Animal Social Complexity

Intelligence, Culture, and Individualized Societies

EDITED BY

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Social and Vocal Complexity in Bats

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The Machiavellian intelligence (MI) hypothesis (Whiten & Byrne 1988; Whiten 1999) proposes that enhanced cognitive abilities permit an individual to exploit others in a group, thereby creating a social environment that favors development of counter-strategies, such as deception or mutual cooperation. Proponents of this idea suggest that as group size increased during hominid evolution, a cognitive arms race resulted in the evolution of larger brains. One of the most robust findings that has been offered in support of the MI hypothesis is that social group size in extant primates positively covaries with relative size of the neocortex—a proxy for enhanced cognitive abilities (Dunbar 1992, 1995). This result holds after controlling for phylogenetic effects (Dunbar & Bever 1998) and is not confounded by visual sensitivity since it occurs within diurnal taxa (Barton & Dunbar 1997). The MI hypothesis has also been applied to other groups. For example, relative size of the neocortex also covaries with group size in carnivores (Barton & Dunbar 1997) and insectivores (Dunbar & Bever 1998). Thus, these results suggest that a complex social environment should select for enhanced cognitive traits in other mammals.

Social interactions require communication. In many primates, social grooming is used to mediate social interactions and maintain social cohesion. Such tactile communication is, however, inadequate for large social groups. The evolution of language seems likely to have enabled the formation of larger hominid groups (Aiello & Dunbar 1993; Dunbar 1993). Al-

though transformational grammar, which can create an infinite combination of phrases and sentences, is only found in humans, other features of human language are found in nonhuman mammals (Pinker & Bloom 1990). These include phonetic units (Richman 1976; Owren & Bernacki 1988; Snowdon 1990; Hauser & Fowler 1991), rhythmicity (Richman 1987), categorical perception (Kuhl & Miller 1975), and syntax-like combinations of discrete sounds that occur nonrandomly and recurrently (Kanwal et al. 1994). In bats and primates, such composite syllables elicit unique neuronal responses, suggesting they have cognitive salience (Esser et al. 1997; Wang 2000). Some bats, cetaceans, and primates can also modify their vocalizations to resemble those emitted by other individuals (Guinee et al. 1983; Boughman 1998; Mitani & Gros-Louis 1998; Smolker & Pepper 1999; Snowdon & Elowson 1999). Thus, social interactions in nonprimate groups may be mediated by vocal communication and, as a consequence, associated with vocal complexity.

In this chapter I define and then compare social complexity to vocal complexity in bats. Bats provide an interesting comparison to primates because these two mammalian orders do not have a recent common ancestor. All species in one suborder, the Microchiroptera, rely on the echoes of high-frequency vocalizations to perceive their world. Perhaps as a consequence, many bat species exhibit a rich repertoire of communication vocalizations (Fenton 1985). Bats also display a wide variety of social organizations that rival primates both in diversity and complexity (Bradbury 1977b). Although my goal in this chapter is to provide an independent test of the MI hypothesis, I also consider alternative scenarios that could give rise to associations among social complexity, relative neocortex volume, and vocal complexity in bats, as well as suggest promising areas for futher study.

Social Complexity

Group Size

Perhaps the most obvious dimension of social complexity is group size. With 936 described species (Findley 1993), bats exhibit unrivaled variation in aggregation size. At one extreme, species from five families have been reported to form colonies in excess of 500,000 individuals, including Mexican free-tailed bats (*Tadarida brasiliensis;* Barbour & Davis 1969), ghost-faced bats (*Mormoops megalophylla;* Barbour & Davis 1969), Sundeval's leaf-nosed

bat (*Hipposideros caffer;* Nowak 1994), bent-winged bats (*Miniopterus schreibersii;* Smithers 1992), and the straw-colored fruit bat (*Eidolon helvum;* Fayenuwo & Halstead 1974). Colony size appears to be evolutionarily labile as other species in each family roost solitarily or in small groups. Important factors influencing colony size include diet, body size, and predation risk (Bradbury & Vehrencamp 1976b). All of the species listed above, except the straw-colored fruit bat, weigh 20 grams or less, capture abundant insect prey using echolocation, and roost in caves where they are inaccessible to most predators. Straw-colored fruit bats, in contrast, weigh 280 grams, eat fruit, do not echolocate, and roost in tall trees. Species that form small groups or roost solitarily often inhabit hollow trees or roost cryptically in foliage and forage on more dispersed food sources. Small group size is also typical of bat species that hunt and capture vertebrate prey (Norberg & Fenton 1988), including the false vampire bat (*Vampyrum spectrum*) and woolly false vampire bat (*Chrotopterus auritus*) in the family Phyllostomatidae and the yellow-winged bat (*Lavia frons*), lesser false vampire bat (*Megaderma spasma*), and ghost bat (*Macroderma gigas*) in the family Megadermatidae.

Colony size may not, however, be the same as social group size. Dunbar (1993) has argued that while group size is ultimately determined by ecological factors, the upper limit to social group size for any primate is set by cognitive constraints. Those constraints dictate the number of social relationships one animal can maintain by personal contact. Unfortunately, the average size of social groups in most colonial roosting bats is unknown. Where detailed studies have been conducted, colonies are often composed of multiple social groups, usually consisting of small groups (less than 30) of females that utilize and defend traditional roosting and foraging sites, i.e., common vampire bats (*Desmodus rotundus;* Wilkinson 1985a), greater spear-nosed bats (*Phyllostomus hastatus;* McCracken & Bradbury 1981), Bechstein's bats (*Myotis bechsteini;* Kerth & Konig 1999), and greater white-lined bats (*Saccopteryx bilineata;* Bradbury & Vehrencamp 1976a).

