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Experimental evidence for group hunting via eavesdropping in echolocating bats

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Group foraging has been suggested as an important factor for the evolution of sociality. However, visual cues are predominantly used to gain information about group members' foraging success in diurnally foraging animals such as birds, where group foraging has been studied most intensively. By contrast, nocturnal animals, such as bats, would have to rely on other cues or signals to coordinate foraging. We investigated the role of echolocation calls as inadvertently produced cues for social foraging in the insectivorous bat *Noctilio albiventris*. Females of this species live in small groups, forage over water bodies for swarming insects and have an extremely short daily activity period. We predicted and confirmed that (i) free-ranging bats are attracted by playbacks of echolocation calls produced during prey capture, and that (ii) bats of the same social unit forage together to benefit from passive information transfer via the change in group members' echolocation calls upon finding prey. Network analysis of high-resolution automated radio telemetry confirmed that group members flew within the predicted maximum hearing distance 94 ± 6 per cent of the time. Thus, echolocation calls also serve as intraspecific communication cues. Sociality appears to allow for more effective group foraging strategies via eavesdropping on acoustical cues of group members in nocturnal mammals.

Keywords: information transfer; network; *Noctilio albiventris*; sociality

1. INTRODUCTION

Although many animals from a multitude of taxa live in groups, at least during part of their lives (Krause & Ruxton 2002), the ultimate and proximate factors underlying sociality often remain unresolved. One main advantage of living in groups is access to socially acquirable information, such as about the best mating partners, and information on the presence or absence of predators and food (Danchin *et al.* 2004; Dall 2005). Socially acquired information can be gained either in the form of evolved signals where individuals 'deliberately' provide personal information to others or as cues, which are inadvert by-products of individual activities, e.g. feeding behaviour can convey information about the presence or quality of food (Dall 2005). In fact, sharing information about food is thought to represent a major driving factor for the evolution of sociality, especially in species exploiting resources with a patchy and ephemeral distribution (Barta 1992; Beauchamp 1997; Buckley 1997*b*; Safi & Kerth 2007).

Several taxa of social diurnal birds commonly use cues, usually visual cues, during foraging (Brown 1986; Buckley 1997*a,b*; Beauchamp 2001). However, social foraging in strictly nocturnal animals such as owls and bats was thought to be limited due to the importance of visual cues in information transfer (Beauchamp (2007), but see Wilkinson (1992)). Contrary to most other nocturnal animals, echolocating bats produce auditory cues while foraging, which contain information that could potentially be used by other foraging bats: 'search-phase' echolocation calls that are emitted while a bat is searching for prey, which change to 'feeding buzzes' (FBs) when prey is encountered. Indeed, bats are attracted to the FBs of conspecifics (Barclay 1982; Balcombe 1988; Fenton 2003; Gillam 2007), but, thus far, it remained unclear whether eavesdropping affects group foraging behaviour and hence sociality of bats.

We investigated social foraging in the lesser bulldog bat, *Noctilio albiventris*. The species is fairly common, lives in social groups year-round and is often seen flying in small groups over open bodies of water. The diet of *N. albiventris* consists mainly of insects (Tamsitt & Valdivieso 1963; Hooper & Brown 1968; Howell & Burch 1973; Whitaker & Findley 1980; Gonçalves *et al.* 2007), but little information beyond the level of order or about prey ecology is available.

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However, due to the fact that *N. albiventris* forages over open water, the diet was expected to consist of ephemeral but locally abundant swarming insects (Jones & Rydell 2003). Finding ephemeral prey, such as insect swarms, is difficult as their occurrence is unpredictable in space and time. At the same time, insect swarms are a rich and nonmonopolizable resource, reducing effects of intraspecific competition. Ephemeral and nonmonopolizable diets have in fact been linked with social foraging and group living in theoretical and comparative studies of birds and male bats from the temperate zones (Beauchamp 1997; Buckley 1997b; Beauchamp 2002; Safi & Kerth 2007). This makes *N. albiventris* an ideal candidate for the studies of social foraging in echolocating bats. *Noctilio albiventris* has an extremely short-activity period just after sunset (Hooper & Brown 1968), which implies that foraging must be very efficient in spite of the fact that unlike many other insect species, those swarming over water often do not have ears or behavioural strategies against bat attacks (Jones & Rydell 2003).

