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Abstract

The evolution of sociality is a central theme in evolutionary biology. The vast majority of bats are social, which has been explained in terms of the benefits of communal breeding. However, the causes for segregated male groups remain unknown. In a comparative study, we tested whether diet and morphological adaptations to specific foraging styles, two factors known to influence the occurrence of information transfer, can predict male sociality. Our results suggest that the species most likely to benefit frominformation transfer - namely, those preying on ephemeral insects and with morphological adaptations to feeding in open habitat - are more likely to form male groups. Our findings also indicate that solitary life was the ancestral state of males and sociality evolved in several lineages. Beyond their significance for explaining the existence of male groups in bats, our findings highlight the importance of information transfer in the evolution of animal sociality.

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Comparative Analyses Suggest That Information Transfer Promoted Sociality in Male Bats in the Temperate Zone

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abstract: The evolution of sociality is a central theme in evolutionary biology. The vast majority of bats are social, which has been explained in terms of the benefits of communal breeding. However, the causes for segregated male groups remain unknown. In a comparative study, we tested whether diet and morphological adaptations to specific foraging styles, two factors known to influence the occurrence of information transfer, can predict male sociality. Our results suggest that the species most likely to benefit from information transfer—namely, those preying on ephemeral insects and with morphological adaptations to feeding in open habitat—are more likely to form male groups. Our findings also indicate that solitary life was the ancestral state of males and sociality evolved in several lineages. Beyond their significance for explaining the existence of male groups in bats, our findings highlight the importance of information transfer in the evolution of animal sociality.

Keywords: information center, local enhancement, group living, Chiroptera, social system, sexual segregation.

Information sharing is an important benefit of group living (Beauchamp et al. 1997; Barta and Giraldeau 2001; Valone and Templeton 2002). Animals can enhance their fitness by obtaining information from conspecifics about the type, location, or amount of currently available resources, such as food (Buckley 1997*a*, 1997*b*). Thus, information transfer about food plays an important role in the evolution of group living in social animals (Buckley 1997*b*; Beauchamp 1999; Barta and Giraldeau 2001; Valone and Templeton 2002).

Bats are of great interest in studying the evolution of sociality because the majority of the 1,000-plus species worldwide are social, despite profound ecological differences among them (Bradbury 1977; Kunz and Pierson 1994; McCracken and Wilkinson 2000). For several reasons, including those related to conservation, most studies on the sociobiology and ecology of bats have focused on breeding colonies. As a consequence we have a relatively good understanding of sociality in female bats but know much less about sociality in male bats. The existence of female aggregations in bats has been explained in terms of benefits of communal breeding, while the occurrence of multimale-multifemale aggregations is probably influenced by mating strategies (McCracken and Wilkinson 2000; Zubaid et al. 2006). However, the selective pressures favoring segregated male groups are largely unknown, even though knowledge of these forces is crucial for a complete understanding of the evolution of sociality in bats.

In temperate zone bats, two of the three annual phases are characterized by mixed-sex aggregations (hibernation during winter and mating in fall; Bradbury 1977). The sexes usually segregate during the third phase, in spring and summer, when in most species the females form breeding colonies. In sexually segregated species the males are usually solitary during this time, but in some species males form separate groups (Altringham and Senior 2005), for example, in *Vespertilio murinus* (Safi 2006).

Using a comparative approach, we attempt to assess the importance of information transfer about food as a possible key factor in the evolution of segregated male groups in temperate zone bats. All microbats use echolocation to orient themselves during foraging (Neuweiler 1984). "Eavesdropping" on echolocation calls has been described in several species (Balcombe and Fenton 1988; Fenton 2003), and a few empirical studies have investigated in-

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formation transfer about food (e.g., *Nycticeius humeralis*: Wilkinson 1992; *Myotis bechsteinii*: Kerth et al. 2001). Yet the overall importance of information transfer about food for the evolution of sociality in bats remains unknown, due to a lack of comparative studies.

Because there are insufficient data on information transfer in different bat species, we focused in our comparative analyses on two well-studied factors that are known to correlate with the occurrence of information transfer.

