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# Mammalian Social Learning:

Comparative and Ecological Perspectives

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## Social influences on foraging in bats

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### Introduction

Theory developed over the past decade (e.g. Boyd and Richerson 1985, 1988, Laland *et al.* 1993, 1996, Barta and Szep 1995) predicts that the extent to which socially mediated biases are to be expected in the transmission of behaviours among animals should depend on environmental predictability, fitness effects associated with adopting alternative behavioural variants, and social organisation. If the environment fluctuates rapidly, social transmission will fail to track those changes. On the other hand, if the environment changes slowly or predictably, social learning can be favoured if it reduces costs associated with individual learning. The rate at which novel behaviours will spread through a population by social learning is also influenced by the types of interactions permitted by the social organisation. Transmission among unrelated animals in the same generation (horizontal) or among unrelated animals across generations (oblique) permits more rapid change than transmission from parents to offspring (vertical). Consequently, social learning may be especially important when unrelated animals have frequent opportunities to interact while making decisions that affect their survival and reproduction.

With over 900 described species, the order Chiroptera almost certainly contains more species predisposed to social learning than any other order of mammals for at least four reasons. 1. Most bat species exhibit communal roosting during all or part of the year. With over 80% of bat species occurring in tropical regions, communal roosting is often associated with mating or rearing young, rather than hibernating. Because lactating bats often make multiple feeding trips in a night (Wilkinson 1992, Wilkinson and Boughman 1998), communal nursery roosts seem especially likely to provide numerous opportunities for acquiring information about the location of food or other resources. 2. Many bat species also move seasonally between traditional roosts. In some temperate species, mating and hibernation occurs at winter roosts. In some migratory species, such as the lesser long-nosed bat, *Leptonycteris curasoae* (Figure 11.1 Wilkinson and Fleming 1996), individuals may utilise several roost sites separated by as much as 1000 km. Naive young bats almost certainly follow older bats (Wilkinson 1992) to alternative roost sites, as would

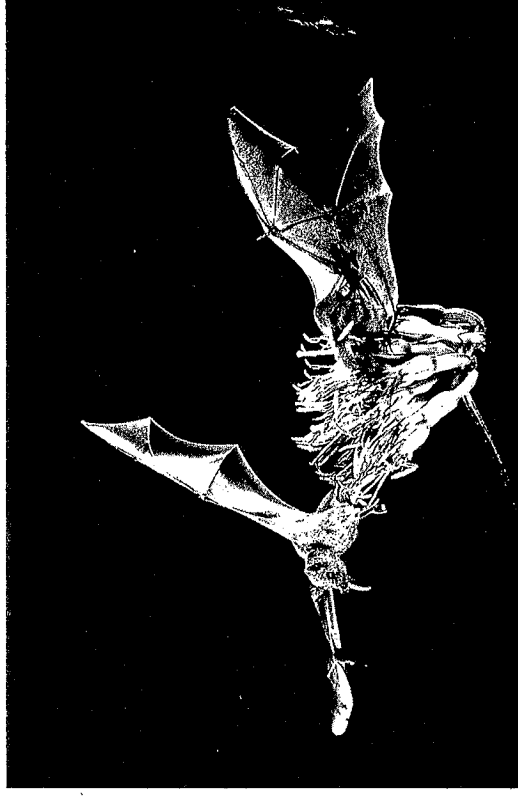


Figure 11.1. Lesser long-nosed bats.

be expected given the potential costs associated with mistakes. 3. For their size, bats are exceptionally long-lived and often exhibit female philopatry. For example, banding studies have revealed that 10 g little brown bats, *Myotis lucifugus* (Keen and Hitchcock 1980), and 20 g greater horseshoe bats, *Rhinolophus ferrumequinum* (Jones *et al.* 1995), can survive 30 years or more. Our own studies have indicated that 35 g female common vampire bats, *Desmodus rotundus*, and 80 g female greater spear-nosed bats, *Phyllostomus hastatus*, can live 16 years in the wild (G.S. Wilkinson, unpublished results). Given that most species give birth to only one young, individuals in social groups vary in foraging experience. 4. All microchiropteran species use echolocation for orientation and many use it to capture prey. Because calling rate increases during prey attacks, echolocating bats broadcast their foraging activity to other individuals in their vicinity.

