



## Postweaning maternal food provisioning in a bat with a complex hunting strategy



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### ARTICLE INFO

#### Article history:

Received 7 December 2012

Initial acceptance 8 January 2013

Final acceptance 18 March 2013

Available online 2 May 2013

MS. number: 12-00924R

#### Keywords:

common big-eared bat

extended parental care

female care

gleaning insectivore

maternal tuition

*Micronycteris microtis*

postweaning investment

prey transfer

prolonged offspring dependence

social learning

Adult animals of many taxa exhibit extended parental care by transferring food to inexperienced offspring, thus allocating nutritional and sometimes even informational benefits such as the acquisition of adult dietary preferences and foraging skills. In bats, postweaning food provisioning is severely understudied, despite the taxon's diverse and complex foraging strategies. The Neotropical common big-eared bat, *Micronycteris microtis*, preys on relatively large insects gleaned from vegetation, finding its silent and motionless prey by echolocation. The demands of this cognitively challenging hunting strategy make *M. microtis* a likely candidate for maternal postweaning food provisioning. We studied five free-living mother–pup pairs in their night roost using infrared video recordings. Each mother exclusively fed her own pup and mother–pup recognition was mutual. Provisioned pups were volant and had started their own hunting attempts. Weaned pups were provisioned for 5 subsequent months with a variety of insects, reflecting the adult diet. Mothers transferred over 50% of their prey to pups. Maternal prey transfers declined as pups matured, whereas the pups' own prey captures increased. During prey transfers, aggressive behaviour between mothers and pups was rare. We argue that postweaning maternal food provisioning might yield two informational benefits for *M. microtis* pups. First, learning how to handle large and well-defended prey is mandatory for inexperienced pups and could be practised with prey items provided by their mothers. Second, acoustically characteristic echo images of prey items could be gained during mother–pup prey transfers, probably facilitating the successful acquisition of *M. microtis*'s complex hunting strategy.

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Parental care is exhibited in a wide range of taxa ranging from invertebrates to mammals (reviewed in Rosenblatt & Snowdon 1996) as a highly diverse strategy aiming to increase offspring survival and, ultimately, the fitness of caregivers (reviewed in Clutton-Brock 1991; Royle et al. 2012). Protection and food provisioning are the most prevalent forms of parental care (Clutton-Brock 1991; Rosenblatt 2003). It is hypothesized that parental care has evolved independently multiple times, being favourable whenever benefits of care outweigh the costs, for example in habitats with limited food availability and high predation risk (Klug & Bonsall 2010; Gardner & Smiseth 2011). Nutritional parental care, that is, adults providing offspring with food, has multiple advantages (Farmer 2000). Adults can use resources unavailable to offspring (e.g. because the latter cannot digest or exploit them). Moreover, provisioned offspring can invest more energy in growth than in maintenance, thus developing faster and shortening the period of their life cycle in which they are most vulnerable to

predation. Correspondingly, a recently developed mathematical model aiming to explain the evolution of parental food provisioning suggests that it is most likely to evolve when parents are more efficient at feeding their offspring than offspring are at self-feeding or when parents are more efficient at feeding than at guarding offspring against predators (Gardner & Smiseth 2011).

In mammals, nearly all nutritional parental care is provided by females through lactation (Pond 1977; Lee 1998). However, females or both parents may provide dependent offspring with additional solid food during and after weaning, often with the help of older siblings. Two main hypotheses have been proposed to explain the functional significance of postweaning food provisioning from parents and/or helpers to infants (Brown et al. 2004). The 'nutritional hypothesis' assumes that transferred food items provide offspring with valuable nutrients during the critical period in which they become independent and successful foragers, whereas the 'informational hypothesis' states that food transfers facilitate the acquisition of adult dietary knowledge and food-processing skills (Brown et al. 2004). There is convincing evidence for both, not mutually exclusive, hypotheses in certain altricial birds (Heinsohn 1991; Langen 2000; Russell et al. 2004; Radford & Ridley 2006),

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primates (reviewed in Brown et al. 2004) and social carnivores (Canidae: e.g. Moehlan 1979; Hyaenidae: e.g. Owens & Owens 1984; Herpestidae: e.g. Doolan & Macdonald 1999).

Postweaning food transfers from adults to offspring predominantly occur in cooperative breeders, namely callitrichid primates (tamarins and marmosets; reviewed in Feistner & McGrew 1989; Brown et al. 2004) and social carnivores (reviewed in Clutton-Brock 1991). However, extended postweaning parental care is also found in solitary species such as certain felids (reviewed in Caro & Hauser 1992; Kitchener 1999), especially if they hunt large and/or dangerous prey (Caro 1994).