1. *Diet*. If food is patchily distributed and ephemeral (i.e., clumped but unpredictable in time and space), sociality can enhance the foraging efficiency of individuals by providing opportunities for information transfer among group members (Barta and Szep 1992; Beauchamp et al. 1997). If male sociality in bats has evolved to promote information transfer about food, we expect to find male groups predominantly in species that prey on ephemeral insects, such as caddis flies, mayflies, and aphids.

2. *Morphology*. Wing morphology reflects a bat species' adaptation to its foraging habitat, as well as its costs of locomotion (Norberg and Rayner 1987). Wing morphology should influence the occurrence of male sociality for two reasons. First, one of the major costs of sociality is local resource competition, which can restrict the emergence of groups or at least limit their size (Doran 1997; Blumstein et al. 2001). Broad-winged species are agile and can pursue their prey in dense habitats (e.g., inside forests) but face high costs of locomotion. Narrow-winged species are adapted to foraging in open space, where they fly quickly and efficiently (Norberg and Rayner 1987). Because narrow-winged species have smaller costs of flying than broad-winged species, they can reduce local resource competition by spreading out over large areas. Second, narrow-winged species that fly in open space have relatively low maximum amplitudes of echolocation frequencies, narrow frequency bands, and loud echolocation calls (Neuweiler 1984; Schnitzler et al. 2003). All of these parameters make their calls and thus the information about prey availability audible over a larger distance. Thus, species adapted to foraging in open space could exchange information over a larger range than species foraging in dense habitats, thereby increasing the benefits of information transfer (Buckley 1997*b*). Because of the combination of these two processes, we expect to find social males more often in narrow-winged than in broad-winged species.

Material and Methods

We restricted our study to temperate zone bats because more data are available than for tropical species and because they provide a more homogeneous data set (Safi and Kerth 2004). By screening almost 100 original publications and the references therein as well as several textbooks, we gathered data on the social organization, diet, and morphology of 45 bat species from North America and Europe (approximately 50% of the bat species present in the area; Hutson et al. 2001; data are available as an Excel file or in tab-delimited ASCII format; see appendix [available in the online edition of the *American Naturalist*] for data file and references).

Because published information about the social organization of male bats is incomplete, we decided to use only three levels of male social organization: solitary, social, and unknown. We then searched for differences between the two social systems (social and solitary) and used them to make predictions about the social system of those species classified as unknown.

The males of a bat species were considered to be social if at least one publication reported male groups during the breeding season of the females (10 species). If a publication reported the sex ratios of bat aggregations, we considered an aggregation a male group if it consisted of a majority of males and no breeding females were present. However, most studies reported only male groups (or used similar expressions such as "bachelor groups") without giving any further details about the sex ratio or the number of individuals. Where the sex ratio was known, the percentage of males ranged from 80% to 100%. The number of reported individuals per male group ranged from seven individuals in *Nyctalus noctula* (Cerveny and Bürger 1989) to 247 in *Vespertilio murinus* (Safi 2006). We considered the males of a bat species solitary if no publication reported male groups and at least one publication explicitly stated that the males are solitary or generally solitary (19 species). The status of the remaining 16 species was classified as unknown, as we found neither a study stating that males are solitary nor one reporting male groups.

We found data on the diet for all 45 species. Dietary composition was usually given as the proportion (volume or number of occurrences) of arthropods found in the feces, at the level of the order in the case of insects or at the level of the class for all other prey. Following Safi and

Figure 1: According to the maximum parsimony reconstruction, the ancestral state of the social organization of temperate zone male bats was solitary life. The color of the final branches (tip of the tree) indicates the type of male social organization: red for species with social males, blue for species with solitary males, and gray for species with unknown male social organization. The colors of the lower level branches and nodes refer to the maximum parsimony reconstruction: light red for social ancestors, light blue for solitary ancestors, and light gray for unresolved ancestral social organization. The reconstruction suggests that solitary life was the ancestral state for males.

