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Sex differences in population genetics, home range size and habitat use of the parti-coloured bat (Vespertilio murinus, Linnaeus 1758) in Switzerland and their consequences for conservation

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Short title: Sexual segregation and conservation

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Keywords: Chiroptera, genetic diversity, PIT-tag, radio-tracking, sexual segregation

Introduction

One important factor causing population declines in various species is a high degree of specialization (Arita 1993; Johnson 2002; Jones et al. 2003; Purvis et al. 2000; Safi and Kerth 2004; Vazquez and Simberloff 2002). When relevant resources decline, specialists seem to suffer more from habitat changes than generalists because they cannot switch to other available resources (Harcourt et al. 2002; Hopkins et al. 2002; Wilson et al. 1999). Likewise, age- or sex-specific niche specialization could increase a species susceptibility to habitat changes, although as a whole the species may use diverse and still abundant resources (Bolnick et al. 2003; Durell 2000). Pronounced sex-specific niche partitioning is particularly likely to occur in species in which males and females live in separate groups outside the mating season (Bowyer 2004). This kind of social organization is termed (social) sexual segregation and in mammals it is often linked to sexual size dimorphism (Mysterud 2000; Ruckstuhl and Neuhaus 2002). Since sexually segregated species often show sex-specific differences in ecology, morphology and behaviour, they may require sex-specific conservation approaches (Bowyer 2004; Durell 2000).

We used the parti-colored bat (*Vespertilio murinus*), a species with pronounced sexual segregation (Baagøe 2001; Rydell and Baagøe 1994), to study whether ecological, morphological and behavioural differences between the sexes are occurring that are relevant for conservation. For each sex we determined body size, genetic population structure, habitat use, and activity pattern at the roost. The parti-colored bat is a Palae-arctic species distributed over large areas of north-eastern Europe and Asia (Baagøe 2001; Rydell and Baagøe 1994). The species is absent in southern Europe and reaches its western limit of reproduction in the Netherlands and Switzerland (Baagøe 2001; Jansen 2002). In Switzerland, where our study was conducted, the species is rare and listed as "potentially

vulnerable with uncertainties regarding the distribution of the species" (Nievergelt et al. 2003).

Male parti-colored bats form large colonies containing up to 250 males (Baagøe 2001) whereas the males in most other European bats are solitary during summer (in contrast to females). Roosts of both sexes are found in the roofs of houses, under tiles or in crevices during a short period of about three months from April until July (Baagøe 2001; Rydell and Baagøe 1994). Long and narrow wings enable the parti-colored bat to pursue its prey, largely Diptera, Trichoptera and other small insects, in fast flight in open space (Beck 1995; Jaberg et al. 1998). The few studies that investigated habitat use in parti-colored bats reported foraging over large water bodies such as lakes and rivers, as well as over open agricultural landscapes and forests (Baagøe 2001; Jaberg et al. 1998; Rydell and Baagøe 1994).

Sexual segregation, which can result from sex-specific ecological, morphological and behavioural differences, may require a more detailed conservation approach than the usual focus on the species as a whole (Catry et al. 2005; Durell 2000; Rubin and Bleich 2005). Using a combination of behavioural and genetic data, our study aims to investigate such sex-specific differences in order to characterize ecological niches and population genetics of each sex in a sexually segregating bat species. We want to understand the extent to which a sex-specific view could change and potentially improve conservation efforts compared to the more commonly adopted scale of conservation, the species level.

Methods

Sampling and body size measurements

To compare genetic-structure and -diversity, as well as body size measurements between sexes and among colonies, we caught bats in three female and two male colonies. Two female colonies (F1 and F2) occurred in Switzerland and the third in north-eastern