In addition to being predominantly cooperative breeders, species with extended parental care often rely on a broad diet and/or exhibit complex foraging strategies, such as the well-studied meerkats, *Suricata suricatta* (reviewed in Thornton & Clutton-Brock 2011), or callitrichid primates (reviewed in Brown et al. 2004). Conceivably the most crucial element of any foraging strategy is the handling of live, mobile and well-defended prey. The acquisition of prey-handling skills is further aggravated by the fact that, on their own, inexperienced individuals lack ample opportunities to improve their skills and that dealing with well-defended prey may be dangerous (Thornton & Clutton-Brock 2011). Therefore, it has been argued that, in some species, food transfers from adults to offspring represent a crucial form of vertical knowledge transmission that promotes the development of prey-handling skills (Thornton & Clutton-Brock 2011). This argument applies especially to species exhibiting complex foraging strategies.

In bats, there is little evidence of postweaning food transfers from adults to offspring (reviewed in Altringham 2011). This is striking as many bat species employ complex hunting strategies (Hill & Smith 1984; Schnitzler & Kalko 1998; Schnitzler et al. 2003) which should make parental provisioning with prey items highly beneficial for inexperienced offspring by facilitating the development of prey-handling and hunting skills (Jones 2000). Most bats display uniparental care, with females exclusively providing both nutritional support and non-nutritional care such as allogrooming, protection, transport and thermoregulation (Jones 2000; Kunz & Hood 2000). Maternal food provisioning after weaning has been observed in only a small number of species, mainly in captivity (Brown et al. 1983; Wilkinson 1984; Delpietro & Russo 2002; Raghuram & Marimuthu 2007). So far, the only conclusive field evidence of offspring being provisioned with additional food during and after weaning comes from the common vampire bat *Desmodus rotundus* (Wilkinson 1984) and possibly also the false vampire bat, *Vampyrus spectrum* (Vehrencamp et al. 1977).

The common big-eared bat, *Micronycteris microtis* (Phyllostomidae) is a promising candidate for postweaning maternal food provisioning. This Neotropical leaf-nosed bat is a small insectivore (5–7 g) that is widespread in Central American evergreen and deciduous forests (Alonso-Mejía & Medellín 1991). It lives in social groups of 3–10 individuals (Alonso-Mejía & Medellín 1991; I. Geipel, unpublished data) and consistently uses night roosts for feeding and resting. Night roosts can be identified by the accumulation of large numbers of discarded insect wings on the ground (Alonso-Mejía & Medellín 1991). *Micronycteris microtis* feeds on relatively large prey compared to its own body size. Its diet consists of large insects that are gleaned from vegetation, including beetles (Coleoptera), katydids (Orthoptera), caterpillars and moths (Lepidoptera), cicadas (Cicadina), dragonflies (Anisoptera) and occasionally small vertebrates (Kalka & Kalko 2006; Santana et al. 2011). The bats forage within the vegetation of dense rainforest understory, finding silent and motionless prey solely by echolocation, presumably using acoustic search images (Geipel et al. 2013) which represents a cognitively challenging hunting strategy ('narrow space active gleaning forager' sensu Denzinger & Schnitzler 2004). Moreover, the

relatively large and often well-defended prey needs to be subdued, handled and transported back to the safety of the night roost before consumption, all of which can pose severe problems for inexperienced individuals. The complex hunting strategy and the associated demands of prey handling make *M. microtis* a suitable candidate to investigate maternal food provisioning in bats. In Panama, the species is seasonally monoestrous with parturitions of a single offspring occurring at the beginning of the rainy season in late May; the single pups are nursed until June (Alonso-Mejía & Medellín 1991; I. Geipel, unpublished data). As in most bat species studied to date (Kunz & Hood 2000), *M. microtis* pups receive maternal care through lactation but no additional paternal care (I. Geipel, personal observations). Nevertheless, it is conceivable that pups would benefit greatly from extended maternal care after weaning (i.e. the provisioning with solid food) because it would allow them to master the species' difficult hunting strategy without the risk of starvation, thus receiving both nutritional and informational benefits (sensu Brown et al. 2004).

In this study, we investigated whether and to what extent postweaning maternal food provisioning occurs in free-living *M. microtis*. We hypothesized that mothers provide only their own pups with food. Moreover, we hypothesized that prey transfers from mothers to pups are directed, voluntary actions of mothers, that is, that they are not preceded by maternal aggression towards the soliciting pup and do not represent pups' food-stealing attempts. Additionally, we predicted that postweaning maternal food provisioning would decline when pups become more experienced hunters. Furthermore, we hypothesized that pups would become more skilled at handling transferred prey as they mature.