Social groups could be maintained by recognition and memory of individuals or by using a cue indicating group membership. Individual recognition must occur in female vampire bats to enable them to share blood reciprocally with roostmates (Wilkinson 1984). Individual differences in vocalizations could be used for recognition and have been described for echolocation calls of many species (Habersetzer 1981; Suga et al. 1987; Jones et al. 1992; Rydell 1993; Masters et al. 1995; Obrist 1995; Guillen et al. 2000). In contrast, female greater spear-nosed bats use group-specific contact calls

to recognize groupmates while foraging (Boughman & Wilkinson 1998), much like parrots (see Chapter 11). Similarly, female fishing bats, *Noctilio leporinus,* scent-mark groupmates presumably to facilitate group recognition while foraging (Brooke 1997). Group membership tags may occur in other species because their use reduces the cognitive burden associated with recognizing group members in a large aggregation. However, to ensure honest signaling, group-specific cues need to be costly or difficult to acquire (Grafen 1990). Vocal learning in greater spear-nosed bats takes time, consistent with this requirement (Boughman 1998).

Group Stability

A second dimension likely to influence social complexity is group stability. The stability of bat roosting groups depends on individual longevity, roost fidelity, and affiliations among individuals. For their body size, bats are extraordinarily long-lived. Twenty of 41 longevity records for bats exceed 15 years (Tuttle & Stevenson 1982). The most long-lived species include greater long-eared bats (*Plecotus auritus*) and little brown bats (*Myotis lucifugus*), which have been recaptured 30 years after initial banding (Keen & Hitchcock 1980; Lehmann et al. 1992), and greater horseshoe bats (*Rhinolophus ferrumequinum*), which have survived 26 years (Ransome 1991). All three of these species weigh 25 grams or less. Most long-lived bat species are temperate insectivores, give birth to a single young each year and hibernate over winter. Whether temperate species live longer than tropical species is unclear since less information on lifespan is available for most tropical species. Some of the large flying foxes live more than 20 years (Tuttle & Stevenson 1982) and long lifespan could be characteristic of other *Pteropus* species that reproduce once per year (Racey & Entwhistle 2000). In the New World tropics, female common vampire bats and greater spear-nosed bats give birth once per year and have been recaptured after 15 years (Wilkinson & Boughman 1998; Tschapka & Wilkinson 1999) and 22 years (G. Wilkinson, personal observation), respectively. A female common vampire bat has even survived 30 years in captivity (U. Schmidt, personal communication). In contrast, neotropical fruit bats which give birth twice per year, such as the Jamaican fruit bat (*Artibeus jamaicensis*) and short-tailed fruit bat (*Carollia perspicillata*), live no more than nine years (Fleming 1988; Gardner et al. 1991).

A review of roost fidelity indicates that 14 of 43 species of bats rarely switch roosts whereas 25 frequently change roosts (Lewis 1995). High fidel-

ity to a single roost is positively associated with the use of permanent roost sites, such as caves, mines, or buildings, and inversely associated with roost availability. Mark-recapture and molecular genetic studies have recently documented that females exhibit natal philopatry and roost fidelity in several temperate-region bat species. For example, female greater long-eared bats (Entwhistle et al. 2000; Burland et al. 2001), greater mouse-eared bats (*Myotis myotis;* Petri et al. 1997), evening bats (*Nycticeius humeralis;* Wilkinson 1992), and greater horseshoe bats (Rossiter et al. 2000) typically reproduce in the colonies where they were born. In each of these species, maternity colonies are persistently used for decades, suggesting that natal philopatry leads to long-term associations among individuals in a colony. Nevertheless, average pairwise relatedness among females in a colony does not differ from zero where it has been estimated (Wilkinson 1992; Kerth & Konig 1999; Burland et al. 2001). Low relatedness between females apparently results from male dispersal, extra-colony mating, high first-year mortality and low male reproductive skew (Watt & Fenton 1995; Rossiter et al. 2000; Burland et al. 2001).

Most bat species that frequently switch roosts exhibit low group stability. For example, even though pallid bats *(Antrozous pallidus)* often roost together in rocky cracks (Vaughan & O'Shea 1976), these groups do not persist through the reproductive season (Lewis 1996). In the tropics, many bats that switch roosts form female roosting groups, but these groups show relatively low compositional stability over time. Examples include the Jamaican fruit bat in Panama (Morrison 1987), tent-making fruit bat (*Uroderma bilobatum;* Lewis 1992), great fruit bat (*Artibeus literatus;* Morrison 1980), short-tailed fruit bats (Fleming 1988), and greater white-lined bats. Greater white-lined bats differ from all other bat species in that males exhibit natal philopatry to a colony whereas females disperse (Bradbury & Vehrencamp 1976a).

