Isotopic Data Do Not Support Food Sharing Within Large Networks of Female Vampire Bats (*Desmodus rotundus*)

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Abstract

Reciprocal altruism is considered to be particularly stable when occurring in small networks. Using a stable isotope approach, we tested in colonies of vampire bats (*Desmodus rotundus*) whether food sharing occurs among few or many females; vampires are known to regurgitate recently ingested blood for starving conspecifics. Accordingly, the isotopic signatures of vampires depend not only on individual prey choice but also on the extent of food sharing among isotopically contrasting conspecifics. By measuring the stable carbon isotope ratio in tissues with varying isotopic retention in individual vampires (blood: approx. 2 wk; wing membrane tissue: approx. 2 mo; fur: >6 mo), we estimated the variation in the percentages of carbon derived from pasture (via blood from cattle and horses). We expected to find narrow ranges of percentages in individual vampires, because we anticipated food sharing only within small female networks if food sharing happened at all. Overall, vampire bats obtained $79.2 \pm 12.3\%$ of carbon from grazers. The range of percentages was small within the majority of individuals in relation to that across all individuals, suggesting that most vampires were isotopic specialists. We expected females to be more isotopically generalistic than males, as food sharing was observed to occur more often between females than between males. Indeed, stable isotope evidence suggested that more females obtained carbon from isotopically contrasting sources than males. This pattern is consistent with food sharing in small groups of female vampires, provided that food sharing occurred at all.

Introduction

Besides kin selection, altruistic behaviour may evolve if the donor of help can expect to get help in return (Trivers 1971; but see Clutton-Brock 2009). This help can either be reciprocated by the receiver (direct reciprocity; Axelrod & Hamilton 1981) or by a third individual that has witnessed the altruistic act (indirect reciprocity; Nowak & Sigmund 1998). However, both direct and indirect reciprocity require the individuals to memorise the actions of their conspecifics and to act accordingly. A third, simpler mechanism that does not involve higher cognitive abilities is provided by generalised reciprocity, where an individual copies the cooperative behaviour it experiences. Despite the fact that altruistic individuals are vulnerable to exploitation by cheaters that gain benefits from cooperators, but refuse to reciprocate the help, theoretical models show that this form of reciprocity can evolve under a wide range of conditions, for instance, in small groups (Boyd & Richerson 1988; Hamilton & Taborsky 2005; Pfeiffer et al. 2005; Nowak & Roch 2007; Iwagami & Masuda 2010), in viscous or assorted populations (Rankin & Taborsky 2009) or even without any assumptions about the interaction structure between group members (Barta et al. 2011).

Although reciprocal altruism has already been confirmed for a variety of captive animals such as rats and primates (Hemelrijk & Ek 1991; Hauser et al. 2003; Rutte & Taborsky 2007, 2008), evidence from natural populations is rare; one prominent example being blood sharing in the common vampire bats, *Desmodus rotundus* (Wilkinson 1984). Vampires feed mostly on blood from large wild mammals, such as tapirs and peccaries, or from livestock, such as cattle and horses (Greenhall & Schmidt 1988; Delpietro et al. 1992; Voigt & Kelm 2006). Individual vampires are frequently at risk of starvation, because successful foraging is unlikely (Wilkinson 1984). Therefore, starving individuals depend on blood regurgitated and shared by social partners of their daytime roosts. Sharing of regurgitated blood has most often been observed in vampires between mother–offspring dyads (77 of 110 observations during 400 h of observation; Wilkinson 1984). In the majority of other cases, donors and recipients were either related or frequently roosted together in case of unrelated dyads (Wilkinson 1984). In general, vampire bats could interact and share food with many colony members. However, besides limited behavioural observations, little is known about whether or not vampires share food with many colony members. Frequent food sharing between few unrelated individuals would confirm vampire bats to apply direct reciprocity, while blood sharing among many colony members would bear evidence for generalised reciprocity.

