Information transfer in bats

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Synopsis

Here I review, and present new, evidence indicating that bats gain information about their environment, i.e. the location or quality of food, roosting sites, predators or mates, from other bats. Four mechanisms—local enhancement, social facilitation, imitative learning, and intentional signalling—of acquiring or transmitting information are described. Local enhancement or inadvertent direction to a resource has been demonstrated for two situations—eavesdropping and following. Playback experiments with several species show that insectivorous bats approach echolocation calls. Non-random departures from nursery colonies have been described for several species; in *Nycticeius humeralis* individuals improve their foraging success by following previously successful foragers to feeding sites. Social facilitation may occur in at least one group-foraging species where *per capita* feeding attempts increase with group size. Imitative learning has been reported for several species learning to feed under novel situations in the laboratory, but the data are consistent with local enhancement and individual learning. Matching of echolocation call frequency in one species provides the best evidence for imitative learning, while matching of isolation calls to directive calls may simply reflect heritable ontogenetic change.

Intentional or voluntary signalling occurs among bats during courtship, attempted predation, resource defence and resource advertisement. For each of these situations evidence from one or more species indicates that the type or frequency of vocalization changes depending on the identity of potential receivers of the signal. In a few cases, such as defensive calls while feeding from horses in *Desmodus rotundus* and group foraging calls in *Phyllostomus hastatus*, individuals selectively give or withhold calls depending on whether or not individuals are from the same social group. Signalling situations relevant to recent theory regarding honest advertisement are identified as exciting opportunities for further study.

Introduction

Although many bats are notable for their ability to extract information from the environment by using echolocation, in this paper I evaluate evidence indicating that bats also obtain information about the location or quality of

food, roosting sites or mates from conspecifics. I focus on auditory signals because this sensory modality has received the most study. To clarify function I distinguish four mechanisms for information transfer—local enhancement, social facilitation, imitative learning and intentional signalling. Although some of these terms were developed to describe social learning, they differ from each other with respect to the potential costs and benefits associated with information transfer. Therefore, by categorizing bat behaviours with these terms I hope to illuminate the ecological and evolutionary conditions that favour information transfer.

Local enhancement refers to one organism inadvertently directing the behaviour of another to some region of the environment. While local enhancement is often used for situations where animals can observe each other feed, inadvertent direction to a resource can occur away from feeding sites if animals forage from a central place. For this reason, cases in which animals follow conspecifics from a colony to feeding or roosting sites represent examples of local enhancement. Local enhancement is not advantageous to the animal which is followed unless group foraging is beneficial or information about the location of unpredictable resources is exchanged over time. As I have argued elsewhere (Wilkinson 1992b), information exchange can result from conditional following without reciprocity.

Social facilitation operates when individual feeding rate is improved in the presence of a conspecific. Thus, in contrast to local enhancement, all members of a group benefit immediately from sharing information about the location of a foraging site. While many forms of social facilitation are possible, here I emphasize cases of group foraging involving transfer of information about feeding sites or individual identity.

Imitative learning permits more rapid acquisition of novel behaviours than does trial-and-error learning, and could allow group-living individuals to share feeding skills (Giraldeau 1984). Imitation can be inadvertent if a naive individual observes a knowledgeable animal, or directed, i.e. involving teaching, if a knowledgeable animal repeats a behaviour more often in the presence than in the absence of a naive conspecific. Genetic models predict that imitative learning should be favoured by natural selection when the environment is predictable and individual learning is either inaccurate or costly to make accurate (Boyd & Richerson 1988). Distinguishing imitation from local enhancement and trial-and-error learning is, however, difficult. The best evidence for imitation is association of a particular motor pattern with a novel behaviour (Galef 1988). Because unnecessary repetitions of a behaviour consume energy and may increase predation risk, teaching should be very uncommon.

Intentional signalling requires that signals should be produced only in association with particular aspects of the environment and should be under voluntary control. For example, alarm and food calls alert conspecifics about particular features of an individual's immediate environment. Whether or

not intentional signals provide honest information is controversial (Hauser & Nelson 1991). Until recently, behavioural ecologists thought that signals rarely provide accurate information and function to manipulate the behaviour of recipients for individual gain (Krebs & Dawkins 1984). Honest signalling was assumed to be limited to close relatives or long-term associates, thereby enhancing inclusive (Hamilton 1964) or direct fitness through reciprocity (Axelrod & Hamilton 1981), respectively. However, recent theory suggests that signals should provide honest information because only costly signals that still provide a net benefit to the signaller represent evolutionarily stable strategies (Grafen 1990; Maynard Smith 1991). Because this controversy is unlikely to be settled without more evidence, I identify possible cases of intentional signalling where deception could occur.