Despite tremendous ecological diversity and apparent opportunities for social learning, few studies have directly considered the degree to which social learning occurs in bats. Therefore, here we describe how three learning problems – choosing a diet, finding resources and communicating while foraging – may involve social learning in some species of bats and discuss evidence for socially mediated biases where available. We then use a recent model for animal social learning (Laland *et al.* 1996) to determine if variation in feeding patch longevity and foraging success predicts differences in following behaviour exhibited by evening bats, *Nycticeius humeralis*, greater spear-nosed bats

and common vampire bats. Qualitative agreement between the model predictions and frequency of following across species support using bats as model systems for studying social learning and information transfer at communal roosts.

### Opportunities for social learning in bats

#### Diet preference

Many species of bats form dense roosting clusters in caves, hollow trees or foliage. Despite the darkness of these sites, at least four different situations provide nonvisual cues about dietary preferences to roostmates. First, individuals may be able to smell or taste food which has adhered to the fur of neighbours. For example, in the process of visiting flowers many nectar feeding bats become covered in pollen, which is subsequently ingested while grooming at a communal roost. Some species, e.g. lesser long-nosed bats (Howell 1979) and lesser spear-nosed bats, *P. discolor* (G.S. Wilkinson and J.W. Boughman, unpublished results), groom roostmates and could ingest pollen from their fur. Horizontal transmission of flower preferences will probably depend on female social group stability, as this factor appears to determine allogrooming frequency across species (Wilkinson 1987).

Second, roostmates may acquire dietary information from faeces. Bat pollinated flowers and bat dispersed fruits often produce conspicuous, pungent odours which attract bats (Pijl 1961, Helverson 1993). Because fruit bats frequently defaecate within minutes after feeding (Werner and Gardner 1978), faecal odour can provide a prompt dietary cue. Socially mediated preferences caused by exposure to faecal odours seems plausible given the olfactory sensitivity of many fruit eating bats (Bhatnagar and Kallen 1974, Schmidt 1975).

Third, species which capture or collect large prey items, either fruit or animal, often bring some food items back to a day or night roost for consumption where these items could be smelled, felt or tasted by roostmates. For example, the fishing bat (*Noctilio leporinus*) consumes fish (Bloedel 1955), pallid bats, *Antrozous pallidus*, eat scorpions (Bell 1982), large slit-faced bats, *Nycterus grandis*, eat grasshoppers, fish and frogs (Fenton *et al.* 1981), fringe-lipped bats, *Trachops cirrhosus*, eat frogs (Tuttle and Ryan 1981), short-tailed fruit bats, *Carollia perspicillata*, eat *Piper* fruit (Fleming 1988), false vampire bats, *Vampyrum spectrum*, eat birds with noticeable odours (Vehrencamp *et al.* 1977), and greater spear-nosed bats consume large insects and a variety of fruit items (Wilkinson and Boughman 1998) in roosts. We have observed a female greater spear-nosed bat steal a large grasshopper from the mouth of a roost-

mate confirming that dietary information can be shared when food is consumed in the roost.

Finally, dietary preferences may be acquired if parents provision young. For example, nocturnal observations in a hollow tree revealed that an adult male false vampire bat returned with and subsequently shared a ground dove (*Columbina talpacoti*) with a juvenile (G.S. Wilkinson, unpublished results). Similarly, food sharing by regurgitation occurs frequently between females and young in common vampire bats (Wilkinson 1984), and may help juveniles learn the taste and smell of blood consumed by the mother. Common vampire bats have been reported to exhibit preferences for particular breeds of cattle and horses (Turner 1975).

#### Resource location

Microchiropteran bats find food in one of three ways: searching independently, following other bats from the roost to a feeding site, or approaching bats that are actively hunting or feeding. The latter two situations represent examples of social learning in which one bat attends to echolocation calls or other cues provided by another bat. Social learning can benefit a follower by reducing the energetic costs associated with searching and increasing the probability of finding food. However, following may cost a searcher to the extent that recruitment of another forager reduces individual consumption rates (Vickery *et al.* 1991). Following is expected, therefore, when rich food patches are short-lived and difficult to find (Waltz 1982, Barta and Szep 1995) – ecological situations likely to be common for many species.