We used an isotopic approach to assess the extent of food sharing in two colonies of *D. rotundus* in Costa Rica. A previous study at the same site indicated that vampires mostly feed on blood from grazing livestock, that is, they are members of a food web that is based on plants with a C4 photosynthetic pathway of CO_2 fixation (Voigt & Kelm 2006). Our study site, La Selva Biological Station (LSBS), is almost completely surrounded by pasture and farmland (Hartshorn & Hammel 1994). Thus, vampire bats roosting in hollow trees within the boundaries of the reserve have the choice between rainforest mammals of the pristine forest, for example, collared peccary (*Tayassu tayacu*), or livestock, such as domestic cattle (*Bos taurus*) and horses (*Equus caballus*). As collared peccary feed mostly on seeds and roots of rainforest plants, they should carry a carbon signature of plants with a predominant C3 photosynthetic pathway of CO_2 fixation (i.e. dicotyledons), whereas both cattle and horse feed predominantly on C4 grass of the surrounding pasture (i.e. monocotyledons). As the stable carbon isotope composition of

the potential vampire prey is variable, one can discern the relative contribution of the isotopically contrasting prey categories to the vampires' diet by looking at the stable carbon isotope ratio of vampires, that is, the analysis of a single tissue provides an integrative and quantitative retrospective view on a consumer's diet during the period when tissue components were replaced. This isotopic approach can be refined by looking at several tissues within the same individual, because tissues differ in isotopic retention times (e.g. Tieszen et al. 1983). Therefore, it is possible to assess the degree of individual specialisation based on the within-individual variation in stable isotope ratios in several tissues (Newsome et al. 2009; Matich et al. 2011; see Fig. 1). In the remainder of the text, we will define a dietary specialist as an animal whose dietary niche is substantially smaller than the total niche width, here defined as the between-individual variation in dietary choice (Bolnick et al. 2003, 2007).

In our study, we looked at the ranges of stable isotope ratios in several tissues of adult vampires as a proxy for the extent of isotopic specialisation and food sharing among colony members (see Fig. 1). We analysed stable carbon and nitrogen isotope ratios in three tissues that varied in isotopic retention: (1) whole blood as a short-term (approx. 2 wk: Voigt et al. 2003; Míron et al. 2006), (2) wing membrane tissue as a mid-term (approx. 2 mo: Voigt et al. 2003) and (3) fur as a long-term integrator (>6 mo: Voigt et al. 2003). We expected vampires to be dietary specialists on livestock, because vampire bats feed usually on the most abundant large mammals, such as livestock (Voigt & Kelm 2006). In the remainder of the text, we will use the term isotopic generalist/specialist instead of dietary generalist/specialist, because the isotopic signature of vampire bats is not only indicative of their own dietary choice but also of the likelihood of obtaining regurgitated blood from other vampire bats (see Martínez del Rio et al. 2009 for the concept of isotopic specialisation). Isotopic specialist vampire bats should have a similar stable isotope ratio in all of their body tissues, whereas isotopic generalists should have varying stable isotope ratios in their body tissues given that they receive blood carbon from isotopically contrasting prey and conspecifics.