Because few studies on bats have been designed to assess information transfer, below I review cases of bat social interactions involving vocalizations which could represent examples of local enhancement, social facilitation, imitative learning or intentional signalling. Where function is uncertain, I provide possible adaptive explanations. My objective is two-fold: to illustrate the diversity of vocal signals used by bats to mediate social behaviour and to stimulate further work on communication call function in bats.

Local enhancement

Eavesdropping

Because most insectivorous bats use an active detection system for capturing prey, echolocation pulses, especially those used for capturing prey, can provide information about the location of feeding sites to other bats. Aggregations of bats at rich feeding sites could form more quickly if individuals responded to each other's vocalizations than if they independently discovered prey patches by searching. Accordingly, groups of several temperate insectivorous bat species have been observed forming rapidly around ephemeral insect patches, e.g. *Myotis* spp. (Fenton & Morris 1976; Bell 1980), *Pipistrellus pipistrellus* (Racey & Swift 1985), *P. kuhlii* (Barak & Yom-Tov 1989). That eavesdropping leads to group formation has been demonstrated with playback experiments for adult and recently volant *Myotis lucifugus* which approached speakers broadcasting echolocation calls emitted by both *M. lucifugus* and *Eptesicus fuscus* (Barclay 1982). Playbacks to *Lasiurus borealis* indicate that this species responds only to conspecifics (Balcombe & Fenton 1988).

Eavesdropping as a method for acquiring information about foraging sites should differ between species, depending on frequency and amplitude of echolocation pulses, as well as on the presence of obstructions between foragers, because atmospheric attenuation has larger effects on high- than on low-frequency sounds (Griffin 1971). Atmospheric attenuation can vary from 0.2 to 15 dB/m depending on frequency and humidity, and adds to the 6 dB loss per distance doubling caused by spherical spreading (Griffin 1971;

Lawrence & Simmons 1982). Many insectivorous bats partially overcome attenuation by producing echolocation calls with amplitudes in excess of 110 dB at 10 cm (Griffin & Novick 1955). In contrast, phyllostomid bats produce much quieter echolocation calls of 75 dB at 10 cm (Griffin & Novick 1955). To illustrate the consequences of frequency and amplitude variation on eavesdropping, I have estimated the distance a 110 dB or a 75 dB sound would travel before reaching 0 dB under several temperature and humidity conditions experienced by temperate and tropical bats (Fig. 1), using ANSI predictive equations (Acoustical Society of America 1978). These calculations predict that an *Eptesicus fuscus* emitting 110 dB, 40 kHz calls (Masters, Jacobs & Simmons 1991) on a 30 °C evening with 100% relative humidity can detect conspecifics calling at 60 m. In contrast, a *Leptonycteris curasoae* with 75 dB, 35 kHz calls (Howell 1974) should detect conspecifics within 20 m on a 30 °C, 25% relative humidity night, while *Glossophaga soricina* with 75 dB, 100 kHz calls (Griffin & Novick 1955) would hear conspecifics no more than 9 m away on a 30 °C, 100% relative humidity night. Actual detection distances may be substantially less if obstructions, such as trees or bushes, are present in the foraging area or if there is noise from wind or insects that would mask the echolocation signal and raise the detectability threshold above 0 dB. Conversely, longer distances may be possible for bats foraging over water because the water surface reflects sound and can act as a wave guide (Wiley & Richards 1978).