## METHODS

### *Study Site and Animals*

We observed two social groups of *M. microtis* in 2003, 2008 and 2009 in their respective night roosts on Barro Colorado Island at the Smithsonian Tropical Research Institute, Panama (9°9'17N, 79°51'53W). Both night roosts were located underneath outdoor staircases of concrete buildings of the research station located in secondary semideciduous tropical lowland rainforest (Leigh 1999). Night roosts are used by *M. microtis* for feeding, resting and self-grooming. In 2003, a social group of eight individuals, including three mothers with their respective offspring, was observed over a 3-month period from 16 August to 3 November. In 2008/2009, a second group consisting of eight individuals, including two mothers with their respective offspring, was recorded from 14 May to 20 February. The rest of the groups were composed of adults. We videorecorded the bats in 2003 for a total of 24 nights (1800–0600 hours) and in 2008/2009 for a total of 39 half nights (1800–0100 hours). All field work was approved by the Smithsonian Institutional Animal Care and Use Committee (IACUC; 2008-11-06-24-08) and the Panamanian Environmental Agency (ANAM).

For the video recordings, we used infrared video cameras (2003: VK-121/IR, Sanyo; 2008/2009: DCR-SR 70, Sony Hard Disk Drive, Sony, Japan; DCR-HC39E PAL, Sony HandyCam, Sony, Japan) that were installed on a tripod 1–2 m from the night roost without blocking or interfering with the bats' flight path. The cameras were connected to video recorders (2003: GV-D 900E, Sony, Japan; 2008/2009: GV-D1000E, Sony, Japan) placed out of sight of the night roosts (approximately 3–4 m distance). Video recordings were stored on DV Minivideo tapes (DVM 60 Premium, Sony, Japan). The night roosts were continuously illuminated with infrared lights (850 nm, Conrad, Germany; IR-10-LED, Voltcraft, Germany). Video recordings added up to 483 h of footage (2003: 217 h; 2008/2009: 266 h). Additionally, high-speed infrared video recordings (500 fps; CamRecord CR600x2, Optronis GmbH, Kehl, Germany) of selected

prey transfers were made in 2012 to document postweaning maternal food provisioning in greater detail (see [Supplementary Material](#)).

To identify individual mother–offspring pairs in the video recordings, individuals of both groups were caught and marked. Bats were captured with mist nets (2 × 2 m; Vohwinkel, Velbert, Germany) set about 2.5 m from the night roosts, separately kept in soft cloth bags and processed immediately at the capture site. The individuals were sexed and marked by bleaching their fur in an individual pattern (2003: PLATINUM Blond, Creme Oxyd 3% H<sub>2</sub>O<sub>2</sub>, Glynt, Germany; 2008/2009: Multi Blonde Powder, Blondor, 1.2% H<sub>2</sub>O<sub>2</sub>, Wella Professionals, Procter & Gamble, U.S.A.). The mixture was applied to the bats' fur and carefully removed by washing and brushing. Bats were kept until the fur was completely dry (maximum of 30 min) and released afterwards at the capture site. All bats returned to their roost after release and did not show any noticeable reactions to their bleach marks.

In this paper, we use the term 'pups' to refer to volant subadults that were weaned but still being provided with solid food by their own mothers (f1–f5). Four of the five observed pups were male (p1, p3–p5) and one was a female (p2). The female pup disappeared during our recording period and, shortly after, her mother (f2) vanished as well. In 2003, two pups (p2–p3) were marked after their mothers (p2: 22 days; p3: 5 days). Until marking, the unmarked pups were assigned to their corresponding mothers based on feeding interactions and clustering behaviour. Prey brought to the roost by unmarked pups was equally divided between the two pups until they were marked. In 2008, one mother could not be marked. However, since we observed only one unmarked female constantly feeding a marked pup (p5) in our video recordings, we assigned her to be the mother (f5) of the marked pup. Additionally, sporadic video recordings from unmarked mother–pup dyads were taken at both night roosts in September 2005, August–October 2006 and August 2012. To investigate whether mothers exclusively feed their own pups, we only used data from marked mother–pup dyads.

#### Data Analysis

We watched the video footage in real time and recorded all prey brought to the roost and transfers of prey for every mother–pup dyad in the night roost. For each observed prey transfer from mother to pup, several parameters were analysed as count data: (1) reactions of own pup, other pups and/or adults towards the mother entering the roost (reaction/no reaction); (2) initiation of prey transfer (take-over initiated by pup/handover initiated by mother); (3) aggressive behaviour of mothers and pups during prey transfer (yes/no); (4) latency of maternal prey transfer after entering the roost (immediate/late); (5) prey size (small/medium/large); (6) prey type (to insect order); (7) pups' prey handling during transfer (with/without wing usage) and consumption (constant/rare/no wing usage). To investigate whether pups recognized their mothers, we quantified the reactions of own pups, other pups and/or adults towards the entering mother (parameter 1) and we monitored whether a pup or conspecific adult lifted its head and followed the entering mother with obvious head and ear movements. We scored aggression during transfers (parameter 3) by monitoring the occurrence of displacement or wing flapping. To investigate whether the mother consumed parts of the prey before handing it over to her pup, we noted the latency of maternal prey transfer after entering the roost (parameter 4). Prey size classes (parameter 5) were based on size estimation in comparison to the bat's body size (small: ≤1 cm; medium: 1–3 cm; large: ≥3 cm). If possible, prey was classified to insect order based on simple prey characteristics (parameter 6). To investigate whether pups became more skilled at handling prey as they matured, we noted their amount of wing

