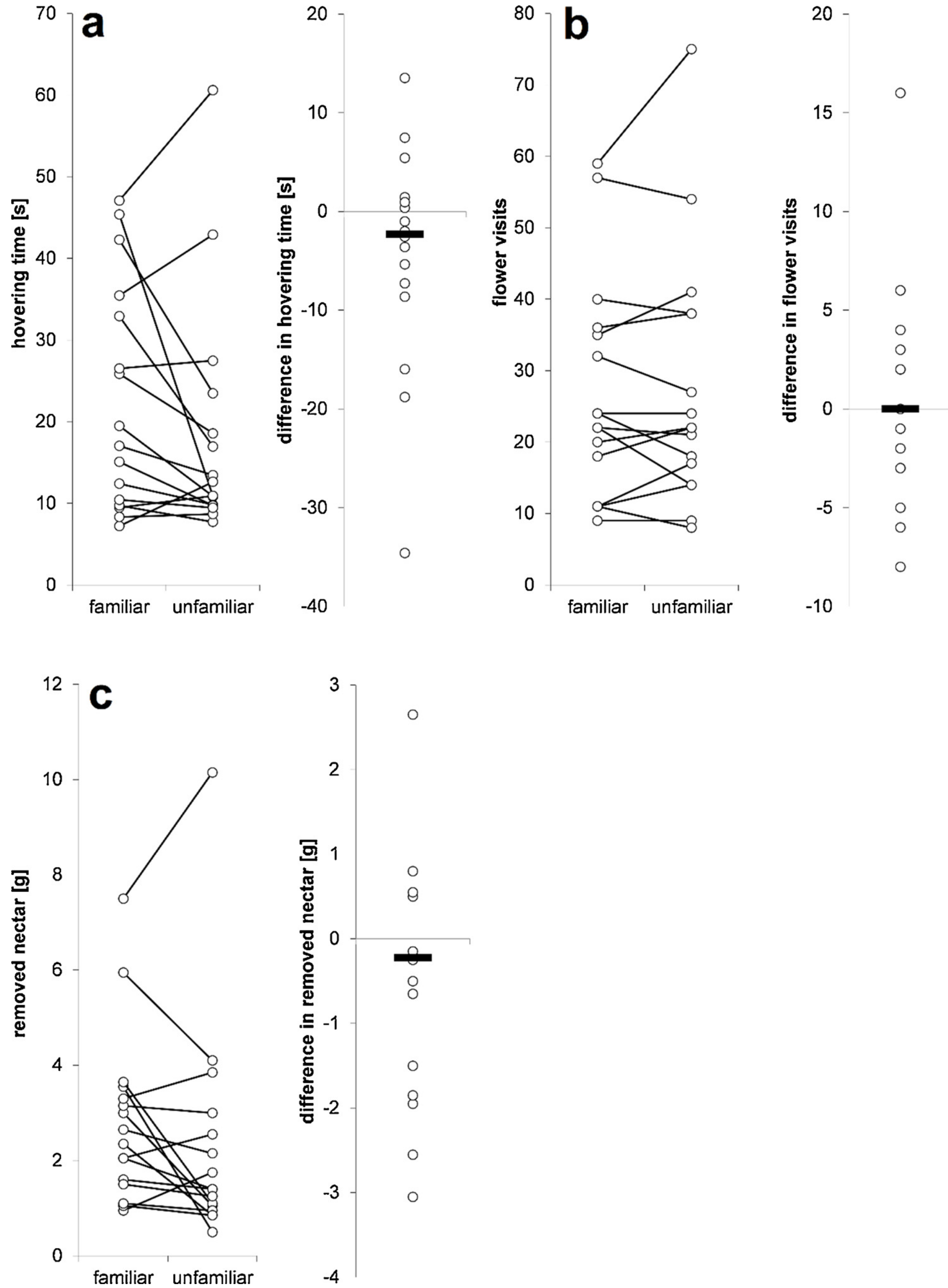

Fig. 2. Choice experiment. Pups (n = 16) showed no significant differences in their behaviour towards the familiar and unfamiliar flavoured nectar, neither in the total hovering time (a, paired t-test: $t = 1.55$, $df = 15$, $p = 0.14$), nor in the number of flower visits (b, paired t-test: $t = -0.48$, $df = 15$, $p = 0.64$) or the amount of removed nectar (c, paired t-test: $t = 1.51$, $df = 15$, $p = 0.15$). Pairwise differences between test situations are plotted on the right side of each plot. Respective median differences are indicated by solid lines.

amount of removed nectar was 5.1 ± 3.8 g (paired t-test: $t = 1.51$, $df = 15$, $p = 0.15$) (Fig. 2c), but nectar occasionally spilled out due to heavy wind gusts, resulting in only limited reliability for this measurement. Subsequently tested mothers did also show no preferences (hovering time: paired t-test: $t = 1.17$, $df = 15$, $p = 0.26$; number of flower visits: paired t-test: $t = 0.31$, $df = 15$, $p = 0.76$) (Supplementary Table S3).