If foraging success declines in the presence of conspecifics, then bats should modify their echolocation calls in the presence of conspecifics to reduce eavesdropping. One method for decreasing transmission distance is to increase call frequency. Reduction of eavesdropping could explain cases where more energy
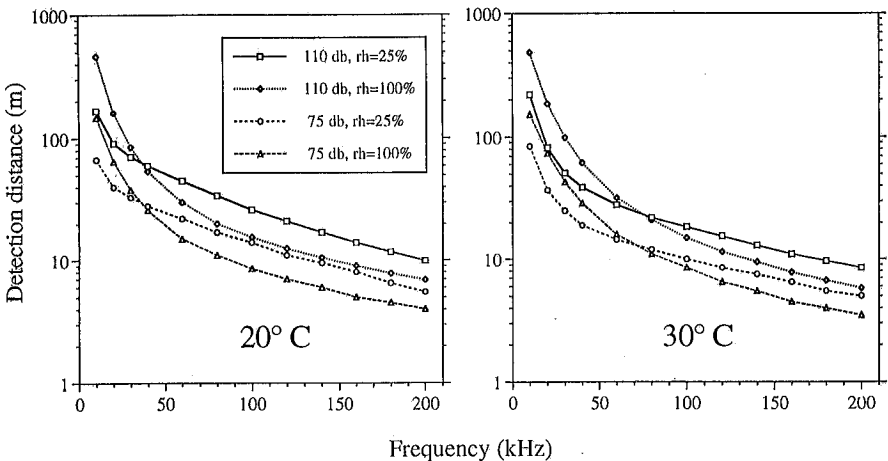

Fig. 1. Distance at which a 110 dB or 75 dB signal of a given frequency will decrease to 0 dB. Attenuation occurs through spherical spreading and atmospheric absorption.

is put into high-frequency components of a call, e.g. by foraging *Rhinolophus rouxi* (Neuweiler, Metzner, Heilmann, Rubsamen, Eckrich & Costa 1986). Alternatively, echolocation may be used less frequently. Observations of *Antrozous pallidus* (Bell 1982) and *Macrotus californicus* (Bell 1985) not using echolocation while capturing prey may, therefore, represent behavioural adaptations to avoid alerting competitors to the presence of large food items rather than to avoid alerting prey to imminent capture. In support of this proposition, ultrasonic hearing organs have never been described (D. Yager pers. comm.) for two favourite prey items of *Antrozous pallidus*, scorpions and Jerusalem crickets (Hatt 1923).

Following

An alternative, but not exclusive, mechanism for locating feeding sites is to follow conspecifics. Following behaviour is expected when resources are unpredictable but persist long enough for multiple foraging trips to be profitable. Although many, if not most, temperate insectivorous bats may experience such food dispersion, only individuals which make multiple foraging trips per night and gather at a common site between trips can benefit from following. These conditions occur in some species during lactation when young are left at a communal nursery roost and females take several foraging trips per night to meet the energetic demands of producing milk. Recent efforts to monitor departure intervals from communal roosts have demonstrated that at least three temperate insectivores, *Eptesicus fuscus* (Brigham & Fenton 1986), *Pipistrellus pipistrellus* (Speakman, Bullock, Eales & Racey 1992) and *Nycticeius humeralis* (Wilkinson 1992b), depart in small clusters more often than would be expected by chance. Although Speakman *et al.* (1992) suggest that clustered departures may be due to a bottleneck at the roost exit, clustered departures of *N. humeralis* occurred after the initial evening exodus between 2200 and 0500, at a time when departures were sufficiently infrequent to preclude a bottleneck (Wilkinson 1992b).

Evidence from variation in prey density, location of foraging radio-tagged individuals, and individual weights before and after departing within 10 s of a previously successful or unsuccessful forager provide strong evidence that *N. humeralis* follow each other in order to improve foraging success (Wilkinson 1992b). At least 20% of departing animals did not gain weight while out of the roost, indicating that they failed to locate ephemeral, rich prey patches. On average, 16% of second or later departures occurred within 10 s of the departure of another bat. Because radio-telemetry data indicate that females sometimes change feeding sites within and between nights as well as forage with other bats, we postulate that following occurs only after independent searching has failed. Following apparently improves foraging success because the weights of bats that followed previously successful foragers were greater than the weights of bats that did not follow (Fig. 2).
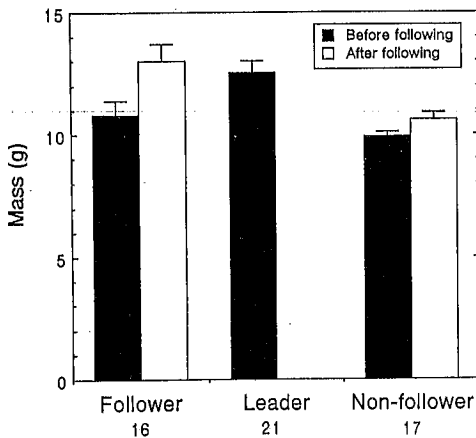
Fig. 2. Average (±SE) weight of *Nycticeius humeralis* after a foraging trip (before following) and, on the same night, after a subsequent trip on which they followed another bat (after following).