usage during transfers and the subsequent prey consumption (parameter 7). In addition to the count data, we obtained metric data (see below) on prey brought to the roost by mothers and pups, maternal prey transfer, maternal aggression, maternal prey consumption before transfer, prey size and pups' prey handling (i.e. wing usage). To get comparable data per night, we calculated mean values per hour per night for all metric parameters. Subsequently, these values were averaged per month to analyse the relation between certain metric parameters and time of year (which serves as an estimate for pup age). Data from 2003 and 2008/2009 were pooled (63 observation dates, five mother–pup pairs). We applied sequential Bonferroni corrections following [Holm \(1979\)](#). Count data were analysed using chi-square tests. We conducted ANOVAs to test whether a certain prey size class was transferred preferentially and whether pups' wing usage differed according to prey size class. We used linear regressions to test for a relation between time of year (i.e. pup age) and the metric variables prey brought to the roost by mothers and pups, maternal prey transfer, maternal aggression, maternal prey consumption before transfer and pups' wing usage. Kolmogorov–Smirnov tests were used to ascertain that residuals did not deviate significantly from a normal distribution. Statistical outliers were identified using Studentized deleted residuals ([Fox 1991](#)) and excluded from further analyses when the residuals' absolute value exceeded four ([Urban & Mayerl 2011](#)). Data could not be analysed with a single model because pups never transferred any prey items and prey size was only determined for prey transfers and not for all prey brought to the roost. All statistical tests were performed using SPSS version 20 (IBM Corporation, New York, U.S.A.).

## RESULTS

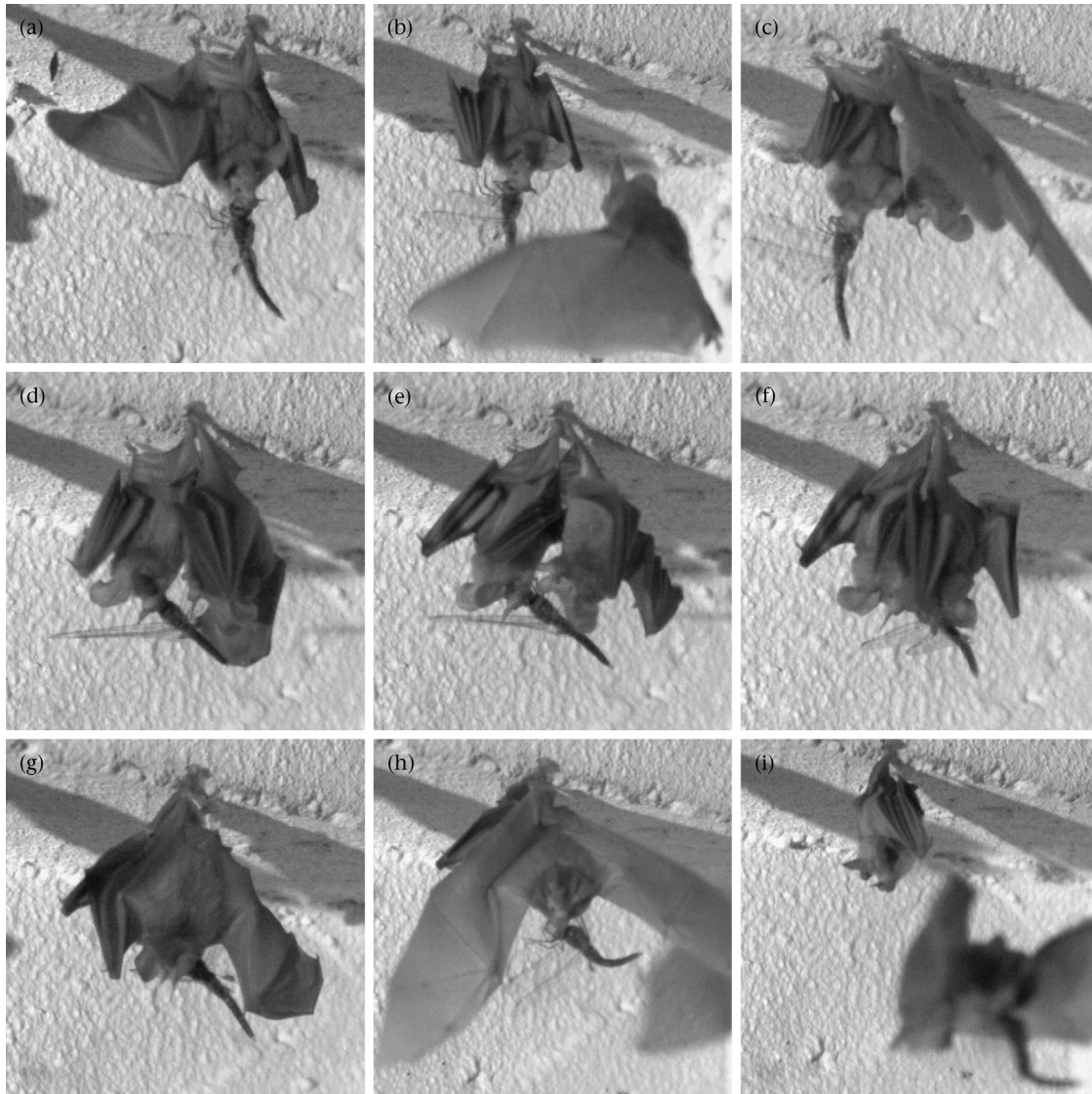
### Postweaning Maternal Food Provisioning