We hypothesized that *N. albiventris* uses the acoustical cues that group members inadvertently emit during prey detection and capture, presumably to increase foraging efficiency. Furthermore, we predicted that individuals, who emerge from their roosts together, maintain social cohesion by flying within hearing distance of each other. This would allow them to find food sources more efficiently, enabling them to catch enough of their small and ephemeral prey during the short foraging period. To test our hypotheses, we performed playback experiments and expected *N. albiventris* to be (i) attracted to playbacks of conspecific FBs. In addition, we monitored bats with an automated telemetry system expecting that (ii) individuals spend a high proportion of time foraging within hearing distance of group members.

2. MATERIAL AND METHODS
(a) *Study site*
Our main study site was the village Gamboa (09.07° N; 079.41° W) in Panama, and surrounding water bodies, the Panama Canal and the Chagres River. An additional study site for recording and playbacks was Barro Colorado Island (BCI, 09.10° N; 079.51° W). The entire study area is covered by semi-deciduous tropical lowland rainforest with a distinct wet and dry season (Windsor 1990; Leigh 1999).

(b) *Playback experiments*
We conducted playback experiments from 6 October to 30 November 2007 and 4–26 June 2008. We recorded foraging *N. albiventris*, whose calls were discernible from those of other bat species flying over water by their distinctive patterns and frequencies, from the shores of the Chagres River (four sites) and BCI (two sites) with a condenser ultrasound microphone (CM16/CMPA) and the software RECORDER USGH v. 3.4 (Avisoft, Berlin, Germany) onto the hard disk of a laptop computer. All recordings were made with a sampling rate of 250 kHz and a bit rate of 16. In the software SASLAB PRO v. 4.40, we then identified six sequences of 1.5 s duration of FBs and search calls (SCs) of single individuals from each site, which were free of heterospecific calls. So each 1.5 s element contained varying numbers of calls as they naturally occurred. We filtered out background noise outside of the species-specific frequency range (bandpass filter: 35–75 kHz) from

these sequences to ensure that the animals were really reacting to the presented stimulus. For each of the six recording sites, we composed one SC file and one FB file of 3 min duration each, composed of the repeated six fragments in random order. As controls, we created a file consisting of white noise (WN) covering the call frequencies of the bats (32–75 kHz) and a silence file, both also lasting 3 min.

For the playback trials, we selected five sites, along the shores of the Chagres River (four sites) and on BCI (one site) where foraging *N. albiventris* had been observed previously. Each site had direct access to the water that was clear of floating vegetation. We limited playback trials to nights without wind or rain. During experiments, we placed an Ultrasonic Dynamic Speaker (ScanSpeak) as close to the water as possible and connected it to the laptop computer via an Ultrasound Gate Player 116. Playbacks were started as soon as the first *Noctilio* sp. were seen over the water or 5 min after they had first been seen on the previous playback night. During each playback session, a selection of the 3 min files was then played back in the following order: silence—stimulus 1—silence—stimulus 2—silence—stimulus 3. The order of the stimuli, i.e. FB, SC and WN, was random. We played back at the same site only after a minimum of 5 and a maximum of 108 days, and a maximum of six times, spread over a period of eight months to avoid habituation of the bats. We played back the files from all recording sites, but one from a different recording site each time at every playback site to avoid the fact that the bats were reacting to playback of calls of familiar individuals. We calibrated the loudspeaker prior to each experiment to ensure that files were played back at approximately the same sound pressure level (SPL). For this purpose, we played the SC file of the respective session at a distance of 5 m from the microphone and simultaneously recorded it. We then adjusted the volume of the loudspeaker until the intensity (derived from the spectrogram) of the playback matched that of the original file in sound intensity. For detailed information on the frequency response of microphone and loudspeaker, see product descriptions on www.avisoft.com.