We hypothesised that – if blood sharing occurs at all – blood is not shared among all members of a colony. Accordingly, we predicted that the within-individual variation of isotopic composition should be small in relation to the between-individual variation, if vampires are dietary specialists and share either no
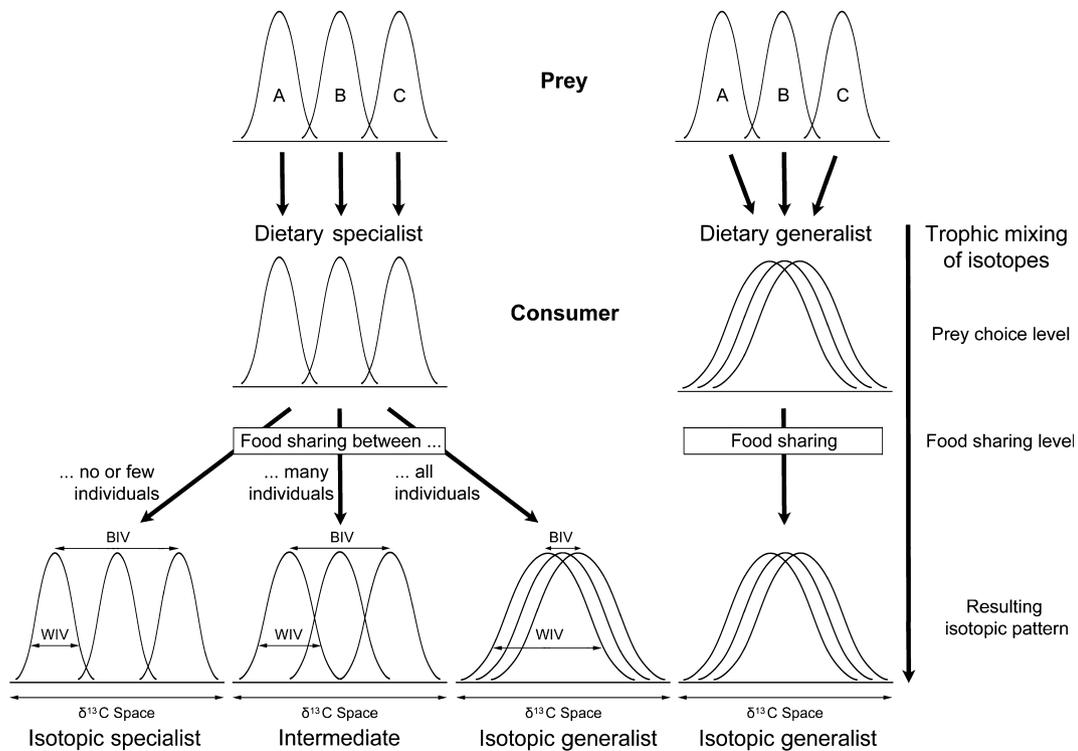
Fig. 1: Schematic description of how food sharing may alter the isotopic signature of individual vampire bats when involved in reciprocal food sharing. On the prey-choice level, vampire bats are *dietary specialists* if they feed only on a few prey individuals (A, B, C), and they are *dietary generalists* if they feed on a variety of prey individuals. On the food-sharing level, dietary generalists will have variable stable isotope ratios in tissues, irrespective of whether or not they are involved in food sharing. Thus, dietary generalists are always *isotopic generalists*. In dietary specialists, reciprocal food sharing may lead to isotopic variation in the body according to the level of food sharing. If food is frequently shared within a network of dietary specialists, vampires become *isotopic generalists*. However, when food is shared only with a small subset of dietary specialists or not shared at all, then vampire bats are *isotopic specialists*. With increasing numbers of vampire bats involved in reciprocal food sharing, the within-individual variation (WIV) of stable isotope ratios will increase, and the between-individual variation (BIV) will decrease.

blood or share blood only with few colony members (Fig. 1). As mostly female vampire bats have been observed to engage in reciprocal altruism, we predicted females to be more isotopic generalists than males.

Methods

Field Work

We studied common vampire bats, *D. rotundus* in the rainforest adjacent to LSBS in Costa Rica (10°25′, 84°00′W) in December 2009. LSBS lies within the Caribbean lowlands of Costa Rica (Heredia Province) and comprises 1615 ha of privately owned tropical rain forest with adjacent pastures used for livestock farming. On 3rd and 12th of December, we captured a total of 34 adult vampire bats (12 males, 22 females) in front of two daytime roosts by setting up one or two mist nets (6–9 m length, 2.5 m height; Ecotone, Gdynia, Poland) between 1800 and 2000 h.

Roost A comprised <30 individuals and roost B more than 100 individuals (C.C. Voigt, pers. obs.). None of the captured females was pregnant or lactating.

Immediately after capture, we collected approx. 50 μl of blood from each vampire by puncturing the antebrachial wing vein with a sterile needle (Sterican 0.6 mm × 25 mm; Braun, Melsungen, Germany) and by transferring droplets of blood with a Na-heparinized microhaematocrit tube (Hecht, Sondheim, Germany) into Eppendorf tubes. Afterwards, we cut some hair with small scissors from the dorsal interspacular region. We then took a biopsy of the wing membrane tissue from each wing with sterile biopsy punches (3 mm diameter). Blood, fur and wing punches were stored in three separate plastic tubes for each individual before drying samples in a drying oven at 40°C until constant mass. All bats were released at the site of capture. Based on the wing punches of bats, we ensured that samples were not collected repeatedly from the same animals.