Weaned *M. microtis* pups were provisioned with solid food by their mothers for at least 5 successive months (mid-June to mid-November). In 2003, the first observed maternal prey transfer occurred on 8 August and the last transfer on 3 November. It is probable that maternal prey transfers occurred before August as well. However, these were not recorded, as our observations only started in August 2003. In 2008, the first observed maternal prey transfer occurred on 4 June and the last transfer on 4 November. Maternal food provisioning occurred on a regular basis, as we have additional anecdotal evidence for frequent maternal prey transfers from 2005, 2006 and 2012 (we excluded these data sets from our detailed analyses since the bats were not individually marked).

In total, we observed 1777 prey brought to the roost by five mothers and five pups. Of these, mothers brought 83.1% and pups 16.9%. Of the prey observed to be brought to the roost by the mother, 53.7% were transferred to pups ([Fig. 1](#)). Pups never transferred prey items. Prey transfers happened almost exclusively between mothers and their own pups, with only one exception where a prey item was transferred from a mother (f1) to an alien pup (p2). Moreover, a small prey item was transferred from an unmarked adult of unknown sex to a marked female pup (p2); the adult was not the pup's mother. We also observed three prey transfers from an adult male to a marked male pup (p4). The identity of the adult male was determined with certainty as he was bleach marked and his penis was clearly visible on the video recordings during the prey transfers. In conclusion, pups were on rare occasions (five of 797 cases, 0.6%) provisioned by adults other than their respective mothers.

### Prey Brought to the Roost and Transfer Over Time

The number of prey transferred from mothers to pups declined significantly over time (linear regression:  $r^2 = 0.925$ ,  $F_{1,4} = 36.903$ ,



**Figure 1.** Maternal prey transfer of a dragonfly. The picture series gained from high-speed video recordings reveals the details of postweaning maternal food provisioning in *M. microtis*. A mother returns to the night roost with prey (a) and is immediately approached by her volant pup (b), which lands close to her (c). Subsequently, the mother turns around (d) and offers the prey to her pup (e). During prey transfer, the pup grasps the prey with its mouth (f) and the aid of its wings (g). Afterwards, the pup prepares to take flight (h) and finally carries the prey to a different place in the night roost (i).

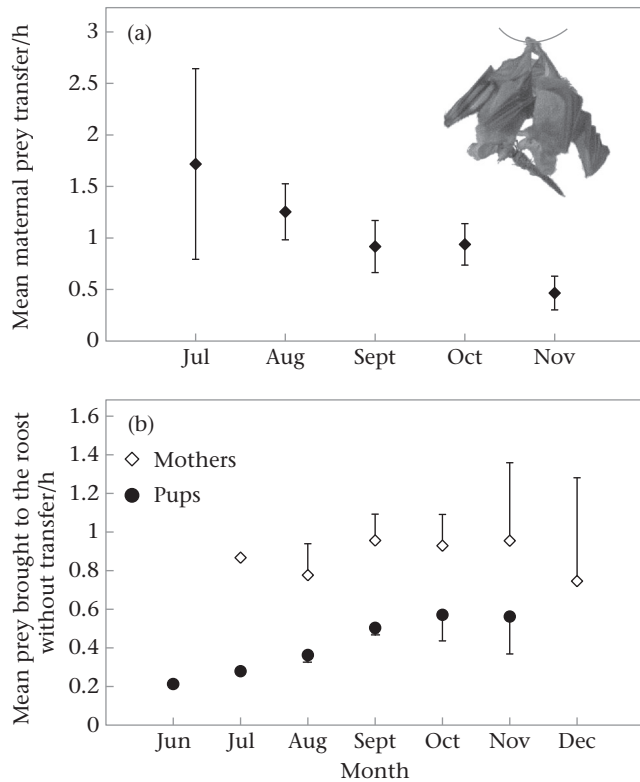
$P = 0.009$ , corrected  $\alpha = 0.01$ ; Fig. 2a); each month, mothers transferred almost 0.3 prey items/h less than in the previous month ( $\beta = -0.281$ ). As pups matured, the number of prey they brought to the roost themselves increased significantly (linear regression:  $r^2 = 0.942$ ,  $F_{1,5} = 64.867$ ,  $P = 0.001$ , corrected  $\alpha = 0.0083$ ; Fig. 2b); each month, pups brought almost 0.1 prey items/h more to the roost than in the previous month ( $\beta = 0.079$ ). At the same time, the number of maternal prey brought to the roost that were not transferred to the pups did not change significantly as pups matured (linear regression:  $r^2 = 0.005$ ,  $F_{1,5} = 0.020$ ,  $P = 0.893$ , corrected  $\alpha = 0.05$ ; Fig. 2b).