Correspondingly, when analysing only the first 15 min of foraging, pups and mothers did not show an only initially present preference in the choice experiment, neither expressed in differences of the hovering time (pups: Wilcoxon signed-rank test: $V = 83$, $n = 16$, $p = 0.46$; mothers: paired t-test: $t = 0.92$, $df = 15$, $p = 0.37$), nor in differences in the number of flower visits (pups: paired t-test: $t = 0.24$, $df = 15$, $p = 0.81$; mothers: paired t-test: $t = 0.29$, $df = 15$, p-value = 0.78).

Data on pup development during husbandry are provided in Supporting Information S5.

3.3. Additional behavioural observations on mouth-to-mouth feeding behaviour

During a total recording time of 22 h over five consecutive nights in 2015, three observed mother-pup pairs showed three main social interactions: breastfeeding, maternal grooming and mouth-to-mouth feeding behaviour. We observed a total number of 29 mouth-to-mouth feeding events with a considerably varying duration from 1 s up to 145 s (median: 9 s). While breastfeeding and grooming was regularly performed in all three mother-pup pairs, mouth-to-mouth feeding behaviour was predominantly (27 of 29 records) observed in the pair with the oldest pup, which became volant five days after terminating behavioural observations. While feeding, pups flipped their tongues rapidly in and out of the slightly opened mouth of their mother, often using forearms and thumbs to adhere to the mother and to manipulate her position. Pups inserted their tongue mostly laterally into the mothers' mouth, sometimes resulting in the tip flipping out at the contralateral side (Fig. 1; Supplementary Videos 1, 2). Mouth-to-mouth feeding events were either observed immediately after mothers returned from a foraging flight back to the roost (16 of 29 records) (Supplementary Video 1), or subsequently after breastfeeding (13 of 29 records) (Supplementary Video 2). Behaviour after mouth-to-mouth feeding was either breastfeeding (20 of 29 records) or another maternal foraging flight (9 of 29 records). Mother-pup social interactions were mainly conducted within the artificial roost, but mothers occasionally took pups along on foraging flights (attached to their body) or placed them somewhere else in the flight cage.

A behaviour closely resembling a mouth-to-mouth feeding event was observed in 2017 during daytime at 16:36 pm, and therefore many hours after the mother's last foraging flight, which makes the regurgitation of nectar highly unlikely. The already volant pup stopped breastfeeding and started licking at its mother's mouth for approximately two minutes. Hereby, it behaved similar to the pups that were observed feeding during the night. After terminating, it instantly continued breastfeeding at the other teat.

3.4. Data availability

The dataset collected and analysed during the current study is available from the corresponding author on reasonable request.