Simultaneously with the playback experiments, we visually recorded the behaviour of the bats according to the following categories: (i) far pass, i.e. a *Noctilio* sp. passing in a direct line in front of the loudspeaker at a distance of 2–10 m. This was used as a means to assess general background activity of bats; (ii) near pass, i.e. a *Noctilio* sp. passing the loudspeaker at a distance of 2 m or less; and (iii) approach, i.e. a *Noctilio* sp. flying directly towards the loudspeaker to a distance of 1 m or less. In addition to the visual observations, we also recorded echolocation calls during each entire playback session. The same microphone as had been used for recording the playback files was placed at a short distance behind the speaker. Playbacks lasted 21 min. Longer playback sessions proved fruitless, as bats were only present over the water for a short-time period.

For analysis of the visual observations, we selected only those playbacks of stimuli where bats had been present and thus within the predicted maximum hearing distance during the immediate pre-playback silence. We compared the number of far passes, near passes and approaches during the pre-playback silence with those during the stimulus in a paired-sample sign test. In addition, we visually scanned the spectrograms of all recorded audio files in SASLAB PRO and noted for every 2 s window whether '*N. albiventris* (NA)' had been recorded or not. Recordings of very closely approaching bats are 'overloaded', which is visible from clipped waveforms

in the spectrogram and this was noted as a second category. Finally, we also included 'other bat species' as a third category. This way of analysing the data was on the one hand, less precise, as all bats in the range of the microphone (which was close to but not identical with the loudspeaker) were recorded regardless of whether they were approaching or passing. On the other hand, we were able to distinguish the calls of *N. albiventris* and *Noctilio leporinus*, which was not always possible with certainty during the visual observations. Finally, we were able to exclude the possibility that additional bat species were attracted by the playbacks. We used non-parametric (Wilcoxon matched-pairs signed-ranks test) tests to analyse the results. We analysed visual observations from 14 playbacks of FBs, 10 of SCs and 8 of WN where *Noctilio* sp. had been visually observed during the pre-playback silence. Calculations were made in INSTAT GRAPHPAD v. 3.0 for Macintosh.

(c) Calculation of hearing distance

We calculated maximum hearing distance based on the attenuation of the sound pressure of echolocation signals using a simplified version of the formula by Stilz (2004). Both geometric and atmospheric attenuations reduce the amount of energy contained in a call as a function of call frequency and distance between sender and receiver. Therefore, the hearing distance is the distance after which the initial sound pressure of an emitted call falls below the hearing threshold of a potential receiver, which is determined by the auditory abilities of the bats and background noise levels. This threshold ranges between 0 and 20 dB SPL in bats (Kick 1982).

We determined the maximum distance of hearing by using the following equation:

$$\text{sound pressure level} = \text{initial sound pressure}$$
$$+ \text{geometric attenuation} + \text{atmospheric attenuation}.$$

We obtained the environmental values needed to calculate atmospheric attenuation in the model for temperature ($t = 27.125°C$), barometric pressure ($p = 109\,125$ pa) and relative air humidity (RH $r = 93.625\%$) from average weather data during the nights we radio-tracked bats (http://www.wunderground.com). Main echolocation frequency was $f = 70$ kHz (own data and Surlykke & Kalko 2008), and SPL of SCs at a distance of 10 cm from the bat was SPL = 134 dB (Surlykke & Kalko 2008). We calculated detection distance for a small insect, such as the typical prey of *N. albiventris* by adding -50 dB target strength to the model (Waters *et al.* 1995). Target strength represents the loss of sound energy as a consequence of the absorption and reflective properties of small insects in the field. In our estimate, we assumed that the SPL of FBs is the same as that of SCs, as published SPLs for the latter are not available (but see Boonman & Jones 2002). Thus, our distance estimates are maximum values, especially also considering the high directionality of echolocation calls.

We calculated a maximum hearing distance of 35–40 m between echolocating bats, depending on the assumed hearing threshold (0 or 20 dB SPL). By contrast, calculated maximum detection distance for a small prey item such as an insect was approximately 4–6 m.