Because followers benefit at the expense of searchers, following would provide higher inclusive fitness if exchanged among relatives than if exchanged among unrelated individuals. However, the average relatedness among leader-follower pairs was -0.12 (SE $= 0.07$, $n = 41$ pairs), estimated by genotypic correlation (Queller & Goodnight 1989) using four polymorphic allozymes (Wilkinson 1992a). Furthermore, only one of ten leader–follower pairs shared the same mitochondrial DNA sequence haplotype (Wilkinson 1992a)—a result to be expected if bats arbitrarily choose colony mates to follow.

These results are consistent with previously unsuccessful foragers simply following a colony member chosen at random on a subsequent trip. The weight data indicate that such a strategy would allow a follower to avoid paying search costs on 80% of subsequent departures. Why do not some females forego independent searching and simply wait to follow another bat? I suspect the energetic demands of lactation are so great in this species that a female which did not attempt to hunt at dusk would not be able to capture enough prey during the night to meet her energy requirements and those of her two or three young. At peak lactation female *N. humeralis* produce half their body weight in milk per day (Steele 1991) and make an average of four foraging trips per night (Wilkinson 1992b).

Social facilitation

Group foraging is commonly observed among bats which forage either close to water or on nectar and pollen. Although some cases of flocking may represent opportunistic aggregations formed by local enhancement, several species forage in persistent groups and exhibit co-ordinated flight.

For example, *Rhynchonycteris naso* (Bradbury & Vehrencamp 1976), *Myotis adversus* (Dwyer 1970), *Pipistrellus kuhlii* (Barak & Yom-Tov 1989), *Noctilio leporinus* (A. Brooke pers. comm.), *Leptonycteris curasoae* (Howell 1979), and *Phyllostomus discolor* (Sazima & Sazima 1977) have all been observed flying one bat after another while hawking insects, gaffing fish or visiting flowers, respectively. Whether such co-ordinated tandem flight provides similar information to conspecifics in each of these situations is currently unknown. Tandem flight may enable bats to monitor the foraging activity of others in the group in order to avoid recently visited feeding sites. Alternatively, fish or insects fleeing from one bat may be more easily captured or detected by other bats in the group. In support of this assertion, *per capita* feeding buzz rate correlated with group size for *P. kuhlii* foraging around street lights (Barak & Yom-Tov 1989).

If foraging success improves as group size increases, then signals that reliably attract conspecifics would be favoured by natural selection. One method for advertising prey availability is to lower the frequency of the terminal buzz in an attack sequence so as to increase detection distance, as has been observed in *P. kuhlii* (Schnitzler, Kalko, Miller & Surlykke 1987) and *Myotis daubentonii* (Kalko & Schnitzler 1989). Whether such calls represent a physiological constraint (Kalko & Schnitzler 1989) or a mechanism for increasing foraging-group size requires further study. Low-frequency calls could also be used to advertise location. For example, the directive calls of *Antrozous pallidus* (O'Shea & Vaughan 1977) appear to recruit conspecifics to roost sites, possibly to improve thermoregulation (Trune & Slobodchikoff 1976).

Co-ordinated tandem flight requires that bats monitor the location of conspecifics, presumably by eavesdropping on echolocation pulses. When foraging groups contain the same individuals over time, e.g. *P. pipistrellus* (Racey & Swift 1985), *N. leporinus* (A. Brooke pers. comm.), *P. discolor* (Wilkinson 1987), and *P. hastatus* (G. S. Wilkinson & J. Boughman unpubl.), individual recognition must also occur. Individual recognition of echolocation cries has been demonstrated in *Eptesicus fuscus* (Masters & Jacobs 1989) and could occur in bats where echolocation pulses differ between individuals, e.g. *P. pipistrellus* (Miller & Degn 1981), *Rhinopoma hardwickii* (Habersetzer 1981), *E. fuscus* (Masters et al. 1991), *Lasiurus borealis* (Brigham, Cebek & Hickey 1989) and *Pteronotus parnellii* (Suga, Niwa, Taniguchi & Margoliash 1987).

Imitative learning

Foraging technique

Imitative learning has been reported for *Eptesicus fuscus*, *Myotis lucifugus* and *Antrozous pallidus* (Gaudet & Fenton 1984). Naive bats allowed to search for mealworms suspended from a wall learned to locate prey more quickly when a knowledgeable bat was present, whereas naive bats allowed to search alone did not discover food during the testing period. Similarly, naive *Phyllostomus*

discolor searching for one accessible food cup among an array of 16 cups in the presence of a knowledgeable conspecific found food more rapidly than did naive bats searching alone (Wilkinson 1987).