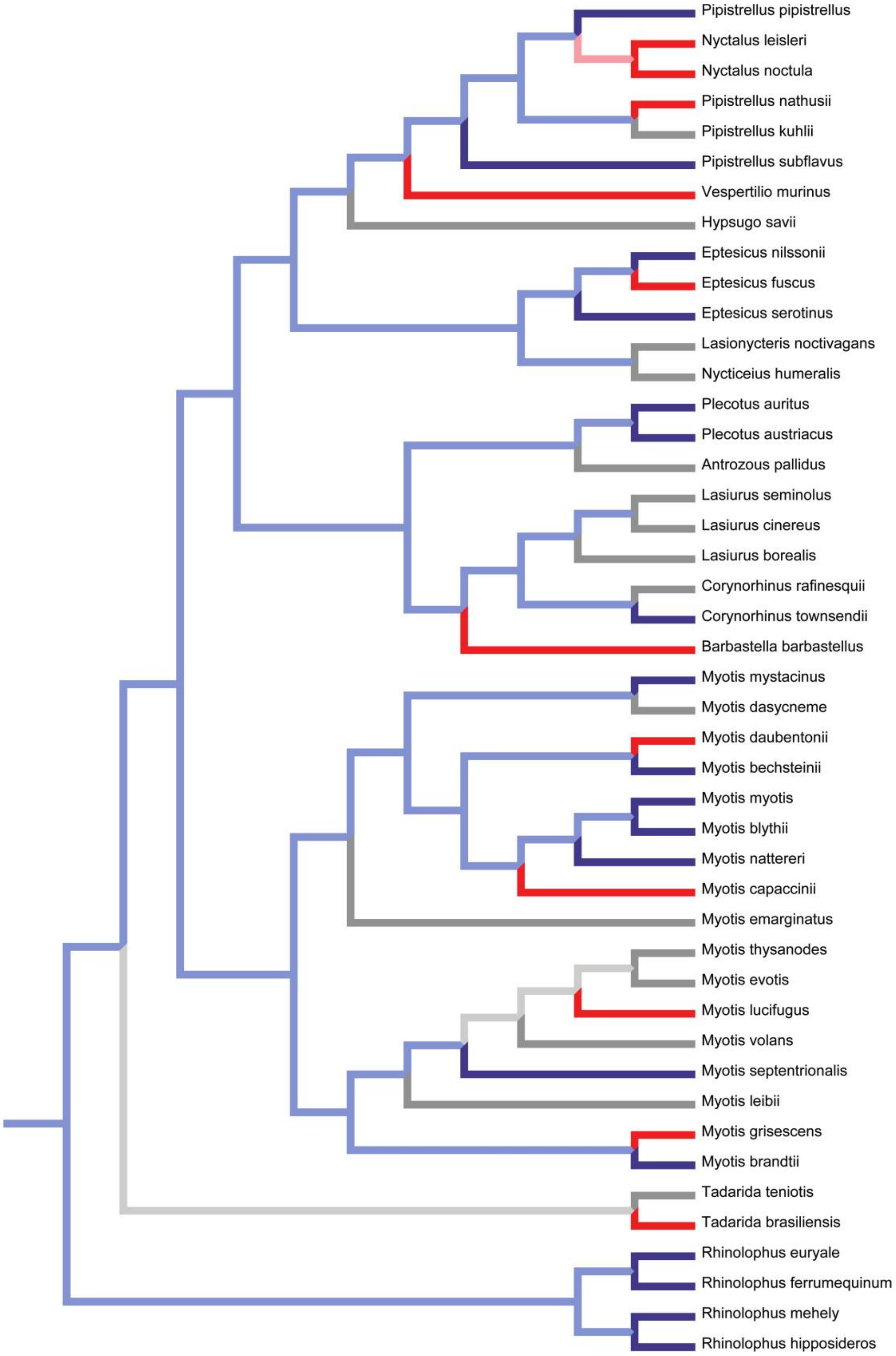
Pipistrellus pipistrellus
Nyctalus leisleri
Nyctalus noctula
Pipistrellus nathusii
Pipistrellus kuhlii
Pipistrellus subflavus
Vespertilio murinus
Hypsugo savii
Eptesicus nilssonii
Eptesicus fuscus
Eptesicus serotinus
Lasionycteris noctivagans
Nycticeius humeralis
Plecotus auritus
Plecotus austriacus
Antrozous pallidus
Lasiurus seminolus
Lasiurus cinereus
Lasiurus borealis
Corynorhinus rafinesquii
Corynorhinus townsendii
Barbastella barbastellus
Myotis mystacinus
Myotis dasycneme
Myotis daubentonii
Myotis bechsteinii
Myotis myotis
Myotis blythii
Myotis nattereri
Myotis capaccinii
Myotis emarginatus
Myotis thysanodes
Myotis evotis
Myotis lucifugus
Myotis volans
Myotis septentrionalis
Myotis leibii
Myotis grisescens
Myotis brandtii
Tadarida teniotis
Tadarida brasiliensis
Rhinolophus euryale
Rhinolophus ferrumequinum
Rhinolophus mehely
Rhinolophus hipposideros