Germany (colony F3), further east and hence closer to the centre of the species' distribution. Both male colonies occurred in Switzerland (M1 and M2). Animals were caught with a harp-trap when emerging from the roost with the exception of the colony F2 where samples were obtained from dead young of the colony. Tissue samples were taken with a sterile biopsy punch (3mm biopsy, Stiefel Laboratorium AG, Switzerland) from the patagial wing membrane and were stored in 96% EtOH. The wing membrane healed completely in all animals that were recaptured after 14 days. From all animals, we determined sex and age (juvenile or adult). In addition, forearm length and body mass were taken from the animals in the colonies F1, M1 and M2. Bats were subsequently marked with passive subcutaneous tags (PIT-tags, Euro-ID, Weilerwist, Germany; see: Kerth and König 1996). All animals were released immediately after processing. Sampling took place in 2000 (colony F2), in 2001 and 2004 for the colony F3, and from 2002 to 2004 (colonies F1, M1 & M2; table 1). Animals were caught and sampled under the licenses of the Swiss federal veterinary office (ZH 78/2002 & NE 2/2002), and the nature and landscape conservation offices of the respective cantons. For colony F3, the license was obtained from the German Landesumweltamt Brandenburg (#4440-236-NF/021-2004).

Population genetics

To analyse population structuring at the maternal level, we sequenced 341 bp of the highly variable mitochondrial control region (D-loop). From each tissue sample, 0.25–2.5 mg of DNA was extracted using a NaCl extraction method (Müllenbach et al. 1989). Double-stranded DNA from the control region was amplified from total cellular DNA using the polymerase chain reaction (PCR) in combination with primers E (Wilkinson and Chapman 1991) and P (Wilkinson et al. 1997). Before analysis, 20-50 ng of mitochondrial DNA was amplified in a PCR reaction with 1x Amplimix buffer (Microsynth, including 1.5 mM $MgCl_2$, 0.2 mM dNTP mix), 0.5 units taq. polymerase (Pharmacia), and 0.24 μM of each primer. Total reaction volume was 25.0 μl. All ingredients are given in final concentrations. A PTC-200

thermocycler (MJ Research) was then programmed to perform 35 cycles of 94°C/30 s, 58°C/45 s, 72°C/60 s after an initial 94°C/4 min step and followed by 72°C/20 min. We tested 5 μl of the PCR-product on a 1.4% agarose gel (1 h: 4.5V/cm) stained with ethidium bromide. PCR products were purified using a Qiagen purification kit and directly sequenced in one direction (primer E) using the ABI prism d-Rhodamine terminator cycle sequencing ready reaction kit (Applied Biosystems). Afterwards we ran them on an ABI Prism 310 capillary sequencer.

To analyse population structuring at the nuclear DNA level, we used three (Paur-3: x-chromosomal; P-20 & NN8: autosomal) micro-satellites, which were developed for other bat species. We used the same PCR-amplification conditions as given in Kerth et al. (2002b), except for NN8, where the annealing temperature was reduced to 40°C. Degrees of heterozygosity were calculated with Arlequin 2.000 (Schneider et al. 2000) and were between 0.81 and 0.84 (Paur-3: for females only). The number of alleles was 13 for Paur-3, 20 for P20, and 22 for NN8. The alignment of the sequence data was done with Sequencher 4.1 (Gene Codes Corp.). Micro-satellite lengths were determined with the program Genotyper (Applied Biosystems). The population structuring (Fst and gene-diversity; Nei 1987) were calculated and analyzed both on mitochondrial and nuclear level using Arlequin 2.000 (Schneider et al. 2000). The population differentiation tests for the significance of the pairwise Fst-differences in Arlequin were run with 1000 permutations (in all other tests the lower default values were taken). Mitochondrial sequences were additionally analysed with Phylip 3.63 to infer phylogenetic relationship of haplotypes (Felsenstein 2004).

Home range size and habitat use

We used radio-telemetry to determine the habitat use and home range size of males and females. In 2002 and 2003, we tracked ten males from the colony M2 and five males from the colony M1. In addition we tracked eight females from the colony F1 in 2003 (table 1). We used medicinal glue (Sauer Hautkleber, Manfred Sauer GmbH, Lobbach, Germany) to

attach the radio transmitters (Holohil BD-2a, Canada) to the animals. The weight of the transmitters (0.96g) never exceeded 7.4% of an animal's body mass. The use of lighter transmitters that met the commonly recommended 5% of the bat's body weight was not possible because of the requirements for range and longevity of transmitters. As a consequence of the foraging ecology of the parti-colored bats, which fly at heights of up to 50 m and at high-speed (up to 30 km/h: Baagøe 1987) following the animals by foot or car was not possible during foraging of the bats. This was even more difficult for females that foraged to a large proportion over a lake. We tracked animals, usually four bats at a time, from two fixed, elevated stations simultaneously, using handheld three or five element Yagi antennae and TRX-1000-S receivers (Wildlife materials, Illinois, USA).