#### Following

Although direct evidence for following is scarce, many species of bats leave communal roosts in groups, as expected if following occurs. For example, many pteropid species depart communal roosts at dusk and fly in groups to feeding areas (Nelson 1965, Thomas and Fenton 1978). Some also make seasonal migrations to track flowering and fruiting plants (Thomas 1983, McWilliam 1986, Richards 1995). Following may occur by visual observation in megachiropteran and some microchiropteran bats (Howell 1979) much as it does in some birds (Brown 1986, Rabenold 1987, Heinrich 1988).

In contrast, aerial insectivores could use echolocation calls for following. Such behaviour would cause clustered departures, as have been observed in many species (Wilkinson 1995). For example, pipistrelles (*Pipistrellus pipistrellus*) depart communal roosts nonrandomly (Speakman *et al.* 1992, 1995) and have been observed following at feeding sites (Racey and Swift 1985). Radio-telemetry studies of evening bats (Wilkinson 1992), common vampire bats

(Wilkinson 1985), lesser spear-nosed bats (G.S. Wilkinson, unpublished results) and greater spear-nosed bats (G.S. Wilkinson and J.W. Boughman, unpublished) have revealed that pairs of individuals sometimes depart together and subsequently feed in the same areas. Evening bats that followed on second foraging trips increased their foraging success, compared with bats that departed independently (Wilkinson 1992). Following can, therefore, facilitate food finding in some species.

With the exception of common vampire bats, in which females will feed simultaneously with their female offspring from the same bite (Wilkinson 1985), little evidence indicates that young bats follow their mothers to feeding sites (Wilkinson 1995). Nevertheless, young bats almost certainly follow adults in other situations. For example, two roost exclusion experiments demonstrated that newly volant evening bats followed adults to new roost sites in hollow trees (Wilkinson 1992). Bats that migrate to feed, hibernate or give birth at traditional sites provide additional examples in which vertical social learning probably occurs. Adults may tolerate the presence of young in these situations because resource competition is weak.

Following also occurs among bats flying in groups. A number of species have been observed flying in tandem within a few feet of each other while feeding on fish, fruit, flowers and insects (Wilkinson 1995). Experimental studies with lesser spear-nosed bats have revealed that naive bats allowed to forage with experienced bats take less time to find hidden food (Wilkinson 1987). On some trials, naive bats flew directly behind knowledgeable bats to the accessible feeding station. We have performed a similar experiment with greater spear-nosed bats, distributing hidden food either evenly or patchily and releasing bats alone or with a 1 min interval between two individuals. After log transformation, analysis of variance revealed a difference between singletons and pairs in the time elapsed to find food ( $F_{1,24} = 8.6$ ;  $P < 0.017$ ). Bats in pairs showed improved food finding only in the patchy environment. Singletons took longer to find food ( $134.3 \pm 1.5$  s) than either the first ( $21.3 \pm 1.7$  s) or the second bat ( $29.4 \pm 1.8$  s). In addition, bats tended to visit the same feeding stations as bats in previous trials, independent of location ( $P < 0.007$ , binomial test), suggesting that olfactory cues may also have influenced food discovery.

#### Eavesdropping

Aerial insectivores emit feeding buzzes, i.e. decrease duration and increase repetition rate of their echolocation calls, as they approach prey (Simmons and Stein 1980). Consequently, information about foraging activity is broadcast to other bats and could be used to locate foraging sites and assess prey abundance.

Several studies have confirmed that some species approach playbacks of feeding buzzes (Barclay 1982, Balcombe and Fenton 1988). Such eavesdropping requires that the bats are sufficiently close to hear each other's biosonar. Detection distances under most environmental conditions are likely to be less than 100 m for many temperate insectivorous bats, and sometimes less than 10 m for bats with low amplitude, high frequency biosonar (Griffin 1971, Wilkinson 1995). Eavesdropping is, therefore, likely to be restricted to aerial insectivores that use relatively loud, low frequency echolocation calls.