Stable aggregations of females that remain together for two or more years have been documented for greater spear-nosed bats (McCracken & Bradbury 1981), fishing bats (Brooke 1997), common vampire bats (Wilkinson 1985a), Jamaican fruit bats in Mexico (Ortega & Arita 1999), Bechstein's bats (Kerth & Konig 1999; Kerth et al. 2000), rufous hairy bats (*Myotis bocagei;* Brosset 1976), African sheath-tailed bats (*Coleura afra;* McWilliam 1987), little free-tailed bats (*Tadarida pumila;* McWilliam 1988), and greater short-nosed fruit bats (*Cynopterus sphinx;* Storz et al. 2000). Resightings of animals marked as infants indicates that both sexes disperse from their natal

group in greater spear-nosed bats, fishing bats, and greater short-nosed fruit bats. In each of these species, females subsequently either join existing groups or assemble into age-structured cohorts, which then exhibit high levels of affiliation. In contrast, female matrilineal kin remain together in common vampire bats, Bechstein's bats, and little free-tailed bats. Two or more females have been recaptured in the same social group after 10 years in greater spear-nosed bats (McCracken & Wilkinson 2000) and after 12 years in common vampire bats (Wilkinson 1985a), suggesting that long-term roostmate affiliation can occur with and without matrilineal relatives present. In several species, notably common vampire bats, Bechstein's bats, and greater short-nosed fruit bats, females often switch roosts, but pairs or small groups of females can be identified that invariably roost together and occasionally join other subgroups. Roost affiliation varies independently of the level of relatedness between the bats (Wilkinson 1985b; Kerth & Konig 1999; Storz et al. 2000). Such fission-fusion movement patterns are characteristic of chimpanzees (Goodall 1986; Nishida 1990), dolphins (Shane et al. 1986; Bearzi et al. 1997; Chapter 2), elephants (Moss & Poole 1983), and some parrots (Bradbury, Chapter 11). More examples of fission-fusion social organization among bats may be revealed as more long-term studies of individually marked animals are conducted.

Mating

In primates, the presence of alliances and coalitions, involving pairs or trios of individuals, has been used to distinguish more complex from less complex societies. In polygamous primates, reproductive skew, i.e., the extent to which high-ranking males monopolize matings, exhibits negative correlated evolution with neocortical size independent of group size (Barton & Dunbar 1997). To the extent that reproductive skew is reduced by alliance formation, this result is consistent with coalition formation influencing social complexity. Bats exhibit considerable variation in mating systems (McCracken & Wilkinson 2000). The most common mating system in bats involves a single male mating with several females (52 percent of 66 species). This mating system can occur either when a male controls access to a group of females or mates sequentially with several females that visit a defended site. Because single males often control access to sites with females, this mating system offers little opportunity for coalitions to form among lower-ranking individuals. Alliances might, on the other hand, occur among individuals in species in

which several males roost and mate with females. Such multimale and multi-female groups have been described for 18 percent of bat species (McCracken & Wilkinson 2000). Alliance formation has not been described for any bat species, but this may reflect the paucity of detailed observational studies of mating behavior in bats rather than absence of this type of behavior.

Cognition and Social Complexity

Group stability in bats has been reported to covary positively with relative neocortex size (Barton & Dunbar 1997), but only two species with purportedly stable groups, common vampire bats and lesser spear-nosed bats (*Phyllostomus discolor*), were used in the analysis. Here I reexamine this question using recent compilations of mating system, colony size, and stability of female groups (McCracken & Wilkinson 2000; Wilkinson & McCracken 2001) together with brain structure volume estimates (Baron et al. 1996) for bats. Because previous work has also found differences in brain-body allometry according to diet among mammals (Pagel & Harvey 1989), I also tested for an effect of diet (insects, vertebrates, fruit, or nectar) on brain size. In dolphins, increased brain size has been proposed to be a consequence of echolocation (Ridgway & Brownson 1984). Consequently, I also compare brain volumes between echolocating and nonecholocating bats. I follow the methods of Dunbar (1992) with the exception that I use species, rather than genera, as the unit of analysis because species within bat genera often differ in each of the social factors under consideration (e.g., Bradbury & Vehrencamp 1976a). To control for differences in body size, which scales allometrically with brain size, I regressed log volume of the neocortex on log volume of the rest of the brain ($F_{1,63} = 5705.2$, $p < 0.0001$), and then used residual neocortex volumes in subsequent analyses.

Residual neocortex volume was independent of colony size ($F_{1,42} = 1.92$, $p = 0.17$), type of mating system ($F_{2,37} = 0.3$, $p = 0.76$), and echolocation ability ($F_{1,63} = 0.08$, $p = 0.78$). In contrast, Figure 12.1 shows that residual neocortex volumes differed according to diet ($F_{3,61} = 4.6$, $p = 0.0061$) and group stability ($F_{1,24} = 8.5$, $p = 0.0075$). In a two-way ANOVA, group stability ($F_{1,21} = 2.4$, $p = 0.13$) explained more variation than diet ($F_{3,21} = 0.6$, $p = 0.61$), but neither factor was significant, indicating that diet and group stability are not independent. Bats that form stable groups or feed on vertebrates or nectar have larger relative neocortex size than bats without stable groups or those that feed on fruit or insects. A previous analysis indicated
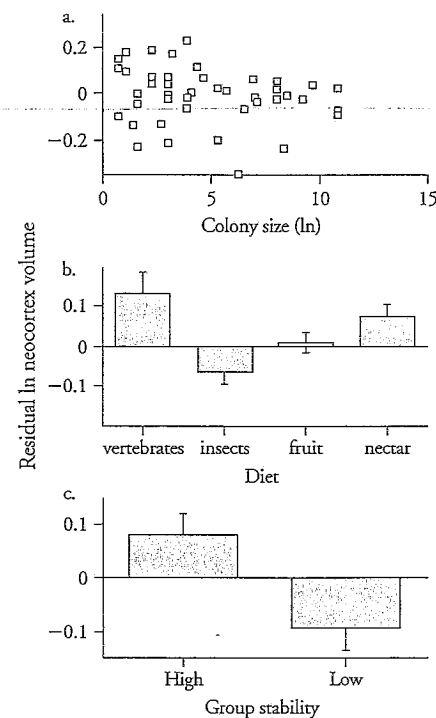