#### Transferred Prey Spectrum and Size

The spectrum of transferred prey items included a variety of differently sized insects such as dragonflies (Fig. 1, Supplementary Videos S1, S2), katydids, caterpillars (Supplementary Video S3), moths or cockroaches, thus reflecting the adult diet. Of the transferred prey items, 17.5% were orthopterans (mainly katydids, some

crickets and very rarely grasshoppers), 15.9% were Lepidoptera (including 12.2% caterpillars and 3.7% moths) and 14.5% were dragonflies (Anisoptera). Smaller numbers of Blattodea (4.2%), Hymenoptera (3.1%), Coleoptera (2.2%), Hemiptera (1.8%; Supplementary Fig. S1), Phasmatodea (1.1%) and one Mantodea (0.1%) were transferred as well. Additionally, spiders were occasionally transferred (3.3%). A large number of transferred prey items (36.3%) were not identifiable in the videos.

No particular prey size class was transferred preferentially; the percentage of small (32.6%), medium (35.2%) and large (32.2%) transferred prey items did not differ significantly (ANOVA:  $F_{2,15} = 1.268$ ,  $P = 0.310$ ). In 14.2% of cases, prey items were partially consumed by the mothers before being transferred to their pups. When partially consuming prey items, mothers fed on them for a mean  $\pm$  SD of  $114 \pm 142$  s (range 2–800 s) before transfer. As pups matured, maternal prey consumption before transfer decreased (linear regression:  $r^2 = 0.915$ ,  $F_{1,3} = 21.525$ ,  $P = 0.043$ , corrected  $\alpha = 0.0125$ ), with a 5.5% decrease per month ( $\beta = -5.533$ ).



**Figure 2.** (a) The mean number of maternal prey transfers/h and (b) the mean number of prey brought to the roost/h without transfers for mothers and pups over time (June–December). Means  $\pm$  SE are shown.

#### Mother–Pup Interactions During Prey Transfers

In the majority of cases (85.2%), pups were already resting in the night roost when mothers returned to transfer prey (Supplementary Video S2). Thus, pups waited for their mothers' return to the night roost significantly more often than they pursued their mothers back to the night roost (chi-square test:  $\chi^2_1 = 392.224$ ,  $P < 0.0001$ , corrected  $\alpha = 0.05$ ), suggesting that tandem flights and joint foraging occur only rarely if ever in *M. microtis*.

Mother–pup recognition was mutual and occurred as soon as mothers or pups entered the night roost. Mothers recognized their own pups (evidenced by the almost complete lack of transfers to alien pups), but pups recognized their mothers as well, as 86.6% of the reactions towards a mother entering the night roost were exclusively from their own pups (chi-square test:  $\chi^2_2 = 643.319$ ,  $P < 0.0001$ , corrected  $\alpha = 0.025$ ). As soon as a mother entered the night roost, her resting pup lifted its head, directed both head and ears towards its mother, following her flight movements, and echolocated (Supplementary Videos S1, S2). Only rarely did other pups (4.8% of cases) or adults (8.6%) also show obvious reactions towards the entering mother. We never observed any pups stealing prey from alien mothers or fellow pups. Mothers initiated 54% of the prey transfers (handovers) and pups 46% (take-overs).

Aggressive behaviour between mother and pup occurred in 8.5% of prey transfers and increased over time (linear regression:  $r^2 = 0.710$ ,  $F_{1,4} = 7.336$ ,  $P = 0.073$ , corrected  $\alpha = 0.0167$ ), with a 1% increase per month ( $\beta = 1.003$ ). However, we observed only mild forms of aggression (such as displacement and wing flapping) but never biting or hitting. During normal, aggression-free prey transfers, mothers actively turned towards their pups and offered them the prey items (Fig. 1, Supplementary Fig. S1, Videos S1–S3).