#### Advertisement

Some bats could also learn where food is located from conspecifics which use audible vocalisations and behaviour to defend a feeding territory. Many aerial insectivores use nonecholocation calls when chasing intruders away from foraging sites, e.g. Daubenton's bats, *Myotis daubentonii* (Wallins 1961), lesser sac-winged bats, *Saccopteryx leptura* (Bradbury and Emmons 1974), northern serotines, *Eptesicus nilssonii* (Rydell 1986), red bats, *Lasiurus borealis* (Hickey and Fenton 1990), and pipistrelles (Miller and Degn 1981). Calling rate is inversely related to prey abundance in pipistrelles; field playback experiments demonstrate that these calls repel conspecifics (Barlow and Jones 1997). Instead of calling and chasing, several large carnivorous megadermatids, including heart-nosed bats, *Cardioderma cor* (Vaughan 1976), yellow-winged bats, *Lavia frons* (Vaughan and Vaughan 1986) and ghost bats, *Macroderma gigas* (Guppy *et al.* 1985, Tidemann *et al.* 1985), give loud audible calls while perched, apparently to advertise territory ownership.

In contrast, a few species emit audible calls which attract conspecifics. Field playbacks demonstrate that loud, broad-band screech calls attract greater spear-nosed bats at cave entrances and foraging sites and elicit additional calling (Wilkinson and Boughman 1998). Observations of LED-tagged bats indicate that these calls function to coordinate foraging activity among females from the same social group. Individuals foraging with social partners appear to benefit from improved defense of flowering or fruiting trees as well as from learning food location from others (Wilkinson and Boughman 1998).

#### Communication

As the previous sections indicate, vocalisations may often mediate how bats learn feeding site location from conspecifics. But, social learning can also influence call production directly. Bats might learn the context in which social calls should be emitted as a consequence of reinforcing social interactions. For example, male hammer-headed bats, *Hypsignathus monstrosus*, increase call repetition rate when females approach (Bradbury 1977). Social reinforcement

could occur in this example because only males with high calling rates mate. Alternatively, under several social situations acoustic modification of vocalisations can be expected.

#### *Social modification of echolocation calls*

Because echolocation calls are effectively designed for orientation and prey capture (Simmons and Stein 1980), extensive modification of signal form in response to conspecifics seems unlikely. Nevertheless, if eavesdropping or following are costly to a searcher, active foragers would be expected to increase frequency, decrease amplitude or decrease echolocation calling rate to reduce the probability of detection while hunting.

Several studies have reported cases of bats modifying the frequency of their echolocation calls when foraging near conspecifics, e.g. hipposiderids (Pye 1972) and emballonurids (Barclay 1983). Such modification reduces similarity among individuals, which may help avoid interference in echo detection and processing by partitioning acoustic space (Haberstetzer 1981). But, when researchers have noted a change in echolocation call frequency, it has increased, not decreased, when conspecifics were encountered, e.g. mouse-tailed bats, *Rhinopoma hardwicki* (Haberstetzer 1981), pipistrelles (Miller and Degen 1981), and northern serotines (Rydell 1993). Furthermore, Obrist (1995) found in four species that calls are shorter and given less frequently when conspecifics are present, as expected if foragers modify their calls to reduce inter-individual detection distance.

In addition, geographic, colony or sex differences in echolocation calls (Neuweiler *et al.* 1986, Heller and Helverson 1989) could result from social modification of calls. However, such differences could also reflect population genetic variation in morphology or differences in foraging behaviour (Rydell 1993). Evidence that echolocation calls can be modified to increase resemblance among colony members has only been obtained for greater horseshoe bats (Jones and Ransome 1993). Mothers were more similar to pups than expected if call similarity was due solely to heritable variation. Furthermore, calls of adult females changed in frequency over their lives and pup calls mirrored these changes.

#### *Social modification of communication calls*

The acoustic structure of communication calls should be influenced by the social environment if this enhances call function. For example, calls which function to form foraging groups or advertise feeding sites should have characteristics which resist attenuation and maximise locating ability. If group composition matters, social calls should also convey caller identity. While calls

that indicate individual identity or kinship can be heritable (Scherrer and Wilkinson 1993), calls that indicate social identity, such as membership in a group or pair, are more likely to be modified by social experience.

Recent work on greater spear-nosed bats indicates that screech call acoustic structure not only conforms to signal design expectations, but also responds to changes in the composition of social groups. Greater spear-nosed bat screech calls are loud and low in frequency, as expected for long distance transmission. These calls also cover a wide frequency range, which improves the ability of other bats to localise the caller. Our observations suggest that females use screech calls not only to coordinate foraging activity (Wilkinson and Boughman 1998), but also to indicate and assess group identity.