We collected hair of three potential host species known from the literature to be commonly approached by vampire bats: domestic cattle (*B. taurus taurus*; n = 11) and horses (*E. caballus*; n = 10) from farmland adjacent to LSBS and of collared peccaries (*Tayassu tajacu*; n = 7) within the boundaries of the forest reserve of LSBS. From each cattle and horse, we collected mane (horses) and dorsal fur (cattle) by cutting off some hair with scissors. As we could not pluck hairs from peccaries directly, we used an extendable 4 m pole with adhesive tape at its tip to brush off some dorsal fur. Hair samples were stored separately for each individual in plastic tubes. All samples were shipped to the Leibniz Institute for Zoo and Wildlife Research (IZW) in Berlin (Germany) for isotopic analysis. All hair samples were cleaned from external contaminants by washing them in a 2:1 chloroform–methanol solution.

Stable Isotope Analyses

Stable carbon isotope ratios of tissue samples were analysed at the stable isotope laboratory of the IZW using an isotope ratio mass spectrometer (Delta V Advantage; Thermo Finnigan, Bremen, Germany) connected to an elemental analyser (Flash elemental analyser; Thermo Finnigan) via a ConFlo III (Thermo Finnigan). We weighed 0.4 mg of material into tin capsules that were later combusted under chemically pure helium gas in the elemental analyser. By convention, we expressed stable isotope ratios using the δ notation in relation to an international standard (Vienna-PeeDee Belemnite for carbon and air N_2 for nitrogen) and used the unit of measurement parts per mil (‰) deviations from the respective standards. To calculate δ values, we used the following equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$; where X is the heavy isotope of either carbon (^{13}C) or nitrogen (^{15}N), and R is ratio of heavy to light isotopes ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). The analytical precision was better than 0.13‰ (one standard deviation) for carbon and 0.14‰ for nitrogen isotopes based on repeated measures of internal protein standards.

To test whether $\delta^{13}C$ of the three tissues (blood, fur and wing punch) differed within individual vampire bats, we used a repeated measures analysis of variance (ANOVA) followed by pairwise Tukey–Kramer tests. We used one-way ANOVA to test whether potential prey differed in $\delta^{13}C$ and $\delta^{15}N$. All tests were conducted two tailed, assuming $\alpha = 5\%$ and by using SYSTAT (version 11.00.01; SPSS, Chicago, IL, USA). Values are presented as $\bar{x} \pm$ one standard deviation, if not stated otherwise.

Isotopic Specialisation of Vampire Bats

To assess host specificity of vampire bats, we studied the within-individual variation in dietary choice based on tissue stable isotope ratios. As consumer tissues differ systematically in stable isotope ratios from the consumer's diet, we corrected stable isotope ratios of consumer tissue by subtracting tissue-specific discrimination factors to infer the dietary stable isotope ratios (Martínez del Rio et al. 2009). We lacked discrimination factors for blood, wing membrane tissue and fur of vampire bats and therefore used the discrimination factors of a similar sized, related bat, *Leptonycteris yerbabuena*, as reference (Voigt et al. 2009). Discrimination of ^{13}C in relation to the diet averaged 1.8 ± 0.2‰, 2.6 ± 0.6‰ and 2.7 ± 0.2‰ for blood, wing membrane tissue and hair, respectively, and discrimination of ^{15}N in relation to the diet averaged 3.5 ± 1.4‰, 4.3 ± 1.3‰ and 3.3 ± 1.5‰ for blood, wing membrane tissue and hair, respectively. A recent study showed that insectivorous *Myotis* species had slightly different discrimination factors for hair: 3.6‰ and 3.5‰ for ^{13}C in relation to the diet and 2.6‰ and 3.2‰ for ^{15}N in relation to the diet (Siemers et al. 2011). Nonetheless, we considered the discrimination factors of *L. yerbabuenae* as more representative for *D. rotundus* because of three reasons: First, nectar-feeding *Leptonycteris* and sanguinivorous *Desmodus* belong to the same family, Phyllostomidae and *Myotis* and *Desmodus* to different families (Vespertilionidae and Phyllostomidae), and we think it is more appropriate to use data from closely related species than from distantly related species. Second, bats of the genus *Leptonycteris* are a generalist nectar feeder that assimilates nitrogen mostly from dietary animal proteins. Indeed, *L. curasoae* from Venezuela have nitrogen isotope ratios similar to insectivorous bats (Nasser et al. 1998), which highlights that this species is probably on the same trophic level as animalivorous bats, at least with respect to the consumption of proteins. Third, we lack discrimination factors for blood and wing tissue membrane in *Myotis*, and it is more consistent to use tissue-specific fractionation factors from a single species, that is, *Leptonycteris*, to control for the effect of trophic discrimination in a target species. Using trophic fractionation factors from various species may add taxonomic effects to the data