#### Prey Handling by Pups

In most cases (99.1%), pups relied on the support of their wings to grasp transferred prey items securely (Supplementary Videos S1–S3). Pups' wing usage often continued during prey consumption as well. This is noteworthy as adults only rarely use their wings during prey consumption (I. Geipel, personal observations). As pups matured, they did not become more skilled at prey handling; the percentage of constant wing usage during prey consumption did not decline significantly over time (linear regression:  $r^2 = 0.464$ ,  $F_{1,5} = 1.095$ ,  $P = 0.354$ , corrected  $\alpha = 0.025$ ;  $\beta = 0.464$ ). The percentage of constant wing usage was highest when consuming large prey items; it was lower when pups consumed small or medium-sized prey (ANOVA:  $F_2 = 4.045$ ,  $P = 0.039$ ; Tukey post hoc tests: large versus small:  $P = 0.049$ ; large versus medium:  $P = 0.090$ ; small versus medium:  $P = 0.941$ ).

#### DISCUSSION

##### Postweaning Maternal Food Provisioning

Our study provides evidence for extended maternal food provisioning of weaned pups with solid food in a free-living insectivorous bat. Regular prey transfers from mothers to their own pups for at least 5 months after weaning were directed, voluntary actions that declined as pups matured and became experienced hunters themselves. Prolonged maternal investment in weaned offspring is exceedingly rare in bats (reviewed in Altringham 2011). We propose that the extended maternal care is crucial for *M. microtis* pups because it provides both nutritional and informational benefits (sensu Brown et al. 2004) by giving pups additional time to master the species' complex hunting strategy without facing the imminent risk of starvation. Our argument corresponds to findings in other bat species (reviewed in Jones 2000) in which the offspring's prolonged dependence on adult food provisions presumably facilitates the acquisition of challenging prey-handling and hunting skills required for carnivory (Vehrencamp et al. 1977; Raghuram & Marimuthu 2007) or sanguivory (Wilkinson 1984; Delpietro & Russo 2002).

##### Mother–Pup Recognition

Two lines of evidence suggested mutual mother–pup recognition in *M. microtis*. First, mothers almost exclusively fed their own pups. Second, pups seemed to recognize their respective mothers when the latter returned to the night roost because pups lifted their head and oriented their ears towards their returning mothers significantly more often than towards other returning conspecifics. It is conceivable that mother–pup recognition before prey transfers is mediated acoustically in *M. microtis* because this would allow recognition in complete darkness over a certain distance (Bradbury & Vehrencamp 2011), thus preventing erroneous landings in the night roost. Vocal mother–pup recognition in bats is well studied (reviewed in Kunz & Hood 2000; Wilkinson 2003) and probably the prevalent form of parent–offspring recognition in this taxon. Acoustically mediated communication between food-providing adults and offspring has also been demonstrated for birds (e.g. Radford & Ridley 2006), meerkats (e.g. Kunc et al. 2007) and primates (e.g. Ruiz-Miranda et al. 1999).

In five of 797 observed prey transfers, pups received solid food from adults other than their respective mothers; the donor bats were both male (three cases) and female (two cases) conspecifics. These nonmaternal food transfers could represent nonadaptive mistakes or adaptive, if rare, forms of alloprovisioning as seen in some cooperatively breeding carnivores (Clutton-Brock 1991), callitrichid primates

(Brown et al. 2004), and altricial birds (Langen 2000). Further detailed work on the social system of *M. microtis*, particularly the genetic relatedness of group members, is necessary to clarify this point.

We considered the prey transfers to be voluntary maternal actions for the following reasons. First, in more than half of the cases, prey transfers were initiated by mothers and not by soliciting pups. Second, when soliciting pups landed next to their mothers, the latter turned towards the pups and actively presented the prey items. Third, we never observed any food-stealing attempts of pups. Fourth, aggressive behaviour between mothers and pups during prey transfers occurred only rarely. When pups attempted to take prey items that mothers were unwilling to deliver, merely mild forms of aggressive behaviour such as displacement or wing flapping occurred and we never observed serious maternal aggression such as biting or hitting the offspring. This contrasts with studies on other species in which mothers may reject soliciting offspring violently (e.g. bats: Strauss et al. 2010; primates: Maestripieri 2002; rodents: König & Markl 1987; birds: Davies 1978). This discrepancy might be attributed to the overall docile nature of adult *M. microtis*, which show little obvious aggression between conspecifics (I. Geipel, personal observation). Moreover, it must be noted that a genetic conflict of interest between mothers and offspring (sensu Trivers 1974) does not necessarily result in an obvious behavioural conflict, for example a weaning conflict with visible maternal aggression towards the soliciting offspring (Gomendio 1991; Bateson 1994). Nevertheless, mild aggressive interactions during prey transfers did occur and tended to increase with increasing pup age. At present, we cannot be certain whether this trend indicates a weaning conflict in *M. microtis* or not.