Greater spear-nosed bat screech calls from different social groups differ in acoustic structure and individuals within groups sound similar (Boughman 1997). Consequently, screech calls contain information to indicate group membership of the caller, but not individual identity. Bats attend to these acoustic differences, as their response to call playbacks depends on the group membership of the bat giving the calls (Boughman and Wilkinson 1998).

Group differences in screech calls cannot result from heritable variation because *P. hastatus* female group mates are unrelated (McCracken and Bradbury 1981). Our data indicate that screech calls are modified through social experience. In a reciprocal transfer experiment that mimics naturally occurring dispersal, acoustic structure of calls changed in response to changes in group composition resulting in increased similarity among bats in the same social group (Boughman 1998). This modification took place among both first year and older, reproductively mature animals.

Few other published studies have demonstrated vocal learning in mammals. There is good evidence, however, that infant lesser spear-nosed bats (Figure 11.2) change characteristics of their isolation calls to match playbacks of maternal directive calls (Esser 1994). Esser (1994) suggests that increased similarity between mother and offspring facilitates individual recognition during retrievals. Whether the genus *Phyllostomus* is exceptional in the capacity for vocal learning or provides an example of a broader phenomenon in bats is unknown at present.

Lesser spear-nosed bats may share more than an ability for vocal learning with greater spear-nosed bats. Both species forage on pollen and nectar in groups (Sazima and Sazima 1977, McCracken and Bradbury 1981, Wilkinson and Boughman 1998), and both respond to greater spear-nosed bat screech call playbacks by approaching the speaker and calling. Lesser spear-nosed bat screech calls sound similar to greater spear-nosed bat screech calls except they are higher in frequency and more trill-like (unpublished data). Additional



Figure 11.2. Lesser spear-nosed bat.

study is needed to determine if lesser spear-nosed bat foraging calls may also change in response to the social environment.

### A test of social learning theory

In a recent paper, Laland *et al.* (1996) developed a model to predict the frequency of social learning at an information centre where animals can acquire information about diet choice and resource location. The frequency of social learning is determined by four variables,  $c$ ,  $e$ ,  $\epsilon$ , and  $s$ , where  $c$  is the probability of social transmission,  $e$  is a measure of environmental predictability, i.e. the probability of patch disappearance,  $\epsilon$  is the probability that a naive forager successfully finds better food by itself and  $s$  indicates the fitness advantage associated with adopting the knowledgeable conspecific's diet or feeding location. Animals are assumed to search for food every day, but social learners can acquire information about better feeding sites without cost from any knowledgeable conspecific prior to foraging.

Numerical analysis of this model reveals three possible outcomes at equilibrium: 1. all individuals learn independently, 2. a polymorphic region where individual and social learners coexist, and 3. a region in which all animals should use both individual and social learning. Qualitatively, individual learn-

ing is favoured when the probability of finding better food by foraging alone is high and the environment changes rapidly. In contrast, socially transmitted information should be used when the probability of finding food by searching is low and the environment changes slowly. Social learning increases mean fitness if  $e + \epsilon < 1$  (Laland *et al.* 1996). Consequently, if the model is valid, we would expect  $e + \epsilon$  to correlate inversely with following.

To test this model we compare  $e + \epsilon$  to the frequency of following in three species: evening bats, greater spear-nosed bats and common vampire bats. Although these three species have very different diets and life histories, all three exhibit following behaviour from a communal roost. Female evening bats follow previously successful foragers at nursery colonies and subsequently improve their own foraging success presumably because they are led to sites where small flies and beetles are temporarily abundant (Wilkinson 1992). Female greater spear-nosed bats follow other females from their social group apparently to defend rich flowering or fruiting trees from other bats (Wilkinson and Boughman 1998). Young female vampire bats fly with their mothers to pastures and sometimes feed from the same wound (Wilkinson 1985). Thus, in each case following can improve access to food.