correction when tissue-specific values are corrected by fractionation factors derived from several species.

We converted δ values into percentage values of carbon derived from the C4 food web using a two source linear mixing model. Mixing models extrapolate the contribution of different dietary sources to an animal tissue based on $\delta^{13}C$ of consumer tissues and on $\delta^{13}C$ of the two food sources (Martínez del Rio et al. 2009). In the case of vampires, we estimated the contribution of vampire tissue from the two sources at the isotopic extreme, that is, the C4 food web as indicated by mean $\delta^{13}C$ of horses and the C3 food web as indicated by the mean $\delta^{13}C$ of collared peccaries. We used IsoError to calculate the relative contribution of C3 and C4 food web to the diet of vampire bats (Phillips & Gregg 2001, 2003; Phillips et al. 2005). This model is based on $\delta^{13}C$ of individual *D. rotundus* that were corrected for trophic discrimination of ^{13}C in relation to the diet ($\delta^{13}C_{corr}$). We assumed blood of the three potential hosts to be similar in carbon concentration and therefore did not perform a concentration-dependant mixing model. We used the range of the three percentage values obtained for each individual as a proxy of individual specialisation. Differences in individual specialisation between males and females were tested with a two-tailed Mann–Whitney U-test. For statistical tests, we used SYSTAT (version 11.00.01; SPSS).

Results

Stable Isotope Ratios of Vampire Bats and Their Potential Prey

We captured 15 adult vampire bats (seven males and eight females) at daytime roost A and 19 adult vampire bats (five males and 14 females) at roost B. $\delta^{13}C$ of bats differed between blood ($-13.8 \pm 2.3‰$), wing tissue ($-12.2 \pm 2.0‰$) and fur ($-11.8 \pm 1.8‰$; $F_{2,101} = 30.6$, p < 0.001; Fig. 2c). Pairwise comparisons revealed that blood was more depleted in ^{13}C than wing tissue ($q = 8.3$, p < 0.001) and fur ($q = 10.5$, p < 0.001). However, wing tissue and fur did not deviate in $\delta^{13}C$ ($q = 2.2$, p > 0.05). Also, $\delta^{15}N$ differed among blood ($9.9 \pm 0.9‰$), wing tissue ($12.4 \pm 1.1‰$) and fur ($11.7 \pm 1.2‰$; $F_{2,101} = 107$; p < 0.0001; Fig. 2d). Blood was more depleted in ^{15}N than wing tissue ($q = 20.1$, p < 0.001) and fur ($q = 14.5$, p < 0.001), and fur was more depleted in ^{15}N than wing tissue ($q = 5.6$, p < 0.001).