Neither of these examples requires observational learning. If solitary bats search less than bats hunting in a group, i.e. demonstrate a 'fear effect' (Galef 1988), then naive bats hunting in a group should locate food more rapidly by individual learning than do solitary bats. Alternatively, if naive bats followed knowledgeable bats, then the area to search would be reduced. Food could then be located by individual learning more quickly as a consequence of local enhancement.

Offspring might also be expected to learn how to feed from observing their mothers or other adults. Although the young of some bat species learn to fly and feed independently of their mothers (Buchler 1980), anecdotal reports on *Eptesicus fuscus* (Brigham & Brigham 1989), *Noctilio albiventris* (Brown, Brown & Grinnell 1983) and *Lavia frons* (Vaughan & Vaughan 1987) indicate that females occasionally associate with recently volant young outside the roost. Video records of *Nycticeius humeralis* departing from an attic roost on three nights reveal that six of 25 recently volant (average age 30 days) pups departed after 2200 within 10 s of an adult female. This represents more paired departures than would be expected ($P < 0.001$, 1000 randomizations) if adults and juveniles were departing at random. However, only two of the six juveniles followed their mothers: the remaining four followed unrelated adult females. In contrast, female *Desmodus rotundus* often feed in the same pastures and sometimes at the same bite with daughters during their first year (Wilkinson 1985). Species with difficult feeding techniques and protracted periods of association between mothers and young, such as *D. rotundus* or *Vampyrum spectrum*, deserve further study to document imitative learning.

Vocalizations

One method for advertising group membership is to adopt a common vocalization. This requires imitation of a call—an uncommon ability in mammals. Observations that *Phyllostomus discolor* infant isolation calls converge on maternal directive calls during a 45-day period after birth have been promoted as evidence for imitative learning (Esser & Schmidt 1989). Since isolation calls closely resemble female directive calls in several species, such as *Tadarida brasiliensis* (Balcombe & McCracken 1992) and *P. hastatus* (D.L. O'Reilly & G.S. Wilkinson unpubl.), directive call imitation could be widespread. However, infant isolation calls should also eventually resemble maternal directive calls if these two call types are ontogenetically related (Brown 1976) and heritable. In support of this suggestion we have estimated significant heritabilities for spectral variables measured from isolation calls of 39 *Nycticeius humeralis* sibling pairs (Scherrer & Wilkinson 1993) and from 22 groups of *Phyllostomus hastatus* (D. L. O'Reilly & G.S. Wilkinson

unpubl.). Because harem male *P. hastatus* typically father all of the young in a female group (McCracken & Bradbury 1977), the young within a group are paternal half-siblings. The recent claim (Rasmuson & Barclay 1992) that isolation calls of *Eptesicus fuscus* are not heritable should be viewed with caution as only two pairs of siblings were measured.

Recent observations of extreme similarity in the constant frequency portion of the echolocation pulse between mother and young *Rhinolophus ferrumequinum* suggest that imitative learning can influence echolocation calls (Jones & Ransome 1993). Deafening experiments have demonstrated that *R. rouxi* need to hear to produce appropriately tuned echolocation pulses (Rubsamen & Schafer 1990). However, the ability to modify echolocation call resting frequency may be a consequence of a matched signal-receiver system and have little functional significance for information transfer except to provide a mechanism for generating individual differences.

Intentional signalling

Mating calls

The most spectacular mating calls in bats occur among epomophorine bats (Wickler & Seibt 1976; Bradbury 1977a) which employ lek or exploded lek mating systems (Bradbury 1981). In addition, a diverse array of microchiropteran species, including *Saccopteryx bilineata* (Bradbury & Emmons 1974), *Cardioderma cor* (Vaughan 1976), *Nyctalus noctula* (Miller & Degn 1981) and *Pipistrellus pipistrellus* (Miller & Degn 1981), use audible calls during courtship. At least for *Hypsignathus monstrosus*, courtship calls represent intentional signals because call rate increases when females approach (Bradbury 1977a). Individual males may also have distinctive courtship calls, e.g. *Epomophorus wahlbergi* (Wickler & Seibt 1976) and *P. pipistrellus* (G. Jones pers. comm.). Further study is needed to determine if variation in some aspect of these calls influences female visitation rates by honestly or deceptively signalling male quality.