To find appropriate elevated points, we first tracked each animal for two nights before starting to collect data. Several elevated points per colony had to be used to cover the entire home range of all individuals and to ensure that contact with the transmitters exceeded 90% of the time. Bearings were taken every eight minutes from both positions (White and Garrott 1990; Wilkinson and Bradbury 1988). Whenever we suspected that the animal was stationary, we homed-in on the signal to check whether that animal was in a roost or had lost its transmitter. Since the aim of the radio-telemetry was to assess the bats' foraging areas and commuting routes, we removed all fixes from the data set that were obtained while animals were staying in the roosts. Positions were calculated from the bearings using SAS-lab statistical software and the program provided in White & Garrot (1990). Finally, we analyzed the radio-telemetry data in ArcView 3.3 with the extension "Animal Movement" (Hooge and Eichenlaub 2000).

Home range size was calculated as 90% minimum convex polygons (MCP), for comparison with other studies, and as 95% and 50% Kernel home ranges (KHR) (White and Garrott 1990). For the KHR calculation the smoothing factor H was determined using the least squares cross validation (LSCV) procedure. Each colony used several roosts during the

tracking sessions. Consequently, commuting distances to foraging areas were measured as the distance of a bearing to the barycentre of all known roosts of a colony. We square root transformed all distances for statistical analyses to obtain normal distribution.

To analyze habitat use and preference, data of ground coverage from the Swiss topological institute were used (Vector25 Swisstopo Primärflächen). This data set represents 44 non-overlapping habitat types at a scale of 1:25'000. However, we restricted our analyses to the five major structures "river", "lake", "open landscape", "forest", and "urbanized areas". The remaining habitat types, which totalled only 1.8±0.9% of individual KHR or MCP home range areas, were pooled and named "rest". We applied compositional analyses (Aebischer et al. 1993) for the comparison of habitat use and preference between sexes. Zero values of habitat types were replaced by 0.01% following (Aebischer et al. 1993). In order to assess habitat preference we compared used habitat with available habitat in the 95% Kernel home ranges (Aebischer et al. 1993; White and Garrott 1990). Preference was calculated within the home range, comparing all habitat types in the home range with the habitat types actually used also within the home range area. This level of analysis applies the detailed view of resource use i.e. Johnson's third-order selection (Aebischer et al. 1993; Johnson 1980). Habitats used were the habitats in the bat's position surrounded by a buffer area (Porter and Church 1987). The buffer area around each location was included to account for inherent inaccuracies in the bearings from two fixed stations, assuming an error of 1° which represents the inaccuracy of reading the compass (mean radius of buffer±SD =53±22 m; min=25 m, max=92 m). For each tracked animal, we included thus a small area with a radius proportional to the mean distance of the bearings of the individual from the two telemetry stations (r=tan(0.5)*mean distance to the stations).

Patterns of roost use

Using automatic transponder readers (Euro ID, Weilerwist, Germany), we monitored four roost entrances of the female colony F1 and two of the male colony M2 to assess activity

patterns at the roosts (Kerth and Reckardt 2003). Both colonies had several other entrances and we concentrated on the ones that were used by most individuals. Thereby we obtained an estimate of the minimum returning rates for marked animals. The male colony M1 roosted behind a shutter. Because the animals entered the roost from all sides, automatic readers were not applicable. In this colony we checked for the presence of marked individuals by using a hand held transponder reader (Kerth and König 1996). Transponders of bats were supplied with time and date. We started the surveillance of the roosts as soon as they were occupied in spring (around mid-April) and ended it after the last individuals had left the roosts in summer (about the end of July).

Results

Colony composition

We caught and marked a total of 405 individuals in three colonies (table 1). In the female colony F1 there was a shift in sex ratio from 91% adult females during the pre-birth period to 100% females during the post-natal time. According to the transponder readings, at least 80% of all marked females from the colony F1 returned to the roost where they were first caught. Fewer males of the colonies M1 and M2 were recorded a second time, minimum percentage were 29% and 57%, respectively. A minimum of 75% of the marked females returned from one year to the next, while 37±9% of the males returned the next year (average calculated from the colonies M1 and M2 colony and the years 2003-2004 and 2002-2003).