Table 1: Species-level comparison between species with social and solitary males using the exact Wilcoxon two-sample test

Predictor and social system	Median (Q1; Q3)[a]	N	Sum of scores	Expected score	Mean score	S	df	P
Proportion of ephemeral insects in the diet						216	1	.002
Social	.16 (.10; .24)	10	216	150	21.6			
Solitary	.06 (.01; .1)	19	219	285	11.5			
Aspect ratio (log-transformed)						145	1	.124
Social	1.85 (1.84; 2.00)	9	144.5	117.0	16.1			
Solitary	1.80 (1.74; 1.87)	16	180.5	208.0	11.3			
Wing loading (log-transformed)						167	1	.182
Social	2.27 (2.09; 2.61)	10	167.0	140.0	16.7			
Social	2.02 (1.87; 2.31)	17	211.0	238.0	12.4			

[a] Q1 and Q3 denote the lower and the upper quartiles.

Kerth (2004), we generated a homologous set of dietary data. From the 18 arthropod classes/orders found in the bat feces, we calculated the proportion of ephemeral insects in the diet, defined as the sum of Trichoptera (caddis flies), Ephemeroptera (mayflies), and Hemiptera (aphids) divided by the sum of the remaining 15 classes/orders.

To quantify flight morphology, we used the most widely used measures, aspect ratio and wing loading. Aspect ratio is the square of the wing area divided by the wing breadth. Higher aspect ratios usually correspond to greater aerodynamic efficiency and lower energy losses in flight (Norberg and Rayner 1987). Wing loading is calculated as the wing area divided by the body mass and represents the weight that the wings have to carry. Species with high wing-loading values forage in open space, rely on speed, and have small, narrow wings relative to their body mass, resulting in low agility and low maneuverability (Norberg and Rayner 1987).

Morphological measures have a strong phylogenetic interdependence in bats (Safi and Kerth 2004; Safi and Dechmann 2005), making the interpretation of interspecies comparisons without phylogenetic correction often questionable. Therefore, as recommended by Garland et al. (1992), we analyzed the data both at the species level, using nonparametric tests or logistic regressions (SAS Institute 1993), and at the level of phylogenetically independent contrasts, using the software CAIC (Purvis and Rambaut 1995). We used a composite tree with equal branch lengths, based on available phylogenetic trees (Ruedi and Mayer 2001; Jones et al. 2002, 2005; Hoofer and Van den Bussche 2003; Stadelmann et al. 2004; fig. 1). Where references disagreed, we gave priority to the most recent molecular phylogenetic analysis. To compare continuous variables in CAIC we used the "crunch" algorithm, as suggested by Purvis and Rambaut (1995). Comparisons between the dichotomous variable "social system" (social vs. solitary) and the continuous measures required the "brunch" algorithm (Purvis and Rambaut 1995). Correlations of phylogenetic independent contrasts were forced through the origin (Garland et al. 1992). In order to meet the assumptions of a random walk model required for the independent contrasts (Purvis and Rambaut 1995), we had to log-transform the proportion of ephemeral insects, enter aspect ratios as raw data, and square-root-transform wing loading.

In addition to the comparative analyses with independent contrasts, we used the program Mesquite (version 1.06) to reconstruct the ancestral state of male social organization using maximum parsimony (Maddison and Maddison 2005). For our species-level analyses we log-transformed aspect ratio and wing loading. Results were regarded as significant if the P values were <0.05. Mean values are given with their standard deviation.