Figure 12.1. Comparison of residual ln neocortex volume to *a)* colony size, *b)* diet, and *c)* the stability of social groups. Mean ± SE shown in *b)* and *c)*. Species with more stable groups include *Coleura afra, Cardioderma cor, Lavia frons, Tadarida pumila, Noctilio leporinus, Artibeus jamaicensis* (Mexico), *Desmodus rotundus, Phyllostomus discolor, P. hastatus, Vampyrum spectrum, Cynopterus sphinx**, *Myotis bocagei,* and *Plecotus auritus.* Species with less stable groups include *Saccopteryx bilineata, Carollia perspcillata, Leptonycteris curasoae, Uroderma bilobatum, Hypsignathus monstrosus**, *Miniopterus australis, M. minor, M. schreibersi, Myotis adversus, M. albescens, M. lucifugus, Nyctalus noctula, P. nanus, P. pipistrellus, Tylonycteris pachypus,* and *T. robustula.* * indicates nonecholocating megachiropteran species.

that group stability predicted the occurrence of cooperative behaviors, such as allogrooming, across five species of phyllostomid bats (Wilkinson 1987). Group stability, as measured by an index of female association among day roosts, also predicted the frequency of food sharing (Wilkinson 1984) and social grooming among vampire bats (Wilkinson 1986). Taken together,

these results suggest that group stability, and possibly social grooming, are key components of social complexity in bats. More information on group stability from additional species is needed to tease apart the effects of group stability and diet on neocortex volume.

Vocal Complexity

Complexity of vocalizations can be defined on at least four levels. First, some animals may have a larger lexicon than others, i.e., use more sounds to convey different meanings. To date, nine different functional categories of vocalizations have been described for bats, i.e., echolocation, infant isolation, maternal directive, mate advertisement, copulation, distress, alarm, contact, and defense (Fenton 1985; Wilkinson 1995). A second level of complexity involves the number and order of sound types, often referred to as syllables, emitted by an individual in a single context. If syllables can be combined in different orders to form composite syllables, then syllable order can contribute to syllable diversity. Composite syllables are produced by some bats (Kanwal et al. 1994; Davidson & Wilkinson 2002) and appear to be important for mate advertisement in at least one species (Davidson & Wilkinson 2001). A third level of complexity involves variation in the acoustic features of calls emitted by different individuals. Such variation is often associated with vocalizations that carry signature information, such as infant isolation calls (Gelfand & McCracken 1986; Jones et al. 1991; Scherrer & Wilkinson 1993), but also has been noted for maternal directive calls (Balcombe & McCracken 1992; Esser & Schubert 1998) and contact calls (Boughman 1997). Finally, the ability to modify vocalizations by learning provides a fourth potential source of complexity. Evidence for vocal learning in bats has been obtained for echolocation calls in greater horseshoe bats (Jones & Ransome 1993), infant isolation calls in lesser spear-nosed bats (Esser 1994), and contact calls in greater spear-nosed bats (Boughman 1998). Below I review the literature on several functional categories of bat vocalizations to determine if any aspect of vocal complexity is related to colony size, group stability, or mating behavior in bats.

Call Repertoires

Repertoires of vocalizations with some information on contextual association have been described for grey-headed flying foxes (*Pteropus poliocephalus*; Nel-

son 1964), short-tailed fruit bats (Porter 1979), little brown bats (Barclay et al. 1979), and greater white-lined bats (Bradbury & Emmons 1974). Insufficient information is available, however, to determine if the usage of different functional call types is associated with social complexity. For example, distress calls have only been described for little brown bats (Fenton et al. 1976), Jamaican fruit bats (August 1979), and pipistrelle bats (*Pipistrellus pipistrellus*; Russ et al. 1998), but also occur in many other microchiropteran and megachiropteran species (personal observation). Maternal directive calls, which are emitted by females when searching for pups, have only been described for species that roost in groups, e.g., pallid bats (Brown 1976), lesser bulldog bats (*Noctilio albiventris*; Brown et al. 1983), Mexican free-tailed bats (Balcombe & McCracken 1992), and lesser spear-nosed bats (Esser & Schmidt 1989). However, it is difficult to assess their distribution since they are not detectable without ultrasound recording equipment.

Recent work on the social calls of Parnell's mustached bats (*Pteronotus parnellii*), has revealed that these bats can combine calls in nonrandom orders to create composite syllables (Kanwal et al. 1994). Two-syllable composites represent a nonrandom subset of the 342 possible disyllabic combinations and constitute 30 percent of the sounds recorded (Kanwal et al. 1994). Playback studies have revealed that frequently used composite syllables elicit specific neuronal responses suggesting that syllable order, which the authors refer to as syntax, may have some behavioral salience (Esser et al. 1997). Unfortunately, the context in which each call variant was produced is unknown because observations were not conducted simultaneously with audio recordings. Observational and playback studies are, therefore, needed to assess syntax context and complexity among this and other species of bats, particularly those that differ in social complexity.