(d) Capture and radio-tracking

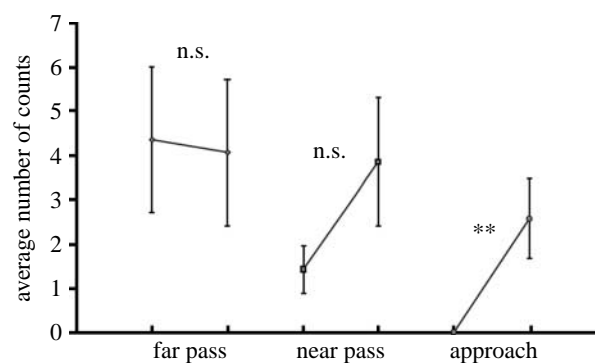We caught groups of bats with a handmade harp trap in the wet season of 2007 during evening emergence from two

Figure 1. Mean number of visual observations ($\pm$s.d.) of far passes, near passes and approaches contrasting between pre-playback silence (left hand values of each category) and playback of FBs (right hand value). Only the difference between approaches during pre-playback silence and FBs was significant (asterisks, $p < 0.007$; $n = 14$).

known roosts in buildings in Gamboa. We distinguished social groups by the fact that they emerged simultaneously. Group A (two individuals), group B (three individuals) and group C (three individuals) were all captured on 9 June at roost 1. Group D (five individuals) was captured at roost 2 on 14 June. We glued a 0.6 g transmitter to the dorsal fur of fully grown, non-pregnant females and released them at the capture site during the same night. Data collection started the following evening and always lasted from emergence just after sunset until all bats had returned to the roost approximately 1 hour later. Radio-tracking continued until 22 June. Using an automated telemetry system (see below), we confirmed that no bat emerged from the roost again later during the night.

After emerging in the evening, bats foraged over the nearby Panama Canal and Chagres River. Two automated recording units (ARU's) were placed at an elevated point and near the water to determine bearings towards bat radio signals (figure 1; Crofoot 2008). In addition, two to three persons functioned as mobile-tracking units, locating the bats continuously by scanning through the radio-transmitter frequencies, taking compass bearings ($\pm 5°$) for each individual. Whenever the signal of a bat was located, we scanned through all the other frequencies within half a minute. We used the maximum-likelihood estimator by Lenth (1981) as implemented in LOAS (Ecological Software Solutions, Inc.) to tri-, quadr- or quintangulate individual locations. We tested the location accuracy by using precisely known locations of bats (i.e. roosts) and by placing radio transmitters at five terrestrial locations within the study site. We used the triangulation method with one mobile observer and the two ARU's to estimate the locations of these transmitters from 300 to 800 m distance to each receiver. We determined five locations during each trial and averaged their error in metres. The location accuracy was determined as the average location error of the five trials and amounted to 30 ± 3.7 m (distance $\pm$s.d.).

Only the recorded positions of foraging bats observed over intervals of at least 5 min were compared to avoid pseudo-replication (Otis 1999). Based on the calculated maximum hearing distance, bats were counted as having foraged in a group, when they had been localized within 40 m or less. We determined the total number of co-locations (C) between individual female bats as well as the total number of

observations (P) for each bat. We then calculated the percentage of observations when each bat was foraging with at least one other bat ($C/(P+C)$).

From the observed co-locations, we created an undirected weighted network representative of the social ties between individuals. Vertices represented each bat, while the presence of an edge between two vertices meant that the two bats were observed foraging in a group. The weight of each edge was given by the value C. We constructed a 13×13 adjacency matrix for all bats and calculated the modularity Q for various possible subdivisions of the network. The modularity represented the difference between the number of edges within a 'community' (in our case a social group) and the expected number of edges from a random network, but with the same degree (number of edges from a vertex) distribution of the original network (Newman 2004). The highest Q-value ($0<Q<1$) indicates the most probable structure.

In addition, we visualized group foraging, with Kruskal's non-metric multidimensional scaling using the R statistical package v. 2.7.1 (R Development Core Team 2008). This method estimates the orthogonal coordinates of a set of objects from data measuring distances between them (Venables & Ripley 2002). We used the inverse of the ranked pairwise number of co-locations resulting in a matrix where individuals with few co-locations received a large distance and individuals with many co-locations a short distance. In our example, bats that had foraged together had low pairwise distances, i.e. low dissimilarity. The result was a two-dimensional representation of the pairwise matrix of co-locations of the radio-tracked individuals.