Results

Male groups were reported in 10 vespertilionid species in six different genera from Europe (six species) and North America (four species; fig. 1). Reconstruction of the ancestral state suggested that the ancestral male social organization was solitary (fig. 1).

The proportion of ephemeral insects in the diet was uncorrelated with the morphological variables (species level: Spearman rank-correlation coefficients between -0.04 and 0.28 with $.2 < P < .8$; contrast level using generalized linear models: $0.0 < F < 0.3$, $.6 < P < .9$). At the species level, the proportion of ephemeral insects in the diet was significantly higher for bat species with social males compared to species with solitary males, whereas none of the other measures differed significantly between the two groups (table 1; fig. 2).

After controlling for shared phylogeny, the proportion of ephemeral insects in the diet remained positively correlated with the occurrence of male groups (table 2). How-

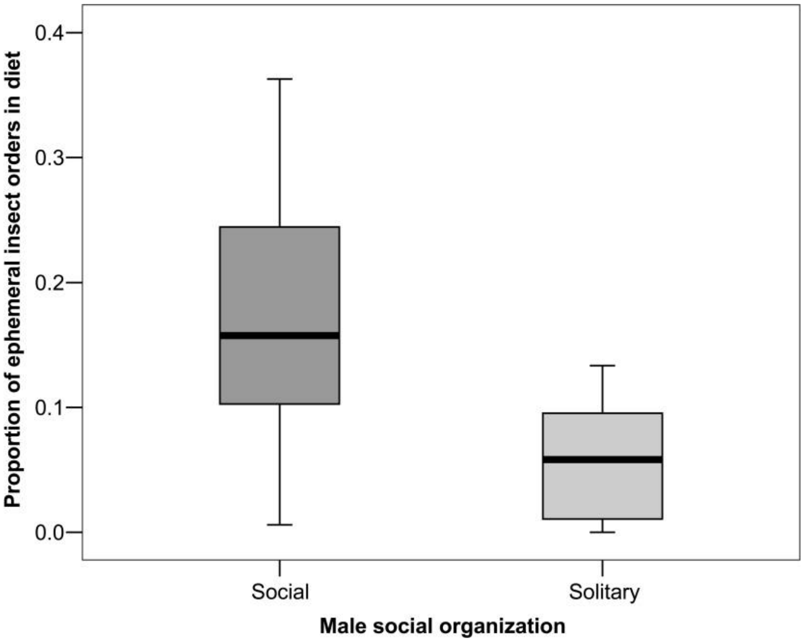

Figure 2: Box plots of the proportion of ephemeral insect orders in the diets of North American and European bats, comparing species in which males are solitary with those in which males are social.

ever, flight morphological variables now also differed significantly between bat species with solitary and social males (table 2). Thus, according to the phylogenetically independent contrasts, bat species more often evolved male sociality with increasing amounts of ephemeral insects in their diet and a morphological adaptation to flight in open space.

To evaluate the relative importance of wing morphology and diet for the evolution of male sociality, we used a single logistic model at the species level in which all factors were tested simultaneously and corrected against each other in a Type III sum-of-squares model. In this model the only remaining significant factor at the species level was the proportion of ephemeral insects in the diet (log-likelihood ratio for Type III analysis: df $= 1$, $\chi^2 = 8.9$, $P = .003$). The analogous method of analysis for the independent contrasts is the use of multiple correlations (Purvis and Rambaut 1995). After correcting for the effect of flight morphology, the proportion of ephemeral insects in the diet and the social organization remained significantly correlated at the level of independent contrasts (corrected for aspect ratio: slope $= 0.15$, $r^2 = 0.6$, SS $= 0.2$, $F = 11.94$, df $= 2, 7$, $P = .006$; corrected for wing loading: slope $= 0.28$, $r^2 = 0.72$, $F = 20.14$, df $= 2, 8$, $P = .002$). Accordingly, after correcting for the proportion of ephemeral insects in the diet, social males still occurred more often in narrow-winged species than in broad-winged species at the level of independent contrasts (aspect ratio: slope $= 0.33$, $r^2 = 0.39$, $F = 4.56$, df $= 2, 7$, $P = .06$; wing loading: slope $= 0.46$, $r^2 = 0.46$, $F = 6.8$, df $= 2, 8$, $P = .02$).