#### *Development of Prey-handling Skills*

Postweaning adult food provisioning may enhance the offspring's prey-handling skills (reviewed in Thornton & Raihani 2008). To date, the most convincing example for this argument stems from wild meerkats (Thornton & McAuliffe 2006). Adults teach inexperienced pups crucial prey-handling skills by providing them with live prey items. A similar rationale is used to explain why many felids confront their offspring with live prey (reviewed in Caro & Hauser 1992). As *M. microtis* hunts relatively large and well-defended prey, providing inexperienced offspring with subdued prey in the safety of the night roost might give them a corresponding opportunity to master the handling and consumption of well-defended prey. When consuming large prey items, pups considerably relied on the support of their wings; this contrasts with the behaviour of skilled adults which rarely use their wings during prey consumption. In our observation period, however, we could not observe pups reducing the amount of wing usage during consumption, that is, becoming more skilled at prey handling. It is possible that a detectable improvement in prey-handling skills would need a longer time span to develop than covered by our study. Nevertheless, we observed that maternal prey consumption before transfers, which is probably important for subduing large, well-defended prey, decreased over time, probably because pups gained more experience at handling prey as they matured. An alternative explanation for the observed decrease in maternal prey consumption before transfers is that certain prey items may have simply been too large to be handled by young pups, which is why mothers consumed them partially before transferring them.

#### *Potential for Social Learning of Hunting Strategy*

When pups became volant, there was little evidence for tandem flights and joint foraging of mother–pup pairs, suggesting that pups started their hunting attempts without the guidance of their

mothers. In several other bat species, mother–pup pairs regularly associate during foraging (reviewed in Jones 2000), presumably to transfer knowledge about hunting skills or suitable prey. However, we were not able to find similar evidence for such observational learning (sensu Gaudet & Fenton 1984) of pups from their foraging mothers in *M. microtis*.

Nevertheless, social learning may be crucial for the development of hunting skills in species with complex feeding strategies (chimpanzees, *Pan troglodytes*: Boesch 1991; orang-utans, *Pongo pygmaeus*: Jaeggi et al. 2008; dolphins, *Stenella frontalis*: Bender et al. 2008; killer whales, *Orcinus orca*: Guinet & Bouvier 1995; bats: Wilkinson 1995) such as *M. microtis*. Jones (2000) suggested that parental provisioning with solid food could provide inexperienced bats with a search image of particular prey items that, in turn, would facilitate the development of their hunting skills. This is a conceivable scenario for *M. microtis* when considering the species' complex hunting strategy. *Micronycteris microtis* gleanes silent and motionless prey from leaves in the dense forest understory using solely echolocation for prey perception (Geipel et al. 2013) and thereby faces the sensorial challenge of acoustic masking effects (sensu Neuweiler 1989). Thus, it has been proposed that *M. microtis* uses acoustic images for prey perception in acoustically cluttered environments (Geipel et al. 2013). Such acoustic search images might be based on innate templates or learned, for example through trial and error or social learning. We hypothesize that *M. microtis* pups may learn acoustic echo images of suitable prey through the maternal transfer of intact prey items. Maternal food transfers were always accompanied by pup echolocation calls, suggesting that pups might learn prey-specific cues such as shape or reflective properties shortly before and during transfer. Therefore, we argue that prey transfers from mothers to pups might be a key factor in the acquisition of the cognitively challenging and complex hunting strategy of *M. microtis*.

#### *Conclusions*

In conclusion, we argue that maternal food provisioning in *M. microtis* could have informational benefits (sensu Brown et al. 2004) in addition to the implicated nutritional benefits for pups. Pups might not only practise how to handle large and well-defended prey in the safety of the night roost but also learn acoustic echo images of prey items during transfers. Corresponding arguments have been proposed to explain the functional significance of postweaning food provisioning in cooperatively breeding carnivores and callitrichid primates (reviewed in Clutton-Brock 1991; Brown et al. 2004). Our study suggests that a noncooperatively breeding bat species may facilitate the successful acquisition of its complex hunting strategy by exploiting social-learning mechanisms predominantly found in cooperative breeders.

#### *Acknowledgments*

Valuable comments by T. Jónsson, M. Metz and M. Tschapka substantially improved the manuscript. We thank P. Smiseth, H. Kunc and two anonymous referees for their helpful suggestions. The Panamanian authorities and the Smithsonian Tropical Research Institute gave both support and research permissions. The Biological Station BCI provided excellent logistics and technical support. We are especially indebted to O. Acevedo for her generous help.

#### *Supplementary Material*

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2013.03.040>.

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