3. RESULTS

(a) *Playback experiments*

We never visually observed a response to playback of WN, and only non-significant responses to playback of SCs. By contrast, playback of FBs caused a significant increase in approaches by *Noctilio* sp. ($p<0.007$; Wilcoxon matched-pairs signed-ranks test; figure 1).

The analysis of the simultaneously recorded audio files confirmed this finding. Only the category 'overloaded', i.e. bats in the immediate vicinity of the loudspeaker, revealed a significant increase in the number of bats approaching the loudspeaker between pre-playback silence ($n=20$; mean $=0.364\pm0.79$) and playback of FBs (mean $=2.409\pm4.687$, $p=0.0156$; Wilcoxon matched-pairs signed-ranks test). The only other comparison that came close to significance was between pre-SC silence 'NA' ($n=19$; mean $=6.64\pm11.03$) and SC playback (mean $=11.06\pm19.10$; $p=0.08$), all other comparisons yielded a $p=0.27$ or greater.

(b) *Radio-tracking*

Several individuals—including all five members of group D—were always triangulated within maximum hearing distance (<40 m) of at least one other bat (for a representative example of a radio-tracking night, see figure 2); the bats foraged socially 94 ± 6 per cent of the time (figure 3). Some of the groups switched roosts after capture, but continued to forage together. Flight trajectories changed from night to night, thus we can be sure that the bats were not simply following established routes.
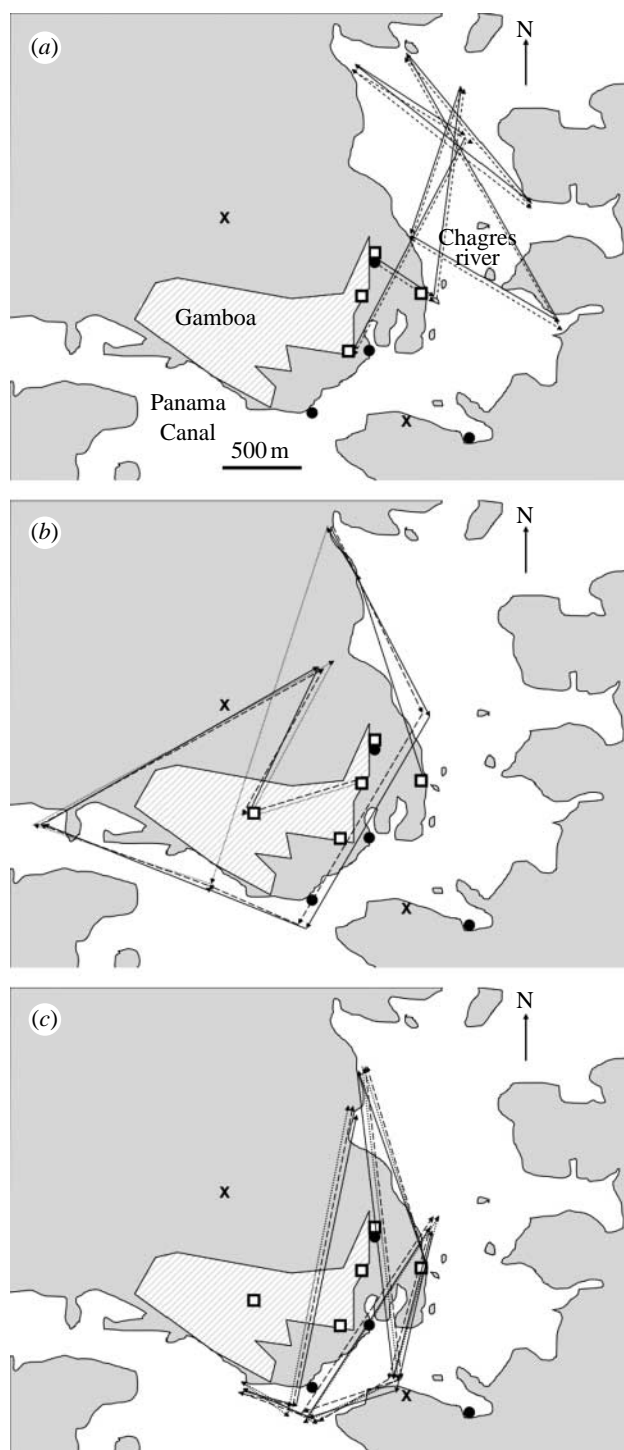