Finally, we applied a series of nonparametric discriminant function analyses (DFAs) to assign the species of unknown status to the classes "social" or "solitary," using

Table 2: Analyses of phylogenetically independent contrasts, generated with the software CAIC and the "brunch" algorithm

	R	R^2	SS	Numerator df	Denominator df	*F*	*P*
Proportion of ephemeral insects in diet (log-transformed)	.15	.63	.20	1	8	13.4	.006
Aspect ratio (raw values)	.37	.42	1.09	1	7	5.34	.05
Wing loading (square-root-transformed)	.22	.43	.42	1	8	6.08	.04

Note: See "Material and Methods" for details.

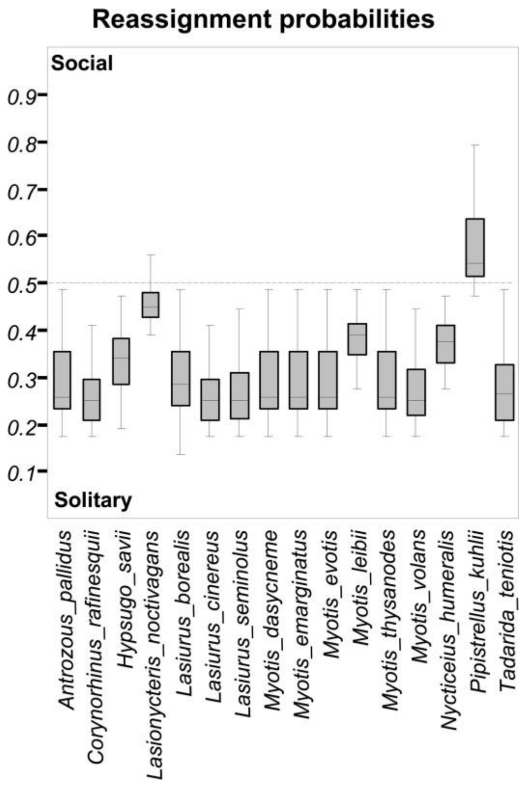

Figure 3: Reassignment probabilities from discriminant function analyses for the 16 species with "unknown" male social organization. The reassignment probabilities are given as the probability of a species being "social," whereas the probability of being "solitary" is (1 − P_{social}). Species were classified as social if the probability was >.5 (=unresolved probability) and solitary if the probability was <.5.

the proportion of ephemeral insects in the diet in a *k* nearest neighbors framework (for $2 \le k \le 28$). The posterior percentage of the species with known male social organization that were reassigned to their correct class in the series of DFA was 94.3% ± 6.0% for the species with solitary males and 58.2% ± 19.2% for the species with social males. Thus species with solitary males had a probability of <6% to be misclassified by the DFA as social. From the 16 species with unknown status, *Pipistrellus kuhlii* was regularly (22 out of 26 times) classified as social with an average probability of 58% ± 10% (fig. 3). The reassignment probability suggests that in *P. kuhlii*, males probably form aggregations. For the 15 remaining species with unknown male social organization, it was impossible to achieve a similar degree of confidence in the predictions regarding their possible male social organization, although the reassignment probabilities observed suggest that most of them have solitary males (fig. 3).

Discussion

Female sociality in temperate zone bats has often been explained in terms of benefits of communal breeding, such as social thermoregulation during pregnancy and lactation (Zubaid et al. 2006). Male sociality cannot be explained with the same benefits, as males do not contribute to parental care. The results of our comparative analyses, regardless of the methods used, show that bat species with social males have a high percentage of Trichoptera (caddis flies), Ephemeroptera (mayflies), and Hemiptera (aphids) in their diet. These three insect orders contain mainly small and highly ephemeral species, characterized by mass emergences of their winged imagos (Borror et al. 1989). The temporal and spatial prey distribution of bat species with social males therefore matches both the theoretical expectations for information transfer in animals and previous empirical data (Buckley 1997*b*; Barta and Giraldeau 2001).