Mate Advertisement Calls

A variety of bat species emit calls that appear to attract females for mating. In most cases these are acoustically simple calls that are emitted repetitively. For example, male hammer-headed bats, *Hypsignathus monstrosus*, emit loud "honks" from a stationary location and increase call repetition rate as females approach (Bradbury 1977a). Similar types of calls are given by Wahlberg's fruit bats (*Epomophorus wahlbergi*; Wickler & Seibt 1976), Gambian epauletted fruit bats (*E. crypturus*; personal observation), and Franquet's fruit bats (*Epomops franqueti*; Bradbury 1981). These epomophorine bats exhibit lek

or exploded lek mating systems in which males gather in groups to display (Bradbury 1981). Whether or not variation in any acoustic aspect of these calls is associated with female visitation rates has not yet been determined.

Several vespertilionid species, including the banana bat (*Pipistrellus nanus*; O'Shea 1980), both phonic types of pipistrelle bat (Gerell-Lundberg & Gerell 1994; Barlow & Jones 1997), Kuhl's pipistrelle (*P. kuhli*; Barak & Yom-Tov 1991), serotine bat and Daubenton's bat (*Eptesicus serotinus* and *Myotis daubentonii*; Miller & Degn 1981), greater mouse-eared bats (Zahn & Dipple 1997), and noctule bat (*Nyctalus noctula*; Sluiter & van Heedt 1966) also emit calls that appear to attract females to mating sites. None of these species are known to form stable female groups. Instead, where information is available, females visit males for short periods to mate (McCracken & Wilkinson 2000). Much as in epomophorine bats, the vespertilionid advertisement calls that have been described have simple acoustic structure, often consisting of repetitive frequency-modulated chirps. Acoustic differences occur in calls emitted by closely related species, but have not been described among individuals (Barlow & Jones 1997).

In contrast, male white-lined bats produce long series of complex vocalizations and defend small territories on the buttresses of large trees that contain up to eight females (Bradbury & Emmons 1974; Davidson & Wilkinson 2001). Calls are produced by males during the day throughout the year and differ from echolocation calls, in general, by being lower in frequency and longer in duration. Analysis of vocalizations from 16 individually marked males at four colonies in Trinidad, West Indies identified 21 simple (Figure 12.2) and 62 composite syllable types. Males differed in estimated repertoire size and in three out of six acoustic features measured from the most common syllable type (Davidson & Wilkinson 2002). The number of composite syllables in a male's repertoire, the number of times a particular element is repeated, and two other acoustic features of the common syllable significantly correlate with the number of females in a male's territory (Davidson & Wilkinson 2001). None of these variables covaries with male body size. Because females do not form stable groups in this species, these results suggest that females prefer to roost with males that produce more complex vocalizations. Although territorial males may not father all of the young in their territory, they do have higher mating success than males without females (Heckel et al. 1999). These results are consistent with some studies in birds that have shown female mating preferences for males with larger repertoires (Catchpole 1980; Heibert et al. 1989). Interestingly, the size of male
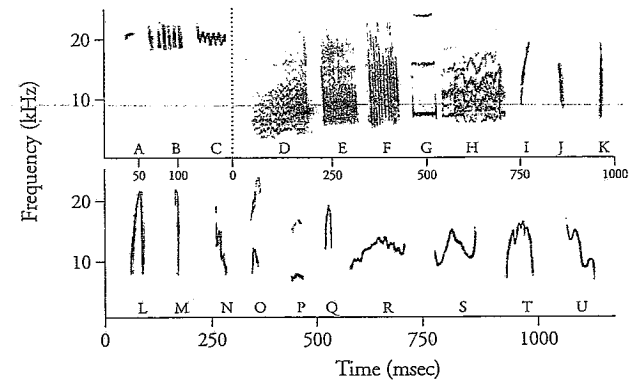
Figure 12.2. Sound spectrograms of representative syllables for 21 different types emitted by male greater white-lined bats (*Saccopteryx bilineata*) during vocal displays.

song repertoires in birds also correlates with the size of brain nuclei associated with song production, presumably as a consequence of past selection to enhance vocal learning (DeVoogd et al. 1993). Whether male repertoire size in greater white-lined bats is influenced by learning and possibly associated with the size of any brain structures remains to be determined. Neuroanatomical comparisons between greater white-lined bats and a congener, such as *S. leptura*, might be revealing since male *S. leptura* do not produce vocal displays. Also, playback studies on greater white-lined bats are needed to demonstrate that male vocalizations influence female roosting patterns.

Echolocation Calls

Echolocation calls are produced by megachiropteran bats in the genus *Rousettus* as well as by all microchiropteran bats. *Rousettus* emit short audible broad-band clicks that permit limited orientation in cave roosts (Suthers 1988). In contrast, microchiropteran bats emit specialized, often ultrasonic, calls that are used for orientation and prey capture. Two echolocation strategies have been recognized and are characterized by differences in signal bandwidth and in how outgoing calls are discriminated from incoming echoes (Fenton 1995). Rhinolophoid species in the Old World and Parnell's mustached bat (family Mormoopidae) in the New World separate pulse and echo by frequency. Echolocation calls emitted by these bats have narrow band-

width (<1 kHz over >80 percent of a call), long duration (5–100 ms), high duty cycle (>50 percent), and consequently, extensive pulse-echo overlap. These bats are often referred to as constant frequency or CF bats. In contrast, all other microchiropteran species separate pulse and echo in time by producing calls of short duration (<5 ms), broad bandwidth (>40 kHz), low duty cycle (<20 percent), and no pulse-echo overlap. These bats are often referred to as frequency modulated or FM bats because they produce calls that sweep through many frequencies in a very short time. These two types of call design have been associated with differences in prey capture technique and auditory processing (Neuweiler 1984), with high duty cycle bats often hunting from perches and relying on Doppler-shift compensation to detect insect wing movements. Although dominant frequency is inversely related to body size in both groups of bats (Heller & Helverson 1989; Fenton et al. 1998; Bogdanowicz et al. 1999; Jones 1999), no evidence yet suggests that echolocation call design covaries with any dimension of social complexity.