For all three species, we assume that  $e$  is the probability that on any given day a feeding site has below average food availability. For evening bats we used samples of prey insect abundance collected in 1 h at dusk using five automated suction traps located at feeding sites about 1 km from a nursery colony (Wilkinson 1992). For each site we estimated the number of consecutive days that prey biomass density was either above or below the mean of all five sites. Patch duration was  $2.55 \pm 0.57$  (SE) days averaged over a six week period. We then calculated  $e$  as the inverse of the mean over all five sites each week. We calculated  $\epsilon$  as the mean proportion of bats returning after their initial foraging trip which had gained weight and, therefore, fed successfully. We used videotape records of bats entering and leaving an attic roost while crawling across a balance to obtain bat weights. Finally, we estimated the proportion of bats which departed within 10 s of another bat on their second or later foraging trip as potential social learners because these bats are close enough to hear and follow the echolocation calls of the previous bat (Wilkinson 1992).

Greater spear-nosed bats consume animal prey and feed on fruit, pollen or nectar of more than 30 different plants (Gardner 1977, Gorchov *et al.* 1995). Consequently, to estimate  $e$  we first examined faecal collections to determine food items in the diet. During December and January over 50% of the diet of greater spear nosed bats includes pollen and nectar of balsa (*Ochroma lagopus*). In May and June 60–80% of the diet consists of *Cecropia peltata* fruit with the remainder comprising large-bodied insects (Wilkinson and Boughman 1998).

We used daily censuses of the number of flowers on 10 balsa trees over a three week period in December–January to determine the average number of consecutive days each tree had more flowers than the mean ( $4.12 \pm 0.92$  days,  $n = 25$ ). Similarly, we used counts of the number of fruits on 10 *Cecropia* trees over a two week period to determine that *C. peltata* patch duration was  $6.29 \pm 0.82$  days ( $n = 14$ ). Although these samples are small, similar phenological patterns have been reported for another population of *C. peltata* (Fleming and Williams 1990). During May–June we also estimated large-bodied insect predictability using 10 Plexiglas impact traps suspended in locations where we had observed greater spear-nosed bats forage. Trap samples indicated a patch duration of  $1.65 \pm 0.20$  days ( $n = 24$ ) for insects. Finally, we weighted estimates of patch duration by the proportion of the diet comprising either insects or *C. peltata*, to obtain an average  $e$  for the May–June period of  $4.67 \pm 0.60$  days.

We estimated  $e$  for greater spear-nosed bats during each season as the proportion of radio-tagged bats that returned briefly to the cave and subsequently departed on a second foraging trip (unpublished data). Following was obtained from observations of LED-tagged females from the same social group that departed the cave roost and flew away together. Captures of bats attracted to playbacks of screech calls at flowering trees confirmed that females from the same roosting group sometimes foraged at the same feeding site (Wilkinson and Boughman 1998).

We assumed that  $e$  for a vampire bat was the reciprocal of the average number of days livestock were present in each pasture, i.e. 6 days (Turner 1975). We estimated  $\epsilon$  as the proportion of bats less than 2 years of age that were netted while entering roosts within 1 h of dawn and had successfully consumed a blood meal, i.e. 67% (Wilkinson 1984). Finally, we used night vision scope observations on two nights of vampire bats departing from a hollow tree between dusk and dawn to calculate the proportion of departures in which one bat left simultaneously with another bat. Group departures are likely to indicate following in vampire bats because night vision scope observations of 67 bats feeding on horses revealed seven instances of two bats drinking together from the same bite (Wilkinson 1985).

A plot of  $e$  or  $\epsilon$  for all three species reveals that no points fell within the region in which all individuals should be social learners (Figure 11.3a). While the feeding environment for greater spear-nosed bats and vampire bats is sufficiently predictable, individual feeding success appears to be too high to favour unconditional social learning. However, vampire bats and greater spear-nosed bats in January are predicted to exhibit a combination of social and individual learning. In contrast, environmental predictability is sufficiently low in evening bats that social learning is not predicted. Greater spear-nosed