After taking phylogenetic relationships into account, social males also occurred more often in species adapted to flight in open habitats. The observed correlation between wing morphology and sociality could have two reasons that both point to the importance of information transfer about food. First, rich ephemeral swarms of insects, which favor information transfer, occur mainly in the open air, and because of spatially and temporally very concentrated nuptial flights (Borror et al. 1989) and due to the fact that swarms are subject to convection, they are short-lived (20–30 min; Brown 1986). Second, the typical structure of the echolocation calls of bats foraging in open air facilitates information transfer. In bats, the temporal pattern of echolocation calls provides information about the foraging success of individuals, which can be perceived by conspecifics that eavesdrop on the calls (Barclay 1982; Balcombe and Fenton 1988; Fenton 2003). Species flying in open space should be able to share information more easily because of the larger range of their calls (Schnitzler et al. 2003). For the parti-colored bats (*Vespertilio murinus*), for example, which typically show male aggregations, other conspecifics in open air are within hearing range at distances of up to 90 m, whereas insects are detectable at distances of at most 6–12 m (distances based on the following values: 27 kHz call frequency, 0 dB detection threshold, target strength of prey −30 dB sound pressure level for large prey and −50 dB sound pressure level for small prey, attenuation calculated for 15°C, 50% relative humidity, and 100 kPa air pressure; Møhl 1988; Holderied and von Helversen 2003; Stilz 2004). Besides the increase in the amount of available information, open aerial foragers may experience lower costs of sociality because of their efficient locomotion. For comparison, coloniality in birds has been explained in terms of the benefits of information transfer in species that forage in open habitats and that are specialized on ephemeral resources such as insect flocks, carcasses, or marine prey (Brown 1986; Buckley 1996; Wright et al. 2003). In the few studies directly addressing information transfer about food in bats, the data support our findings. Information transfer about food occurred among female evening bats (*Nycticeius humeralis*) that forage in the open air (Wilkinson 1992) but was absent among female Bechstein's bats (*Myotis bechsteinii*) that mostly glean their prey from the vegetation (Kerth et al. 2001).

Theoretical studies have emphasized the importance of information sharing in shaping social strategies (Beauchamp et al. 1997; Barta and Giraldeau 2001), and the occurrence of information transfer has been empirically demonstrated in many species, including some bats (King 1991; Buckley 1996; Marzluff et al. 1996; Brooke 1997; Marchetti and Drent 2000; Drapier et al. 2002; Wright et al. 2003; Ratcliffe and Ter Hofstede 2005). In contrast to our findings in bats, comparative studies investigating the importance of increased foraging efficiency for the evolution of bird colonies have come to no general conclusion (Rolland et al. 1998; Beauchamp 1999). We suspect that, in part, this may be attributable to the fact that birds often live in colonies in which breeding is taking place and where sexes with potentially different life-history traits live together.

Conclusions

We have shown that feeding on ephemeral prey and morphological adaptations to flight in open habitats are correlated with the occurrence of male groups in temperate zone bats. Both factors predicting male sociality in a phylogenetic framework are expected to promote the exchange of information among conspecifics. This suggests that information transfer about food may have played a key role in the evolution of male sociality in bats. Two questions not addressed by our study remain. First, why do social males segregate from social females, when one might expect that males would further increase their information gain by joining female aggregations? Second, is information shared during foraging, via some process such as local enhancement, or in the roost (which therefore acts as an "information center")? Theoretically both processes could be involved in information exchange in bats. In some species with male aggregations, local enhancement is more likely because of generally only one continuous foraging trip per night (*Vespertilio murinus*: Safi et al. 2007). In other species, however, roosts could act as information centers because animals usually show several foraging bouts per night (*Nycticeius humeralis*: Wilkinson 1992; or *Nyctalus nactula*: Gebhard and Bogdanowicz 2004). Clearly, to fully understand the different routes to sociality in bats, more empirical studies are needed that investigate the sex-specific ecology and sociobiology of species in which males and females are social but segregated.

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