One possibility worthy of consideration, however, is that the amount of variation in orientation call spectral characteristics may be greater in group-living species to avoid acoustic interference from conspecifics, especially during exodus from densely populated caves or mines. Individual variation in the dominant frequency of the echolocation call has been described for several colony-forming species, including Hardwicke's lesser mouse-tailed bats (*Rhinopoma hardwickei;* Habersetzer 1981), Parnell's mustached bats (Suga et al. 1987), big brown bats (*Eptesicus fuscus;* Masters et al. 1995), northern bats (*E. nilssoni;* Rydell 1993), lesser horseshoe bats (*Rhinolophus hipposideros;* Jones et al. 1992), and Sundeval's leaf-nosed bats (Guillen et al. 2000). Individual differences in call features have, though, also been reported for some solitary roosting species, such as spotted bats (*Euderma maculatum*), hoary bats (*Lasiurus cinereus*), and red bats (*L. borealis;* Obrist 1995). Because age can also influence echolocation call frequency (Jones & Ransome 1993), age-matched comparisons are needed to determine if any aspect of echolocation call variation is associated with colony size.

Isolation Calls

When isolated from their mothers, pups of most, if not all, species of bats produce loud, repetitive calls (Gould et al. 1973; Gould 1975, 1977). These isolation calls often exhibit variation in acoustic structure suggestive of a vocal signature (Brown 1976; Brown et al. 1983; Thomson et al. 1985;

Gelfand & McCracken 1986; Jones et al. 1991; Scherrer & Wilkinson 1993). Playback studies on Mexican free-tailed bats (Balcombe 1990) and little brown bats (Thomson et al. 1985) have demonstrated that isolation calls attract mothers to their young. Recordings of individuals over time show that frequency modulation patterns can be used to distinguish individuals even though frequencies typically increase while durations decrease as pups age (Esser & Schmidt 1989; Jones et al. 1991; Scherrer & Wilkinson 1993). Furthermore, comparison of calls between siblings indicates that many acoustic features are both repeatable and heritable (Scherrer & Wilkinson 1993). Thus, isolation call complexity is expected to increase with group size as the discrimination task for a female becomes more difficult (Beecher 1989).

To test if call complexity is greater for species that form larger colonies, I recorded and analyzed isolation calls from eight species of bats that differ in colony size. These species represent three phylogenetically related groups and include both high duty cycle CF echolocators and low duty cycle FM echolocators. One clade contains three closely related vespertilionid species: evening bats, Schlieffen's bats (*Nycticeinops schlieffenii*), and lesser yellow house bats (*Scotophilus viridis*). The evening bat forms maternity colonies containing up to 1,000 individuals in hollow trees or houses (Scherrer & Wilkinson 1993). Schlieffen's bats roost solitarily under bark (Merwe & Rautenbach 1987). Lesser yellow house bats form colonies in hollow trees or caves that contain up to 100 individuals (Fenton et al. 1977). Females of all three of these species typically produce twins, and pups of similar ages aggregate to form creches while their mothers are away feeding (Figure 12.3).

A second clade includes two molossid bats, Mexican free-tailed bats and little free-tailed bats, both of which produce a single young each year. Mexican free-tailed bats form large maternity colonies (McCracken 1984) with up to 20 million individuals in a single cave. Pup densities on the cave wall can reach 1,000 per square meter. Little free-tailed bats form colonies in attics that contain 20–500 individuals (McWilliam 1988).

The third clade includes one rhinolophid, the bushveld horseshoe bat (*Rhinolophus simulator*), and two hipposiderids, Sundeval's leaf-nosed bat and the short-eared trident bat (*Cleotis percivali*). All three of these species form colonies and use high duty cycle, narrow bandwidth echolocation calls. Colony size varies from several hundred in the bushveld horseshoe bat to many thousand in Sundeval's leaf-nosed bat. Little information is available on colony size for short-eared trident bats, but reports indicate colonies
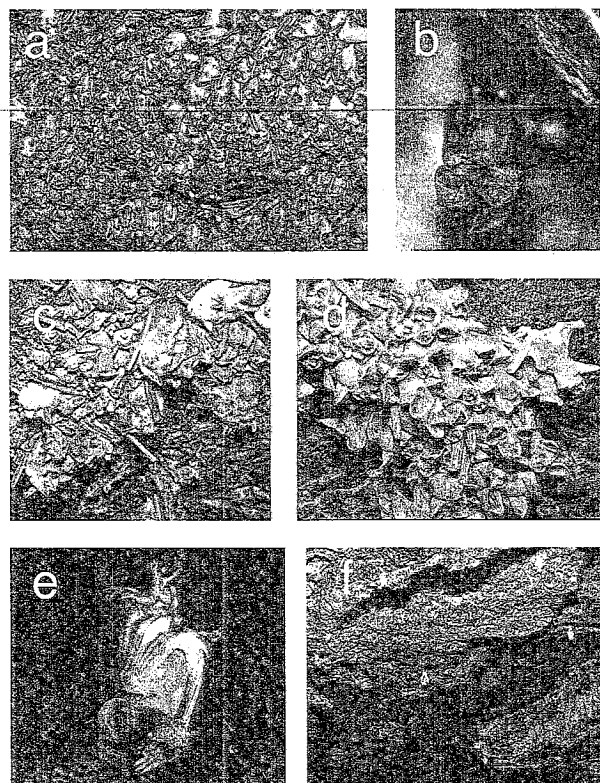
Figure 12.3. Infant aggregations for *a)* Mexican free-tailed bats (*Tadarida brasiliensis;* courtesy of G. McCracken), *b)* Sundeval's leaf-nosed bats (*Hipposideros caffer*), *c)* lesser yellow house bats (*Scotophilus borbonicus*), *d)* bushveld horseshoe bats (*Rhinolophus simulator*), *e)* and *f)* short-eared trident bats (*Cleotis percivali*).