4. Discussion

4.1. Mouth-to-mouth feeding behaviour

Our study demonstrates that lactating female Pallas' long-tongued bats (*Glossophaga soricina*) use mouth-to-mouth feeding behaviour to provide floral nectar to their dependent, nursing pups. We therefore add the first nectarivorous species to the small list of frugivorous (*e.g.* Pierson and Rainey, 1992), sanguivorous (*e.g.* Delpietro and Russo, 2002) and predatory bats (*e.g.* Raghuram and Marimuhtu 2007) that were documented to incorporate sharing of primary food items into parental care. Despite the only anecdotal assessment of mouth-to-mouth feeding in some bat species, there seem to be differences in the temporal ontogenetic onset of this behaviour. Pups of the vampire bat *D. rotundus*, for instance, already start feeding on regurgitated blood when they are still breast-fed and not yet foraging (Schmidt, 1978), while mouth-to-mouth feeding in the predatory bats *Noctilio albiventris*, *Megaderma lyra* and *Micronyteris microtis* seems to be a behaviour whose onset is associated with weaning (Brown et al., 1983; Raghuram and Marimuthu, 2007; Geipel et al., 2013). Although our sample size of continuously observed mother-pup pairs is rather limited, there is no doubt that mouth-to-mouth feeding behaviour in *G. soricina* is already performed long before weaning and can be observed in pups that are not yet volant. While the two mother-pup pairs we observed prior to the verification experiment started mouth-to-mouth feeding at an age of 20 and 29 days, respectively, anecdotal observations of only 9 day old pups licking on their mothers' mouths indicate a certain intraspecific variability (Pink, 1996). This relatively early ontogenetic onset of mouth-to-mouth feeding behaviour in *G. soricina* might be facilitated due to the uniform, fluid consistency of their nectar diet. Unlike, for example, the morphologically extremely variable large insects (cf. Geipel et al., 2013), nectar is a liquid diet like breast milk and does not require sophisticated handling abilities or fully developed adult teeth. It is therefore more comparable to the fluid blood diet of vampire bats, which seem to exhibit a relatively early ontogenetic onset of mouth-to-mouth feeding as well, starting months before weaning (Schmidt, 1978). Our behavioural observations further suggest certain variability in onset, frequency and duration of mouth-to-mouth feeding in *G. soricina*. In contrast to the provision with breast milk, mouth-to-mouth feeding of primary food might be facultative, and its performance is potentially influenced by variable factors like the nutritional state of the involved individuals or the amount of secreted breast milk. Even though we cannot reveal whether mouth-to-mouth feeding events were requested by pups due to an inconspicuous begging behaviour, for instance by licking at their mothers' lips (for soliciting behaviour in vampire bats see Wilkinson, 1990), or proffered by mothers, we observed at least a very active role of feeding pups which used their thumbs to adhere to the mother and to manipulate the position of her head while licking nectar out of her mouth. The tongue flipping technique was similar to the behaviour used by adult bats when extracting nectar from a flower, but the licking behaviour of pups frequently lasted much longer (Tschapka et al., 2015). Comparable, young vampire bats were observed licking for up to 10 min at the adult's mouth (Schmidt, 1978).

Mothers seemed to use regurgitation when providing nectar to their pups. During our behavioural observations, mouth-to-mouth feeding was not exclusively performed right after maternal foraging flights, but also subsequently after phases of breastfeeding during which mothers used their tongues for grooming the pup and themselves. Comparable observations were made by Pink (1996). Hence, it seems unlikely that mothers had stored the respective nectar in the mouth all the time, and we assume that mothers regurgitated previously swallowed nectar when providing it for mouth-to-mouth feeding, a technique also performed by vampire bats with their blood diet (*e.g.* Delpietro and Russo, 2002). The open mouth emission of echolocation calls in *G. soricina* should also impede transportation and storage of nectar inside the mouth cavity (Gessinger, 2016).

Mothers of *G. soricina* exhibit a behaviour that is conceivably beneficial for providing floral nectar to their pups: In contrast to other flower-visiting bat species such as lesser long-nosed bats (*Leptonycteris yerbabuenae)*, they do not leave their non-volant pups behind inside the day-roost when foraging, but rather take them outside in order to place them inconspicuously in the understory vegetation (Pink, 1996 and personal observation AR, MT). Thus, by hiding pups in the vicinity of their current foraging area, mothers should be able to visit and feed them on a regular basis over night.