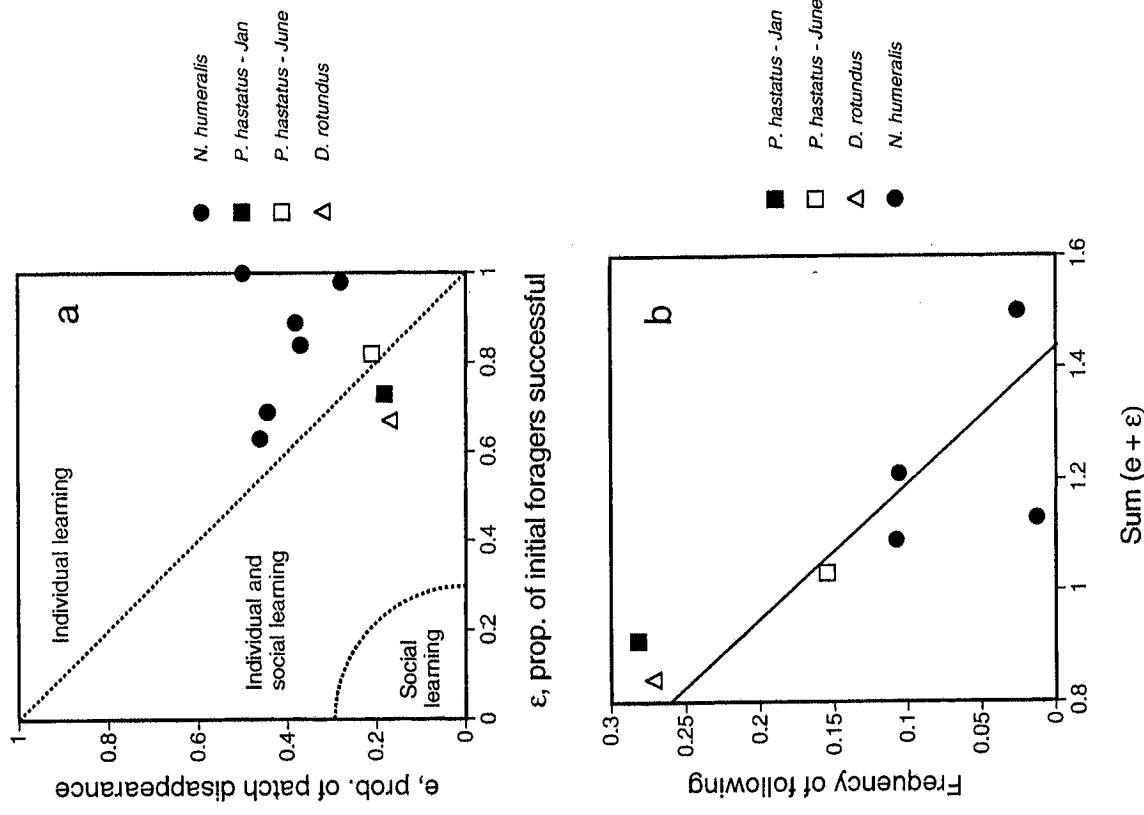


Figure 11.3. (a) Comparison of estimates for the probability of patch disappearance,  $e$ , and proportion of successful foragers,  $\epsilon$ , for evening bats, *Nycticeius humeralis*, greater spear-nosed bats, *Phyllostomus hastatus*, and common vampire bats, *Desmodus rotundus*, to equilibrium predictions made by a model for social transmission at an information centre (Laland *et al.* 1996). (b) Frequency of following from a communal roost for the same three species and time periods indicated in (a) plotted against  $e + \epsilon$  as a qualitative test of the model.

bats in June are predicted to show less social learning than in January because initial foraging success is higher in June.

Even though social learning among evening bats is not expected, adding environmental predictability to initial foraging success successfully predicted the frequency of following behaviour across species (Figure 11.3b). The Spearman rank correlation between  $e + \epsilon$  and the proportion of bats following was  $-0.86$  ( $P = 0.036$ ). Differences in colony sizes between the species do not contribute to this result. In fact, the evening bat colony contained more individuals (between 40 and 80) than either of the other two species and should, therefore, have exhibited the highest frequencies of following behaviour by chance. At the time of observations, the vampire bat tree roost had 27 individuals while only 20 adult female greater spear-nosed bats, on average, were tagged with the same colour LED.

Although our results provide qualitative support for the model in that  $e + \epsilon$  correlates with following frequency, our data do not conform to predictions in that the evening bat points lie in the region where individual learning is expected. We suspect either our estimates of  $e$  or  $\epsilon$  for evening bats are in error or some assumption of the model is incorrect. If evening bats followed each other on initial foraging trips  $\epsilon$  may represent an overestimate because we used foraging success from the first foraging trip to estimate  $\epsilon$ . If following occurred on first foraging trips as often as we estimated it did on subsequent trips, then the  $e$  on  $\epsilon$  points for evening bats would lie within the polymorphic region where individual and social learners are expected.