range from tens to hundreds of bats. All three species give birth to singletons, but the spacing patterns of individuals within a colony differ. Bushveld horseshoe bats form dense aggregations and leave pups in creches (Figure 12.3d), whereas both Sundeval's leaf-nosed bats and short-eared trident bats leave pups in isolated locations, often a meter or more away from other pups (Figure 12.3b, e, f). Given these differences in roosting and echolocation behavior, I also compare vocal complexity to creching behavior and echolocation strategy (high duty cycle versus low duty cycle).

To compare call complexity across species I used comparable methods to quantify acoustic variation and when possible, measured 20 individuals per species. I obtained recordings of infant calls for Mexican free-tailed bats (Balcombe 1990) and evening bats (Scherrer & Wilkinson 1993) that were recorded on tape at 30 ips. All other species were recorded in South Africa in November, 1993, using a quarter-inch Bruel and Kjaer microphone connected to a Bruel and Kjaer sound level meter and a Portable Ultrasound Signal Processor (PUSP), which sampled 8 bits at 410 kHz. PUSP digital recordings were time-expanded 20:1 in the field and recorded with a Marantz PMD-430 cassette recorder. By playing back high-speed recordings at one-eighth speed or using time-expanded recordings for each bat we were able to digitize five nonsequential calls at 44 kHz using a PowerMac computer. Then, for each call we measured 10 time, frequency, and amplitude traits from the waveform, spectrogram, and power spectra, respectively (Figure 12.4), using the sound analysis program CANARY, v. 1.2.

Because call features often change with age as pups grow (Scherrer & Wilkinson 1993), for each species I removed effects of age statistically by computing residuals from regressions of forearm length on each of the 10 acoustic variables. Forearm length is linearly related to age during the first half of lactation in bats (Kunz & Stern 1995). To quantify the complexity in
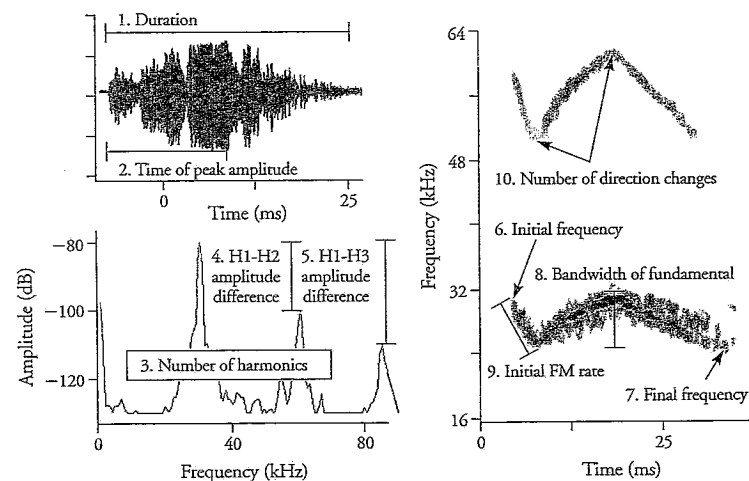

Figure 12.4. Description of 10 acoustic measurements taken on each isolation call.

each variable I used the Shannon-Wiener information statistic, H_s, which I calculated with a model II MANOVA on the regression residuals involving each acoustic variable (Beecher 1989). I then compared total complexity to visual count estimates of colony size obtained when the bats were captured and recorded.

Isolation calls can potentially function as vocal signatures given that there were highly significant differences between individuals in all eight species ($p < 0.0001$, MANOVA). In addition, the total information contained in the isolation calls of each species exhibited a significant positive relationship with colony size (Figure 12.5), as predicted if evolution has acted to increase call complexity. Neither echolocation type nor creching behavior showed significant associations with call complexity. Despite dramatically different forms of echolocation calls, infant isolation calls exhibit considerable acoustic similarity across species, genera, and families. Differences appear only in the degree to which individuals differ in acoustic dimensions, with CF bats showing more variation in the number and relative intensities of harmonics and little variation in duration compared to FM bats. Additional studies are
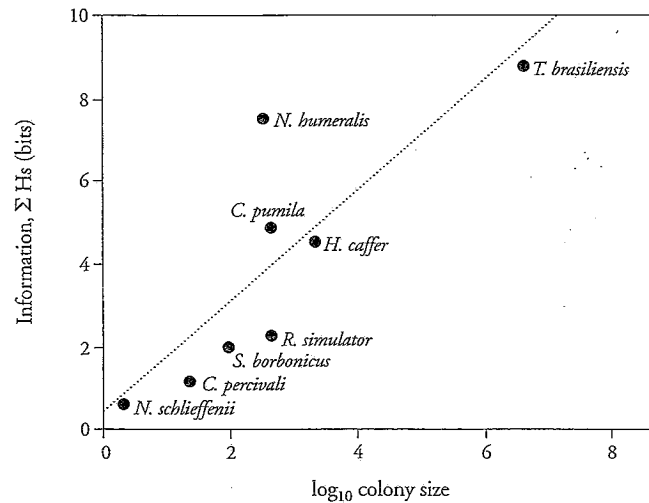