- Insert table 1 here

Body size

We tested for differences in log converted body mass and forearm length between males (N=251) and females in two different reproductive states ($N_{pregnant}$=59, lactating and non-pregnant: N=49; figure 1). The MANOVA revealed significant differences between the three classes males, lactating and non-gravid females, and gravid females (Wilk's lambda=0.6, $F_{4,746}$=54.6, p<0.0001). Pregnant females were heavier than lactating and non-pregnant ones, while males were lighter than both female classes (figure 1). The mean±SD body mass of males was 11.6±0.4 and of lactating or non-pregnant females 12.9±0.2. Hence, females were 11% heavier than males (log body mass: SS=3.3, $F_{2,374}$=111.8, p<0.0001). Forearm length did not differ between sexes or between different reproductive states (log forearm length: SS=0.001, $F_{2,374}$=0.63, p=0.54).

-Insert Figure 1 here-

Population genetics

The analysis of the 341 bp long D-loop sequences of 247 individuals revealed 54 variable loci defining 52 different haplotypes (Genebank accession No. DQ162738-DQ162789). Among those 52 haplotypes, "HT39" was the most frequent one in all colonies (figure 2). HT39 was also the ancestral sequence type from which the other 51 haplotypes derived according to both the maximum parsimony and the maximum likelihood analysis.

Among the 69 adult males sequenced in the colony M1, 24 different haplotypes were found (gene diversity=0.75±0.06). Gene diversity was similar in the second Swiss male colony M2 (0.79±0.05; 31 different haplotypes among 72 sequenced individuals) and not significantly different from that of M1. With an Fst value of 0.007 there was no significant genetic differentiation between the two male colonies (p=0.97) at the mitochondrial level. Both Swiss female colonies F1 (n=48 bats) and F2 (n=10 bats) contained only one haplotype

(HT39); hence gene diversity was zero in both. In contrast, the German female colony F3 had a much higher gene diversity (0.76±0.07; 7 different haplotypes among 24 sequenced individuals), comparable to that of the Swiss male colonies. The low pairwise Fst-values suggested no genetic differentiation between the male colonies in Switzerland and the female colony F3 in Germany (M1-F3: Fst=0.03, p=0.08; M2-F3: Fst=0.02, p=0.07). Also no differentiation was found between the two Swiss female colonies (F1 and F2: pairwise Fst=0.0, p=1). However, pairwise Fst-values suggested a significant differentiation between the two Swiss female colonies F1 & F2 on the one hand and the other three colonies on the other hand (F1/F2 vs. M1, M2 and F3: Fst=0.15, 0.13, 0.16; $p<0.05$).

-Insert figure 2 here-

The three nuclear micro-satellites used in this study showed no heterozygote deficit ($p>0.05$: p20 & p8 for all individuals and paur3 for females only). Despite the low number of micro-satellite loci, gene diversity was 1.0±0.0 for all investigated colonies. Thus, with using only three micro-satellite loci, it was possible to assign a specific allelic combination to every individual at the level of nuclear DNA. As suggested by the high genetic diversity, there was no population differentiation at the level of micro-satellites between any pair of colonies (Fst ranged from zero to max. 0.04; $p>0.05$).

Home range size and habitat use

We used the sample size bootstrap function of "Animal Movement" to verify that sample size obtained from the individuals was high enough to accurately estimate home range size (N_{start}=3, adding 5 new bearings every step, $N_{replicates/step}$=100). Bootstrapping revealed that we had insufficient data from three out of ten radio tracked males in the colony M2 and from one out of eight radio tracked females in the colony F1. We therefore excluded these four individuals from further analysis. No difference in home range size was found

between the members of the two male colonies, but the home range sizes of females were significantly smaller than those of males regardless of the method of analysis (table 3).