The potential prey species of the local vampire bat populations differed in $\delta^{13}C$ ($F_{2,27} = 275$; p < 0.0001; Fig. 2a). Fur from collared peccaries ($-26.9 \pm 0.3‰$) was more depleted in ^{13}C by 10.2‰ than that of cattle (-16.7 ± 2.0; $q = 23$, p < 0.001) and by 15.1‰ than that of horses ($-11.8 \pm 0.66‰$; $q = 33$, p < 0.001). Fur of cattle was more depleted in ^{13}C by 4.9‰ than fur of horses ($q = 12.1$, p < 0.001).
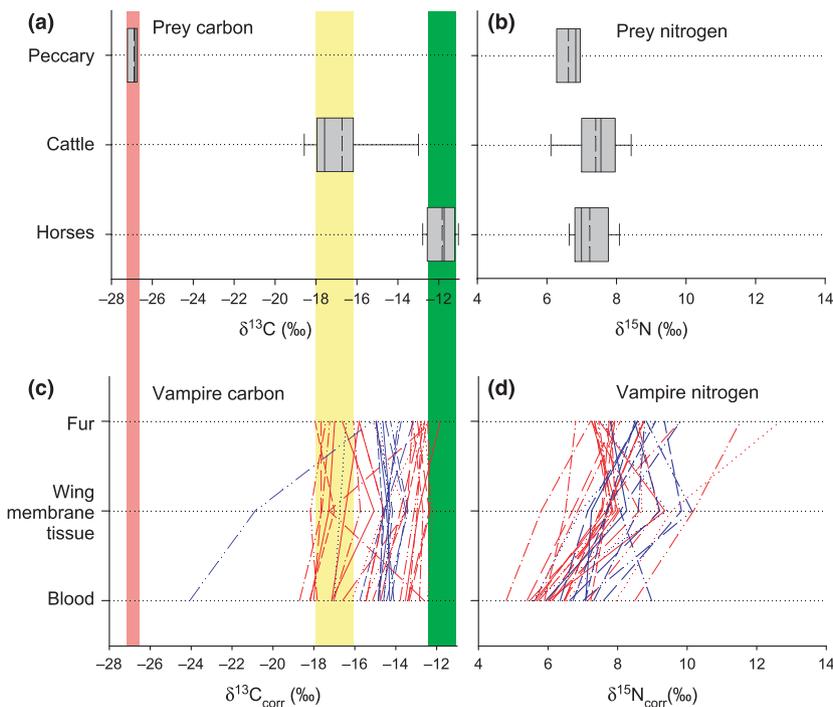

Fig. 2: Stable carbon isotope ratios ($\delta^{13}C$; ‰) and nitrogen isotope ratios ($\delta^{15}N$; ‰) of potential prey for vampire bats (domestic horses, domestic cattle and free-ranging white-collared peccaries; a, b). Box margins in (a) and (b) indicate the 25 and 75 percentiles, whiskers the 5 and 95 percentiles, the solid lines within the boxes the $\bar{x}$ and the dashed lines within the boxes the $\tilde{x}$. Stable carbon isotope ratios ($\delta^{13}C_{corr}$; ‰) and nitrogen isotope ratios ($\delta^{15}N_{corr}$; ‰) of vampire bats corrected for trophic enrichment in ^{13}C and ^{15}N, respectively (c, d). Connecting lines indicate samples from the same individual (fur, wing membrane tissue and blood). Female bats are indicated by red lines and males by blue lines.

δ^{13}C of the three potential prey species indicated that horses belonged to the C4 food web and collared peccaries to the C3 food web, whereas cattle was an intermediate consumer of both food webs. δ^{15}N differed among potential prey groups as well ($F_{2,27}$ = 3.5, p = 0.045; Fig. 2b). According to Tukey–Kramer tests, fur of cattle (7.4 ± 0.8‰) was more enriched in ^{15}N by 0.8‰ than fur of white-collared peccaries (6.6 ± 0.4‰; q = 3.7, p < 0.05), whereas fur of horses (7.3 ± 0.5‰) deviated in nitrogen isotope composition neither from that of cattle (q = 0.9, p > 0.05) nor from that of collared peccary (q = 2.8, p > 0.05).