One obvious assumption of the model that can be questioned is whether either individual or social learning occurs without cost. To put it another way, do both forms of learning provide equally profitable mechanisms for locating food? Animals that follow a knowledgeable conspecific can avoid paying the energetic costs associated with searching. Consequently, the fitness advantage of social learning should be enhanced. This seems likely to increase the parameter space in which social learning will be favoured. Development of models with explicit learning costs is needed to confirm this possibility.

A second possibility is that this model may underestimate the effectiveness of social learning. Because  $\epsilon$  can exceed  $1 - \epsilon$ , the model allows the possibility that social learners are less likely to find preferred food than individual learners. However, in reality individuals who fail to find food by utilising social information will revert to searching, and may still find preferred food. Changing the model to accommodate this possibility seems likely to increase the parameter space allowing polymorphism between individual and social learners and decrease the parameter space where only individual learning is favoured.

## Conclusions

While few studies have yet provided compelling evidence for social learning in bats, qualitative agreement between model predictions and following frequency in an insectivore, an omnivore and a sanguivore suggests that many bats may experience environments in which social transmission of diet or resource location would be favoured by natural selection. Indeed, unless knowledgeable individuals actively avoid interaction, the communal social organisation of many bat species seems to predispose social learning. Because social transmission of foraging site locations can reduce variation in foraging success among individuals (Wenzel and Pickering 1991), social learning could increase survival. Thus, we conjecture that social learning may have played an important role in permitting the extraordinary longevity, relative to body size, displayed by many bats.

In addition to providing model systems for studying social transmission of diet and resource location, bats may also eventually provide some of the best nonhuman, mammalian examples of vocal learning. Although very few species have been studied in detail, vocal repertoires of bats tend to be large (Gould 1977, Fenton 1985, Kanwal *et al.* 1994), with many vocalisations serving unknown communication functions. Further study is clearly needed to determine if the ability of lesser and greater spear-nosed bats to modify their vocalisations and match a conspecific is unique to the genus or more widespread in the order. In either event, more detailed study designed to characterise the process by which these bats perform call matching may provide important insights into how vocal learning among humans has evolved.

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## Social transmission of information in a eusocial rodent, the naked mole-rat (*Heterocephalus glaber*)

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### Introduction

The African mole-rats of the family Bathyergidae are subterranean hystricomorph rodents endemic to sub-Saharan Africa. They occur in a wide range of physically and climatically divergent habitats (from mesic to xeric) and show a diversity of social systems (Jarvis *et al.* 1994, Faulkes *et al.* 1997b, Lacey and Sherman 1997). Of a total of 18 or more species, four are solitary dwelling and plural occupancy of burrows only occurs during the breeding season. At least nine taxa are colonial and, depending on the species, burrows may contain up to approximately 14 individuals. Some, or perhaps all, of these colonial mole-rats are cooperative breeders with colonies composed of a breeding pair and their offspring, who delay dispersal and reproduction until favourable environmental conditions occur (Jarvis and Bennett 1991, Jarvis *et al.* 1994, Faulkes *et al.* 1997b).

Sociality reaches a pinnacle in two other species, the naked mole-rat, *Heterocephalus glaber*, and the Damaraland mole-rat, *Cryptomys damarensis*. Both of these species are cooperative breeders with a high reproductive skew (Sherman *et al.* 1995), as only a small percentage of individuals gain the opportunity to breed. Both species, but the naked mole-rat in particular, have been compared to the social invertebrates like bees, ants and termites. They exhibit the characteristics that define such 'eusocial' insect species (Michener 1969, Wilson 1971), i.e. colonies contain overlapping generations, there is cooperative care of offspring, and there is clear division of reproductive labour in which only a few individuals produce offspring (Jarvis 1981, Jarvis and Bennett 1993). The reproductively suppressed, subordinate group members cooperate in rearing offspring and protecting and maintaining the colony (Jarvis 1981, Lacey and Sherman 1991, Faulkes *et al.* 1991a). One large, dominant female (the 'queen'; Jarvis 1981) controls the reproduction of all the other males and females in a colony that may commonly contain around 100 individuals. The queen mates with one, two or sometimes three specific breeding males (Jarvis 1981, 1991, Lacey and Sherman 1991). Even though

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