Figure 12.5. Infant isolation call complexity, as measured by the information contained in 10 acoustic variables (see text), plotted against log(10) colony size for eight species. A least-squares regression explains 69 percent of the variation in call complexity.

needed to determine if these acoustic differences reflect perceptual differences between species with different echolocation systems.

Discussion and Conclusions

The analysis of neocortical volume presented above is consistent with the hypothesis that group stability has been more important than colony size, mating behavior, or echolocation ability in shaping neocortical volume and presumably, therefore, the cognitive capabilities of bats. This result does not preclude the possibility that social group size has also influenced bat cognitive ability. As noted above, social group sizes are not available for most species of bats, and the MI hypothesis does not necessarily predict any association between colony size and cognitive ability. The association between female group stability and neocortical volume could reflect past social selection for cognitive ability if one assumes that individuals in stable social groups must remember many social transactions. At least one group-living species, the common vampire bat, exhibits evidence of reciprocal food sharing (Wilkinson 1984). A key requirement for the maintenance of reciprocal exchange systems is the presence of a mechanism for detecting cheaters, such as the ability to remember interactions with other members of a social group.

Alternatively, the association between group stability and neocortical volume may be caused by a third, unmeasured, variable. For example, those species that form stable social groups might also face difficult cognitive challenges related to obtaining food, such as finding vertebrate prey. The common vampire bat and the fishing bat are notable in this regard as these two species have some of the largest residual neocortical volumes in the order and face challenging foraging tasks. The relatively large neocortex among nectar-feeding bats might also reflect the cognitive difficulties associated with traveling long distances to food sources that change location frequently. Additional data on group stability as well as more specific comparisons involving aspects of social and cognitive complexity, such as the duration of social relationships or home range size and utilization, may help discriminate between these possibilities.

One interesting parallel between bats and primates is that social grooming appears to be confined to those bats that form stable social groups (Wilkinson 1987). Unfortunately, much less is known about the function of this behavior in bats than in primates. One notable difference is that some bats groom each other to obtain food. Nectar and pollen-feeding bats can become covered in pollen after visiting a flower. This pollen is typically in-

gested by a bat or its roostmates after returning to a communal roost. Nevertheless, not all nectar-feeding bats groom each other, for example, long-nosed bats (*Leptonycteris curasoae*) do not (T. Fleming, personal communication), whereas lesser spear-nosed bats do (personal observation). Long-nosed bats form large colonies and forage in groups (Howell 1979). Absence of social grooming suggests that foraging groups are not stable assemblages of individuals and recent observations on long-nosed bats are consistent with this inference (T. Fleming, personal communication). In contrast, analysis of social grooming among individually marked female vampire bats revealed grooming preferences for some individuals and an association between social grooming episodes and food sharing events (Wilkinson 1986). I hypothesized that bats inspected each other while grooming to determine who might be able to provide or be in need of a blood meal. Whether or not social grooming also functions to maintain social bonds, as has been proposed for primates (Dunbar 1991), remains to be determined.

In contrast to propositions for primates (Dunbar 1993), evidence available to date suggests that social complexity in bats has little general relationship to vocal complexity. This conclusion should, though, remain tentative until direct comparison of vocal complexity between species that form long-term social bonds, such as vampire bats and greater spear-nosed bats, to species with less stable social groups, has been made. On the other hand, repertoire diversity in greater white-lined bats is related to the number of females in a male's territory (Davidson & Wilkinson 2001). Thus, as in some birds and marine mammals (Janik & Slater 1997), sexual selection appears to provide the best explanation for this type of vocal complexity in bats. In addition, colony size appears to have influenced the evolution of infant isolation call complexity in bats. Presumably, similar patterns will be found between colony size and complexity of maternal directive calls in those species where females call to pups to facilitate reunions.

An essential adaptation for the evolution of language is the ability to learn to produce new vocalizations after hearing exemplars. An intriguing question to consider, therefore, is whether vocal learning contributes to call complexity in bats. Several answers are possible. Infant bats begin to produce isolation calls moments after birth. Even at that time, individuals differ in characteristic ways that persist for several subsequent weeks (Scherrer & Wilkinson 1993). Although some evidence indicates that pups may modify acoustic features of their calls in response to sounds they hear (Esser 1994), a consequence of such modication would typically be a reduction, not an increase,

in call complexity as defined by the information available in the calls, according to Beecher (1989). However, if individuals have distinctive signature calls and, in addition, modify a call to match others in their social group, as greater spear-nosed bat females seem to do (Boughman 1998), then within-individual call diversity could increase. Vocal learning could also enhance call complexity if syllables can be acquired from others and syllable order is flexible. Learned vocalizations appear to play key roles in maintaining social cohesion within groups in other taxa, such as parrots (see Chapter 11) and cetaceans (see Chapter 13). Thus, additional studies on vocal learning in bats may prove particularly insightful at understanding how sociality influences vocal complexity in bats.