Dietary Choice and Host Specificity of Vampire Bats

We found two major isotopic food webs for the local vampire bat population in the area of LSBS: pasture dominated by C4 grass as indicated by the isotopic signature of horses and rainforest dominated by C3 dicotyledons as indicated by the isotopic signature of collared peccaries. On average, the local vampire bat population obtained 79.2 ± 12.3% of their carbon from the C4 food web via horses and cattle. We estimated individual host specificity by calculating the range (minimum – maximum) of percentages of carbon derived from the C4 food web as estimated by the stable carbon isotope ratios of the three tissues. On the individual level (within-individual variation), ranges of percentage values averaged 10.8%. On the species level (across all individuals), range values equalled 50.5% for the study population of vampire bats. Thus, individual ranges were only about one-fifth of the range values of the study population, indicating that vampires are rather specialists than generalists. Thirty of 34 vampire bats exhibited ranges lower than 20% (Fig. 3). Only four vampire bats exhibited higher ranges, suggesting regular host switching or blood sharing among vampire bats with contrasting dietary preferences. One of the four vampire bats was a male that recently switched to a C3-dominated food source (Fig. 2c). We found a non-significant trend for a difference in host specificity between males and females (Mann–Whitney U-test: n_1 = 22, n_2 = 12; U = 83; U′ = 181, p = 0.080; Fig. 3).

Discussion

We used an isotopic approach to assess whether vampire bats engage frequently in sharing of regurgitated blood among colony members. In general, we found that vampires of our study population
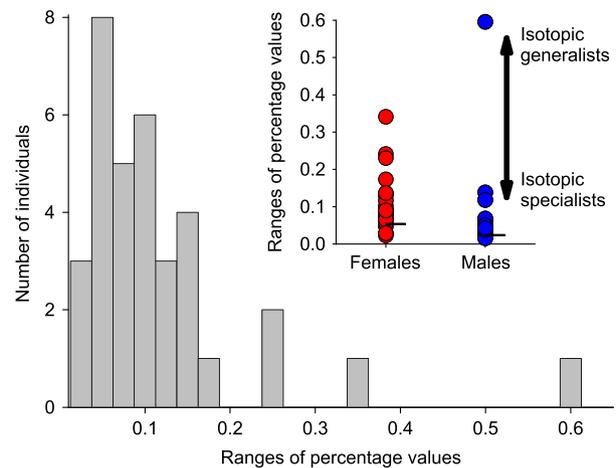

Fig. 3: Frequency distribution of ranges (minimum – maximum) of the relative contribution of carbon from the C4 food web to individual vampire diets. The inserted graph shows individual range values for female (red circles) and male vampire bats (blue circles). The smaller the individual range value, the more specialised is a vampire with respect to the origin of stable carbon isotopes. The $\bar{x}$ is indicated in each sex category by a short horizontal line.

were isotopic specialists, that is, the within-individual variation (approx. 10%) was much lower than the between-individual variation (approx. 50%) of the percentage contribution of blood from the C4 food web to vampire diets. We found a trend that females were more isotopic generalists than males. The results of our study are in line with the notion that food sharing occurs mostly within small networks of female vampires, but not regularly among males or between the sexes, or among large networks of female vampires. Indeed, without previous reports of vampires sharing blood, the results at hand may alternatively indicate that no reciprocal food sharing occurred in this system. However, Wilkinson (1984) made over 100 observations of vampires exchanging regurgitated blood with other colony members. Combining the information of Wilkinson's study with the data of the present study suggests that female vampire bats donate to and receive blood from small subsets of females only. This also meets the theoretical prediction that reciprocal altruism is most likely to evolve if an individual repeatedly interacts with a small network of individuals (Boyd & Richerson 1988; Pfeiffer et al. 2005). Like in some primates, related and unrelated female vampire bats probably form long-term relationships and restrict food sharing to these selected social partners (primates: Packer 1977; Seyfarth & Cheney 1984). Therefore, female vampires seem to

apply direct rather than generalised reciprocity when sharing blood.