Figure 2. Bat foraging movements during one representative evening (15 June 2007); (*a*) group A (two bats), (*b*) group B (three bats) and (*c*) group C (three bats). For explanation of symbols, see (*a*) (crosses, automated tracking site; circles, hand-tracking site; squares, main bat roost). Points in the figure represent fixes where all the animals' signal was heard from the same direction within a maximum of 30 s.

The network analysis of radio-tracked individuals suggested a structure identical to that observed at capture, with a modularity $Q=0.48$, well above the value of 0.3 considered to be a good discriminator between real ($Q>0.3$) and random subdivision ($Q<0.3$, figure 4*a*). The same was true for the visualization method with Kruskal–Wallis' non-metric scaling (figure 4*b*). The four groups that clustered together in both visualization methods were identical with
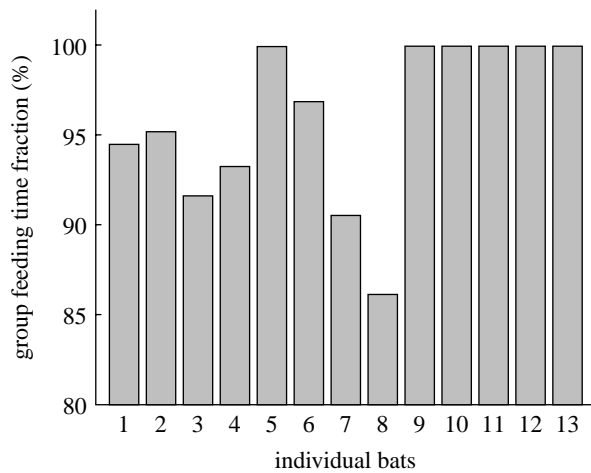
Figure 3. Bar plot of the fraction of time (no. of times a bat was co-located/total no. of observations) bats from roost 1 (groups A–C, bats 1–8) and roost 2 (group D, bats 9–13) foraged with at least one other bat.

the groups that had emerged simultaneously from the same roost, showing that roost members foraged together.

4. DISCUSSION

Social foraging has been postulated as a major reason for the evolution of sociality in animals, yet most studies are either of a theoretical nature (Barta 1992; Buckley 1997b; Sernland 2003; Jackson *et al.* 2008) or observational (e.g. Wilkinson 1992; Buckley 1996; Wilkinson & Boughman 1998; but see Buckley 1997a). Our data strongly suggest that passive information transfer between group members via acoustical rather than visual cues may coordinate foraging of nocturnal flying animals.

Our playback experiments confirm our first prediction that FBs, produced when prey has been detected and is being attacked, attract conspecific bats. This implies that foraging within hearing distance enables *N. albiventris* to profit from inadvertent or passive information transmitted through the change in echolocation call structure of group members that have found an insect swarm, indirectly increasing potential detection distance of prey. Even if our 10-fold estimate of increase in detection distance is too high because FBs are not as loud as SCs, the fact that indirect detection distance can be increased into every direction where there is another bat flying in close proximity probably increases the probability of finding a food resource.

Confirming our second hypothesis as well, we showed that female *N. albiventris*, which emerged from their roost as a group, also foraged together. A similar behaviour had been inferred by monitoring emergence from and return to the roost in female evening bats (Wilkinson 1992). Social foraging was also suspected to be a reason for the formation of stable female groups in *N. leporinus* (Brooke 1997). However, due to methodological limitations, it was not possible to confirm this hypothesis. Our use of an automated telemetry system allowed the simultaneous radio-tracking of groups of bats. Group members were found to be flying within 34.7 m or less of each other between 85 per cent and 100 per cent of the time. Members of groups A–C were occasionally observed leaving their group and foraging on their own. However, usually, they joined the remainder of the group again later

rather than completing the foraging period and returning to the roost on their own. This suggests that although it is important to emerge together from the roost as a group to facilitate social foraging, bats are also able to distinguish their roost mates from other *N. albiventris* foraging in the same area through some unknown cue, probably by their call structure (Masters 1995; S. L. Heucke 2008, unpublished results) and/or olfactory cues (Bouchard 2001). The non-significant trend towards increased bat activity during playbacks of SCs indicates that maybe the louder SCs are used for group cohesion and possibly also finding the right group again.