4.2. Benefits of mouth-to-mouth feeding behaviour and potential implications for vertical social learning

In general, this pre-weaning addition of primary food items like floral nectar can offer various advantages for rearing offspring. It provides energetic benefits for mothers by evading the circuitous route via internal storages and secretion of milk. This benefit might be particularly significant for flying animals like bats, where carrying of energy storages goes along with higher energetic costs than compared to ground-dwelling mammals (Dall and Boyd, 2004). For *G. soricina*, a direct provisioning with regurgitated nectar should be especially advantageous once energy demands of pups rise due to increased physical activities such as wing flapping exercises (Pink, 1996). We originally postulated maternal-mouth-to-mouth feeding to be a valuable opportunity for young bats to socially learn about their parents' dietary preferences and with that about the characteristics of palatable food in general (Galef and Giraldeau, 2001; Galef and Laland, 2005). However, even though pups had ample opportunities to learn about the experimentally induced dietary preference of their mothers and its special characteristics, either directly via mouth-to-mouth feeding, by using olfactory compounds from the fur or breath of mothers (cf. Ratcliffe and ter Hofstede, 2005), or even from the breast milk (cf. Galef and Clark, 1972), they did not prefer the maternally provided nectar over the unfamiliar alternative when foraging alone in the choice experiment. Even though this finding is restricted to a single experiment and should be considered with caution, it might be explained by the bats' ecology. Certainly, most of the documented cases of socially transmitted dietary preferences connected with parental food consumption or provisioning were documented in mammals with mainly opportunistic feeding habits, like for example in rodents and rabbits (*e.g.* Galef and Clark, 1971; Altbäcker et al., 1995; Post et al., 1998), meerkats (Thornton, 2008) or primates (van de Waal et al., 2013). But whereas mammals with opportunistic feeding habits feed on a variety of different food items among which they have to discriminate between palatable and toxic, or easy vs. difficult prey, juvenile flower-visiting bats like *G. soricina* pups might not be subjected to the same constraints. For example, the absence of toxic flowers and the comparatively simple diet of flower-visiting bats that is based on nectar and pollen of chiropterophilous plants with convergently evolved similar signals might have obviated the evolution of specific social learning strategies (Knudsen and Tollsten, 1995); maternal provisioning might probably help pups to recognize nectar as a food source in general. There is further some evidence that preferences for flowers and nectars with distinct chiropterophilous characteristics like sulphur-containing volatiles were genetically added to the bats' innate informational repertoire (von Helversen et al., 2000). A continued provisioning of milk or regurgitated nectar to already foraging pups might further compensate an initial lack of foraging success and enable pups to learn foraging on their own (cf. nutritional hypotheses in Brown et al., 2004).

Besides potential informational and energetic benefits, mouth-to-mouth feeding in *G. soricina* might potentially involve a variety of additional advantages. It could for example represent a cautious way to introduce pups to eating nectar and thus adapt the pups to digest and metabolize their adult diet, as it is discussed for vampire bats (Schmidt, 1978; Müller et al., 1980). It might further be an opportunity for pups to participate in the mother's gastric microbiome (Funkhouser and Bordenstein, 2013) or be a behavioural component to reinforce mother-pup bonding (Mogi et al., 2011). A clue for such an additional, non-nutritional meaning of mouth-to-mouth feeding behaviour in *G. soricina* is probably our anecdotal observation of a pup extensively licking at its mothers' mouth at a time when there was presumably no transfer of regurgitated nectar involved. Likewise, mouth-licking behaviours without provision of food are reported from several other mammals (*e.g.* McFadyen-Ketchum and Porter, 1989), and there is also anecdotal evidence of non-nutritional mouth licking behaviours in pups of other bat species (*e.g. Myotis nattereri*: Dietz et al., 2007; *Saccopteryx bilineata*: personal observation MK).

In summary, our study demonstrates that lactating *G. soricina* provide regurgitated floral nectar via mouth-to-mouth feeding behaviour to their nursing pups, but we are unable to support the hypothesis that parental provisioning helps young bats to learn about foraging by shaping their diet preferences. Nonetheless, there are several pending questions, particularly with regard to potentially associated non-nutritional effects and advantages, but also concerning the circumstances and extent under natural conditions. We are convinced that *G. soricina* and its conspicuous maternal mouth-to-mouth feeding behaviour could be an interesting model for studying parental food provisioning in mammals from different evolutionary, ecological and ethological perspectives.

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Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

All applicable international, national, and institutional guidelines for the care and use of animals were followed. Handling of animals was reduced to the necessary minimum and handling was always performed with respect to the avoidance of stress. Captivity and experiments had no noticeable negative effects on bats' health and all temporarily captive bats in Costa Rica were released after finishing the experiments. Permissions for the work in Costa Rica were granted by the Costa Rican government (permit numbers: ACG-PI-057-2014, ACG-PI-059-2015 and ACG-PI-055-2016).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2019.06.001.