Distinct vocalizations associated with copulation have been described for *Myotis lucifugus* (Barclay & Thomas 1979) and *Hypsignathus monstrosus* (Bradbury 1977a). Barclay & Thomas (1979) argue that copulation calls signal to the female being mated that a male intends to copulate, not fight, with her. Such an interpretation seems unlikely for *H. monstrosus*, since these calls occur at the end of a copulation in this species (Bradbury 1977a). An intriguing alternative hypothesis is that males are signalling their mating success to other females. In many lekking birds, females visit male arenas and observe copulations for several days before selecting a mate (Bradbury & Gibson 1983). Because bat copulations usually occur in darkness, females may need to rely on sound to monitor mating activity. If copulation calls are costly for males to produce, then they could provide reliable indicators of male mating activity. This explanation is consistent with male *M. lucifugus*

not calling during mating when females are in torpor and with call differences among males (Barclay & Thomas 1979).

Alarm calls

Some of the best evidence indicating that non-human animals can associate signals with environmental referents involve species that use different alarm calls for different types of predators (Seyfarth, Cheney & Marler 1980). Among bats, alarm calls have been reported only for *Pteropus poliocephalus* (Nelson 1964). Distinct calls associated with different classes of predators have not been described. However, I suspect that alarm calls may be more common among bats. During my work with nursery colonies of *N. humeralis* and *P. hastatus* I have noticed that once animals have been captured in a roost, subsequent approach with a headlamp causes an increase in the intensity and frequency of audible vocalizations.

Many bats emit loud, low-frequency vocalizations when captured. These distress calls might startle or acoustically impair potential predators. However, they also often attract conspecifics (August 1979). Given the prevalence of this behaviour, playback studies would be useful in determining whether distress calls elicit mobbing behaviour.

Territorial calls

Observations of chases and vocalizations among marked or recognizable individuals indicate that resource defence is particularly common among tropical bats, quite possibly because resource dispersion in these areas is more stable over time than in temperate areas. For example, several emballonurid bats, *Rhynchonycteris naso, Saccopteryx leptura* and *S. bilineata*, maintain group territories by chasing and vocalizing at intruders (Bradbury & Emmons 1974; Bradbury & Vehrencamp 1976). A variety of species that utilize a sit-and-wait foraging strategy defend territories by chasing intruders or vocalizing. Bats which maintain solitary feeding territories include *Hipposideros commersoni* (Vaughan 1977) and *Rhinolophus rouxii* (Neuweiler *et al.* 1986). The megadermatids, *Cardioderma cor* (McWilliam 1987) and *Lavia frons* (Vaughan & Vaughan 1986), form reproductive pairs in which one or both members of the pair defends the territory by chasing and vocalizing at intruders. Among vespertilionids, *Myotis daubentonii* (Wallin 1961) and *M. adversus* (Dwyer 1970) have been observed chasing conspecifics at foraging sites, while *P. pipistrellus* foraging on a regular beat will chase and vocalize at conspecifics when food density is low (Racey & Swift 1985). *D. rotundus* maintain exclusive group feeding areas and will attack, chase and vocalize (Sailler & Schmidt 1978) at non-roost group members that attempt to feed from the same prey animal (Wilkinson 1985). Because some individuals, including relatives, are allowed to feed from the same wound without aggression (Wilkinson 1985), this example demonstrates intentional signalling.

Food calls

At least two species of bats, *Macroderma gigas* and *Phyllostomus hastatus*, give audible vocalizations at feeding sites without evidence of territorial behaviour. *M. gigas*, like other megadermatids, use a sit-and-wait hunting strategy but produce loud chirps while hunting (Tidemann, Priddel, Nelson & Pettigrew 1985). Observations and radio-tracking provide no evidence that these calls advertise feeding territories. In contrast, up to 20 individuals have been observed foraging in a common area and calling at a rate that correlated with hunting activity (Tidemann *et al.* 1985). Further study is needed to determine if these calls advertise food and if social facilitation occurs.