Group foraging could only be beneficial if the increased foraging efficiency outweighs the potential costs of more rapid exploitation of insect swarms (Beauchamp 2005). The latter may not be relevant for our study species, since insect swarms over the water occur mainly during a very narrow time window just around sunset, and because swarms quickly start to scatter as an avoidance mechanism once one or several bats start exploiting them (Jones & Rydell 2003). Quite possibly as a response to this short peak in prey availability, *N. albiventris* spends only approximately 1 hour outside the roost every day, including time needed to commute to and from the foraging areas. Faecal analysis shows that the insects consumed by *N. albiventris* are very small (2–3 mm, D. K. N. Dechmann 2008, personal observation). In addition, the weight difference between emerging and returning bats is 6 g or more ($n = 5$, D. K. N. Dechmann 2008, personal observation), indicating that a large number of insects are being caught during this short foraging period, further corroborating the need for efficient foraging.

Competition for insect swarms with other species might potentially be more important than accelerated patch exploitation. However, there were very few and often no other bat species foraging directly over the water surface while *N. albiventris* was present, as became evident from the audio recordings. The larger and ecologically similar *N. leporinus* forages in the same areas, but appeared later and all other bats we recorded on our audio files foraged higher up in the air, while *N. albiventris* was always seen within approximately 1 m of the water during our experiments. Similarly, on our recordings, *N. albiventris*' main frequency range showed little overlap with calls of other simultaneously foraging bat species, which could mask and interfere with their own calls, making both active and passive foraging more difficult.