References

Altbäcker, V., Hudson, R., Bilkó, Á, 1995. Rabbit-mothers' diet influences pups' later food choice. Ethol 99, 107–116.
Altringham, J.D., 1996. Bats Biology and Behaviour. Reprint 2001. Oxford University Press, New York.
Alvarez, J., Willing, M., Jones, K., Webster, D., 1991. *Glossophaga soricina*. Mamm Species 379, 1–7.
Brown, G.R., Almond, R.E.A., van Bergen, Y., 2004. Begging, stealing, and offering: food transfer in nonhuman primates. Adv. Stud. Behav. 34, 265–295.
Brown, P.E., Brown, T.W., Grinnell, A.D., 1983. Echolocation, development, and vocal communication in the lesser bulldog bat, *Noctilio albiventris*. Behav. Ecol. Sociobiol. (Print) 13, 287–298.
Clarin, T.M.A., Borissov, I., Page, R.A., Ratcliffe, J.M., Siemers, B.M., 2014. Social learning within and across species: information transfer in mouse-eared bats. Can. J. Zool. 92, 129–139.
Dall, S.R.X., Boyd, I.L., 2004. Evolution of mammals: lactation helps mothers to cope with unreliable food supplies. Proc. R Soc. B 271 (1552), 2049–2057.
Delpietro, H.A., Russo, R.G., 2002. Observations of the common vampire bat (*Desmodus rotundus*) and the hairy-legged vampire bat (*Diphylla ecaudata*) in captivity. Mamm. Biol. 67, 65–78.
Dietz, C., von Helversen, O., Nill, D., 2007. Handbuch der Fledermäuse Europas und Nordwestafrikas – Biologie. Kennzeichen, Gefährdung, Kosmos, Stuttgart, Germany.
Engler, S., Rose, A., Knörnschild, M., 2017. Isolation call ontogeny in bat pups (*Glossophaga soricina*). Behav. 154, 267–286.
Fox, J., Bouchet-Valat, M., 2017. Rcmdr: R Commander. R Package Version 2.4-1.
Funkhouser, L.J., Bordenstein, S.R., 2013. Mom knows best: the universality of maternal microbial transmission. PLoS Biol. 11, e1001631.
Galef, B.G., Clark, M.M., 1971. Social factors in the poison avoidance and feeding behavior of wild and domesticated rat pups. J. Comp. Physiol. Psychol. 75, 341–357.
Galef, B.G., Clark, M.M., 1972. Mother's milk and adult presence: two factors determining initial dietary selection by weanling rats. J. Comp. Physiol. Psychol. 78, 220–225.
Galef, B.G., Giraldeau, L.-A., 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim. Behav. 61, 3–15.
Galef, B.G., Laland, K.N., 2005. Social learning in animals: empirical studies and theoretical models. AIBS Bull. 55, 489–499.
Ganesh, A., Mukilan, M., Marimuthu, G., Rajan, K.E., 2016. A novel food preference in the greater short-nosed fruit bat, *Cynopterus sphinx*: mother-pup interaction a strategy for learning. Acta. Chiropterol 18, 193–198.
Geipel, I., Kalko, E.K.V., Wallmeyer, K., Knörnschild, M., 2013. Postweaning maternal food provisioning in a bat with a complex hunting strategy. Anim. Behav. 85, 1435–1441.
Gessinger, G., 2016. Oral Emission of Echolocation Calls in Phyllostomid Bats? Master