When comparing male and female vampire bats with respect to their isotopic specialisation, we found a trend that males were more isotopic specialists than females. There is no reason for an *a priori* assumption that females have more generalist dietary habits than males. For example, nutritional content of blood is very similar in the potential prey types (Voigt & Kelm 2006). Also, behavioural observations confirm that mostly females engage in reciprocal food sharing with their offspring (Wilkinson 1984). In addition, only females have so far been observed to form long-term associations (Wilkinson 1984, 1985a,b). Thus, our current isotopic evidence for food sharing among females is in line with previous direct observations. However, our isotopic evidence may have been confounded by maternal support, that is, food sharing between mother and offspring dyads. Female vampire bats feed their young – both males and females – with regurgitated blood for an average of 348 d (Delpietro & Russo 2002). In addition, young vampire bats accompany their mothers during first foraging flights (Greenhall & Schmidt 1988). Thus, mother and offspring may share a similar isotopic signature, even when the offspring reached maturity. Indeed, we could not distinguish between adult vampire bats and those vampire bats with a fully developed skeleton and adult size that were dependant on their mother. Thus, we cannot rule out the possibility that we falsely assigned (male) vampire bats into the category of adult and independent bats, even though they still depended on regurgitated blood from their mother. This would have hampered our ability to detect gender-specific differences in isotopic specialisation. However, as our data suggest such differences, maternal effects on the isotopic signatures of the studied animals were probably absent or negligible.

We included only three potential prey types in our study, even though vampires are known to feed on a variety of other mammals as well. However, almost all other potential prey types were absent, rare or not accessible at night. For example, even though one of us (CCV) has been working at LSBS for more than 15 yr, he could at no point detect tapirs in the forest surrounding of the station. Vampire bats also have no access to many of the medium-sized mammals such as diurnal Agouti (*Agouti paca*) or nocturnal Paca (*Cuniculus paca*), because these usually hide in borrows when resting. With respect to livestock, we cannot rule out the possibility that vampires may have fed on some other domestic animals, such as, for example, pigs or dogs. However, most of the smaller domestic animals are kept in buildings (at least over night), preventing blood feeding of vampire bats. Therefore, we think that it is reasonable to believe that only the three major large mammals, namely horses, cattle and peccaries, were relevant for vampires at out study site. Moreover, the cryptic presence of other potential prey species would not have influenced the estimation of the relative contribution of blood from the C3 and C4 food web to the diet of vampire bats, because we used the extreme values of horses and peccaries as source values for calculating the mixing model. Intermediate stable isotope values would not interfere with our estimation of the relative contribution of blood from the two isotopically contrasting food webs.

Among the three prey categories available to local vampire bats at our study site, horses were most enriched in ^{13}C, because they obtained almost all of their carbon from C4 grass of the nearby pastures. By contrast, rainforest-dwelling collared peccaries carried an isotopic signature that identified them as consumers of seeds and roots of C3 plants of the forest reserve. Cattle exhibited intermediate values, suggesting that they feed predominantly on C4 grass but complement their diet with herbs with a C3 pathway of CO_2 fixation. The isotopic data of the potential prey species are in line with those obtained in an earlier study for livestock and rainforest mammals (Voigt & Kelm 2006). Vampire bats obtained the majority of their carbon from the C4 food web as indicated by the relative high enrichment in ^{13}C in relation to ^{12}C in all three tissues. This finding is also in agreement with previous studies demonstrating populations of vampire bats to benefit from the expanding livestock industry in Latin America (e.g. Delpietro et al. 1992; Voigt & Kelm 2006). Stable isotope ratios of blood, wing membrane tissue and fur were similar in most vampire individuals, but also showed recent dietary changes in a few individuals towards collared peccaries as indicated by δ^{13}C. Overall, natural prey like peccaries played only a minor or no role in the diet of vampire bats.

Conclusions

In summary, our data indicate a high degree of individual isotopic specialisation in two colonies of vampire bats. This argues against the frequent occurrence of altruistic sharing of regurgitated blood among many colony members. We found a trend for specialisation between males and females that might

indicate blood sharing within small female networks, but not among males, if blood sharing occurred at all. Our observations are in line with the idea that – if food sharing occurs at all in colonies of vampire bats – reciprocal altruism in vampire bats occurs only within small female networks, possibly only within dyads or triads of females that form long-term relationships. Whether or not such networks consist of related or unrelated females cannot be answered with our data set. Hence, our data are not necessarily in support of reciprocal altruism, but could as well be explained by mechanisms of kin selection.

Acknowledgments

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