Coordination of foraging with group members via screech calls, specially produced for this purpose, and thus active information transfer, has been described in another bat, *Phyllostomus hastatus* (Wilkinson & Boughman 1998). However, in *Ph. hastatus*, roosts function as information centres from which successful foragers can be followed to fruiting trees during the next foraging bout of the same night. *Noctilio albiventris* feeds on a short-lived food source that constantly changes in time and space; insect swarms that cannot be exploited repeatedly. In addition, there is usually only one foraging bout per night in *N. albiventris*. Thus, roost members have to stay together and simultaneously exploit food sources. Any bat, which encounters an insect swarm, starts catching prey and thus producing FBs. The information content of these FBs is an unavoidable by-product and useful for other group members (and other *N. albiventris* that happen to be within
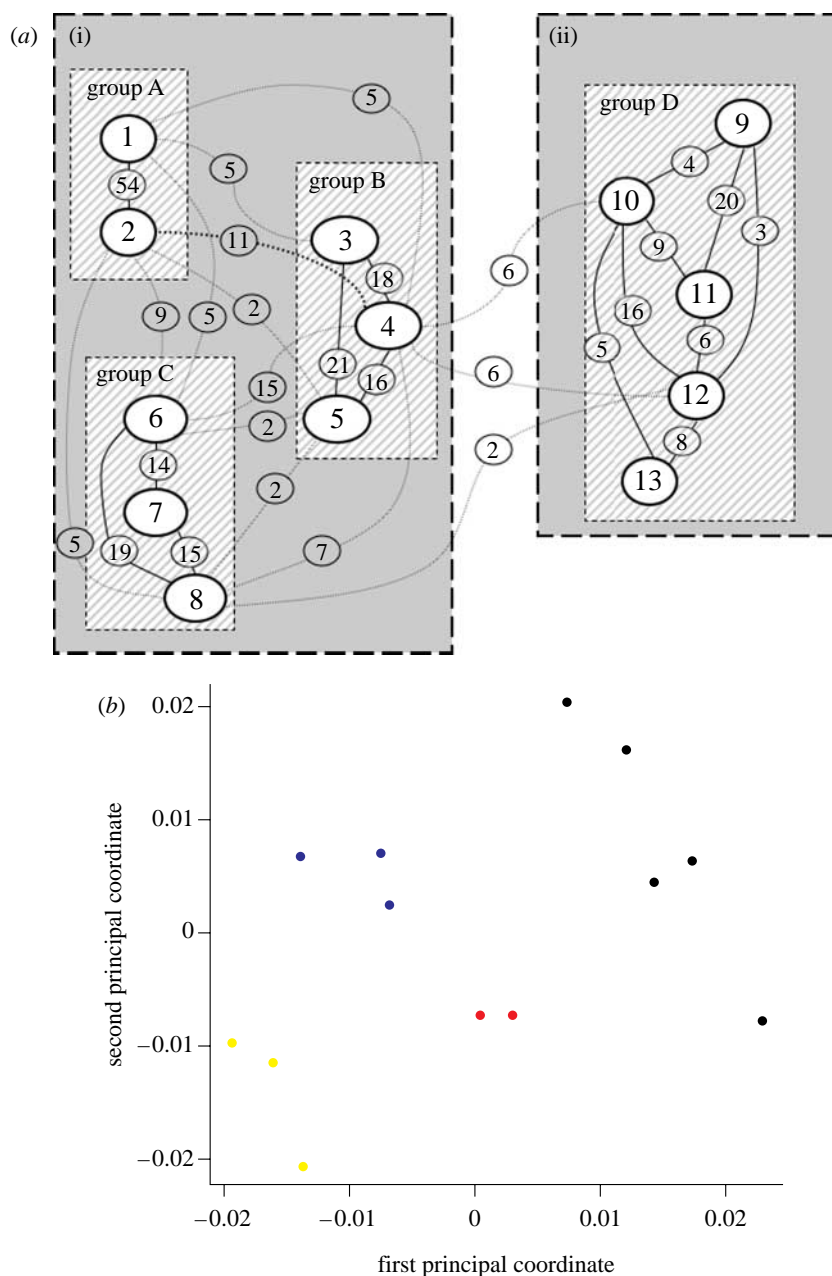
Figure 4. (*a*) Graphical representation of the structure emerging from the network of co-locations of foraging individual bats. Thick-dashed rectangles cluster animals from the same roost. Thin-dashed rectangles cluster animals from the same group. The shown subdivision is obtained as the maximum value of the network modularity ($Q = 0.48$), and it corresponds to the social structure inferred at capture. The bats are represented by a number in a thick oval shape. Bats that foraged together are connected with a thin line. The number of co-locations between two bats is depicted by the number in a thin ellipse breaking the line connecting them. Co-located bats from the same group are connected by a solid line, bats from different social groups by a dotted line ((i) roost 1 and (ii) roost 2). (*b*) Two-dimensional representation co-locations of bats during radio tracking, using a non-metric multidimensional scaling analysis. The distance between individual points is proportional to the inverse of the ranked pairwise number of co-locations. Large distances therefore represent a low number of co-locations, while small distances symbolize a large number of co-locations (red circles, group A; blue circles, group B; yellow circles, group C; black circles, group D).

earshot). Additional active communication via social calls does not seem to be necessary, but cannot be excluded based on our data, even though we never recorded social calls during our experiments.

It had been previously shown that FBs attract conspecific and heterospecific bats (Fenton 2003; Gillam 2007), but it remained unclear whether this was an opportunistic behaviour or the main foraging strategy, and thus potentially linked to the evolution of sociality. In fact, some species may use eavesdropping opportunistically or seasonally, depending on the occurrence of

insect swarms. However, our data from the wet season in Panama make a clear link between emerging to forage as a group and attraction by conspecific echolocation calls. Relatedness between members of socially foraging groups remains unknown, as does the mechanism through which this behaviour is learned and both warrant further investigation.

In summary, we show that social foraging in *N. albiventris* is non-opportunistic and allows a manifold increase in the detection distance of insects and thus potentially more efficient exploitation of patchily

distributed, but rich food sources, which are available only during a narrow time window. Similar to the findings of Ruczynski *et al.* (2007) in the context of roost finding, our results confirm the important role of passive information transfer via auditory cues for sociality in bats and potentially many other animals.

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