Thesis. Institute of Evolutionary Ecology and Conservation Genomics. Faculty of Natural Sciences. University of Ulm, Germany.
Harper, C.J., Swartz, S.M., Brainerd, E.L., 2013. Specialized bat tongue is a hemodynamic nectar mop. PNAS 110, 8852–8857.
Heithaus, E.R., Fleming, T.H., Opler, P.A., 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecol. 56, 841–854.
Holekamp, K.E., Smale, L., 1990. Provisioning and food sharing by lactating spotted hyenas, *Crocuta crocuta* (Mammalia: hyaenidae). Ethol. 86, 191–202.
Hoppitt, W., Laland, K.N., 2013. Social Learning: an Introduction to Mechanisms, Methods and Models. Princeton University Press, Princeton.
Jaeggi, A.V., Van Noordwijk, M.A., Van Schaik, C.P., 2008. Begging for information: mother-offspring food sharing among wild bornean orangutans. Am. J. Primatol. 70, 533–541.
Knudsen, J.T., Tollsten, L., 1995. Floral scent in bat-pollinated plants: a case of convergent evolution. Bot. J. Linn. Soc. 119, 45–57.
Kunz, T.H., Hood, W.R., 2000. Parental care and postnatal growth in the chiroptera. In: Crichton, E.G., Krutzsch, P.H. (Eds.), Reproductive Biology of Bats. Academic Press, London, pp. 415–468.
McFadyen-Ketchum, S.A., Porter, R.H., 1989. Transmission of food preferences in spiny mice (*Acomys cahirinus*) via nose-mouth interaction between mothers and weanlings. Behav. Ecol. Sociobiol. (Print) 24, 59–62.
Mogi, K., Nagasawa, M., Kikusui, T., 2011. Developmental consequences and biological significance of mother-infant bonding. Prog. Neuropsychopharmacol. Biol. Psychiatry 35, 1232–1241.
Müller, H.E., Pinus, M., Schmidt, U., 1980. *Aeromonas hydrophila* als normaler Darmkeim bei Vampirfledermäusen (*Desmodus rotundus*). Zent. Für Veterinärmedizin Reihe. B 27, 419–424.
O'Mara, M.T., Dechmann, D.K.N., Page, R.A., 2014. Frugivorous bats evaluate the quality of social information when choosing novel foods. Behav. Ecol. 25, 1233–1239.
Pierson, E.D., Rainey, W.E., 1992. The biology of flying foxes of the genus *pteropus*: a review. In: In: Wilson, D.E., Graham, G.L. (Eds.), Pacific Island Flying Foxes: Proceedings of an International Conservation Conference, vol. 90. pp. 1–17 Biol Rep.
Pink, B., 1996. Fortpflanzungs- Und Sozialverhalten Der Blütenbesuchenden Fledermausart *Glossophaga soricina* (Phyllostomidae; Glossophaginae). Diploma Thesis. Institut für Zoologie II. Friedrich-Alexander-Universität, Erlangen-Nürnberg.
Post, D.M., McDonald, M.W., Reichman, O.J., 1998. Influence of maternal diet and perishability on caching and consumption behavior of juvenile eastern woodrats. J. Mamm. 79, 156–162.
R Core Team, 2017. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Raghuram, H., Marimuthu, G., 2007. Maternal feeding of offspring with vertebrate prey in captive Indian false vampire bat, *Megaderma lyra*. Acta Chiropterol 9, 437–443.
Raguso, R.A., 2004. Why are some floral nectars scented? Ecology 85, 1486–1494.
Ratcliffe, J.M., Ter Hofstede, H.M., 2005. Roosts as information centres: social learning of food preferences in bats. Biol. Lett. 1, 72–74.
Rose, A., Kolar, M., Tschapka, M., Knörnschild, M., 2016. Learning where to feed: the use of social information in flower-visiting Pallas' long-tongued bats (*Glossophaga soricina*). Anim. Cogn. 19, 251–262.
Ruczynski, I., Siemers, B.M., 2011. Hibernation does not affect memory retention in bats. Biol. Lett. 7, 153–155.
Schmidt, U., 1978. Vampirfledermäuse Familie Desmodontidae (Chiroptera). A. Ziemsen verlag. Wittenberg Lutherstadt.
Thornton, A., 2008. Social learning about novel foods in young meerkats. Anim. Behav. 76, 1411–1421.
Tschapka, M., Dressler, S., 2002. Chiropterophily: on bat-flowers and flower-bats. Curtis's Bot. Mag. 19, 114–125.
Tschapka, M., Gonzalez-Terrazas, T.P., Knörnschild, M., 2015. Nectar uptake in bats using a pumping-tongue mechanism. Sci. Adv. 1, e1500525.
van de Waal, E., Borgeaud, C., Whiten, A., 2013. Potent social learning and conformity shape a wild primate's foraging decisions. Science 340, 483–485.
von Helversen, O., Winkler, L., Bestmann, H., 2000. Sulphur-containing "perfumes" attract flower-visiting bats. J. Comp. Physiol. A 186, 143–153.
Weissgerber, T.L., Milic, N.M., Winham, S.J., Garovic, V.D., 2015. Beyond bar and line graphs: time for a new data presentation paradigm. PLoS Biol. 13, e1002128.
Wilkinson, G.S., 1990. Food sharing in vampire bats. Sci. Am. 262, 76–82.
Wilkinson, G.S., Boughman, J.W., 1999. Social influences on foraging in bats. In: Box, H.O., Gibson, K.R. (Eds.), Mammalian Social Learning: Comparative and Ecological Perspectives. Cambridge University Press, Cambridge, pp. 189–204.
Wright, G.S., Wilkinson, G.S., Moss, C.F., 2011. Social learning of a novel foraging task by big brown bats, *Eptesicus fuscus*. Anim. Behav. 82, 1075–1083.
Wright, G.S., 2016. Social learning and information transfer in bats: conspecific influence regarding roosts, calls, and food. In: Ortega, J. (Ed.), Sociality in Bats. Springer International Publishing Switzerland, pp. 211–230.