For the last two years my students and I have been studying *Phyllostomus hastatus* to determine the function of loud, low-frequency screech vocalizations (Fig. 3) given by flying bats when departing from a roost and at feeding sites (Greenhall 1965). These 75–100 g bats feed on fruit, pollen and insects (Gardner 1977) and have been observed foraging in groups on termites (Bloedel 1955), sapacaia nut fruits (Greenhall 1965), and *Hymenaea courbaril* pollen (McCracken & Bradbury 1981). By monitoring bats flying into and out of a cave roost on video using infra-red illumination, we have discovered that bat departures and screech calls are clustered throughout the night, while
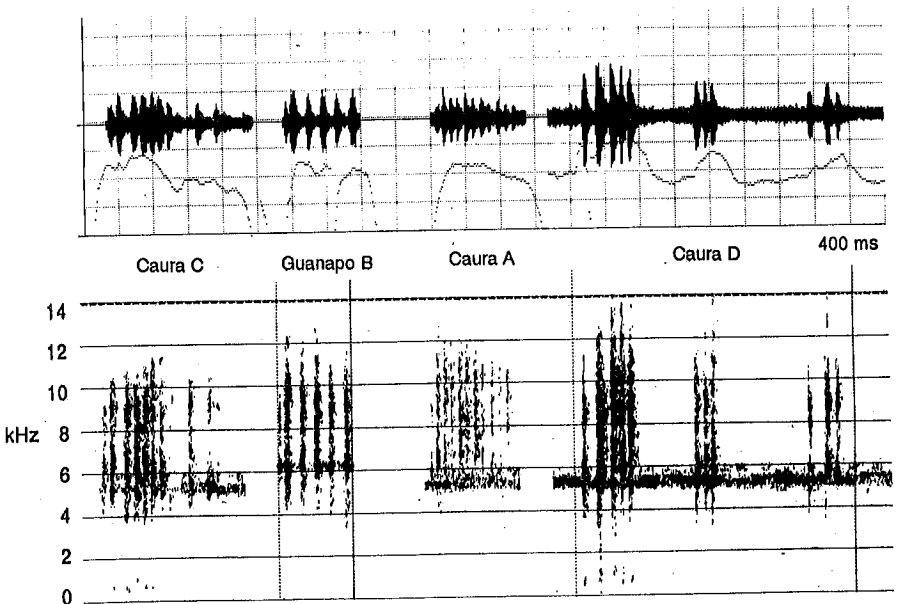

Fig. 3. *Phyllostomus hastatus* screech calls from four individuals recorded at two caves in Trinidad, W. I. The grid interval in the upper portion of the figure is 400 ms.

arrivals are random. By broadcasting screech calls from speakers we have demonstrated that these calls attract conspecifics and elicit additional calling both at the roost site and at flowering balsa trees, *Ochroma lagopus*, where we have observed groups of bats to feed and produce screech calls. We have heard screech calls from groups, but rarely from solitary individuals, flying to feeding sites. By attaching light-emitting diodes of a single colour to all adult females in a roosting group, we have observed group mates departing in pairs and giving screech calls more often than expected. Bats that return to the cave after a feeding trip and fly directly into the cave almost never give screech calls, while those that return, circle and subsequently depart give calls and are accompanied by a group mate more often than expected.

Because screech calls are not confined to either the lactation or the mating period, they do not involve parental care or courtship. Furthermore, an alarm call function seems dubious because screech calls occur frequently at the cave as well as in transit to feeding sites in the absence of any aerial predators. Current evidence suggests that these calls function to recruit conspecific bats into foraging groups and are given at times when group members will hear them. We are currently investigating whether these calls carry information about individual identity and are given by animals which have either located or failed to discover feeding sites. Because adult females within roost groups are unrelated to each other (McCracken 1987) but form stable associations that persist for many years, active advertisement of food sites could be favoured by natural selection through a reciprocal exchange system in this species.

Conclusions

As past reviews (Bradbury 1977b; Fenton 1985) of bat communication have emphasized, the ecological and social diversity of bats in conjunction with their aerial, nocturnal lifestyle suggests that vocal signals play a critical role in mediating social interactions. While this review illustrates that progress has been made in understanding some of the information available to conspecifics from bat vocalizations, many unanswered questions clearly remain. At present, no unambiguous examples of deceptive signalling have been documented, even though situations where deception might be advantageous have been known for some time, such as territorial defence (Bradbury & Emmons 1974), courtship (Bradbury 1977a) and food sharing (Wilkinson 1984). With the availability of inexpensive portable digital instruments capable of recording ultrasound, I anticipate that many exciting discoveries will be forthcoming in the near future.

Acknowledgements

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