-Insert tables 2 and 3 here-

The median distance between roosts and foraging areas was 2.2 km (max. 6.2 km) for the females and 5.2 km (max. 17.8 km) for the males (Generalized Linear Mixed Model: testing for the differences on square root transformed commuting distance between sexes with individual nested in sex as random effect $F_{1,16}$=24.5 p<0.0001). Home range overlap of individuals within colonies ranged from 52% to 79% (90% MCP Males: 70.9±24.5%, females: 53.8±26.4%; 95% KHR males: 60.0±15.0%, females: 54.4±24.4%) and even the 50% KHR core areas overlapped considerably between individuals of the same colony (mean: 29.5±22%). Moreover, no individually exclusive foraging areas were found, but the core areas of males overlapped less than that of the females (50% KHR: males 24.6±18.7%; females: 35.8±24.3%; Wilcoxon two sample test: Z=2.4, df=1 p=0.02).

Female home ranges (95% KHR) were composed mainly of "lake" (54.4%±11.2%), "open landscape" (21.5%±4.2%), "urban area" (16.9%±9.3%), and "forest" (5.6%±4.0%), whereas the home ranges of males contained "open landscapes" (51.0%±2.6%), "forests" (33.0%±7.5%), "urban area" (11.3%±7.7%), and "rivers" (2.3%±0.5%) (figure 3). The sequence or the relative importance in the composition of habitat types was robust regardless of the method used (KHR, MCP, or the projection of actual bearings with a small buffer area on the underlying habitat type). Significant sex-specific differences in the use of the habitats "river", "lake" and "forest" were found (figure 3). The home ranges of females contained more lake and less river and forest than the home ranges of males.

-Insert figure 3 here-

We compared the actual use (preference) of habitats with their availability within the 95% KHR using compositional analyses. Neither males nor females used habitat types according to their availability (females: λ=0.07, χ^2=18.4, d.f.=5 $p<0.05$; males: λ=0.12, χ^2=23.8, d.f.=5 $p<0.001$). Habitat preference for males was ranked: river ≥ open landscape ≥ rest ≥ urban area ≥ forest >> lake. This suggests that the top five habitat types were equally important elements of the home ranges of male parti-colored bats. Only the habitat type "lake", which contributed on average 0.15%±0.02 to the 95% KHR of the males, was significantly underrepresented (t-test: $p<0.02$ for all cross habitat contrasts). Female habitat preference ranked as: urban area ≥ lake >> open landscape ≥ forest ≥ river ≥ rest. Thus, females preferred the two habitats urban area and lake. These two habitats made up 92% of the females' core area (50% KHR), further supporting the importance of them.

Patterns of roost use

The males from the colonies M1 and M2 used seven and nine day-roosts, respectively, and the females used three day-roosts. Most of these roosts were previously unknown and were found by radio-tracking. The three female roosts represent three of the four currently known maternity roosts of the parti-colored bats in Switzerland. Sex-specific patterns of nightly roost use and activity at roost were evident from the roost monitoring. The distribution of transponder readings at roost entrances shows a more aggregated arrival of males at the roost compared to females (figure 4). Females regularly interrupted nigh time foraging and temporarily returned to the roost to nurse their offspring.

-Insert figure 4 here-

Discussion

Effective conservation requires considering all needs of a species in terms of habitat use and population dynamics during all life stages and for both sexes (Foster and Soluk 2006). Our results on habitat use and the genetic population structure of the parti-colored bat in Switzerland suggest that any environmental changes owing to human interference could impact on the species more than expected because of sex-specific niche partitioning.

The observed star shaped minimum spanning networks of the mtDNA sequences suggest that the parti-colored bat population in Switzerland is indeed at the border of the species' range and underwent a rapid expansion since the postglacial re-colonization of the area (e.g. Ruedi and Castella 2003). The high mitochondrial gene diversity found in male colonies but not in female colonies in Switzerland suggests that male parti-colored bats disperse more into this peripheral region and integrate better into existing colonies than females. Re-establishment of a new female colony or population re-growth by immigrating females from other parts of the species distribution area into an existing Swiss colony is rather unlikely, as the demographic isolation of the Swiss female population suggests. This is a surprising finding since the parti-colored bat is known to migrate over long distances (up to 1440 km: Baagøe 2001) and since the males demonstrate that this species can substantially disperse into Switzerland from the main distribution area. The loss of a female colony should therefore influence the population viability in Switzerland more than the loss of a male colony. In addition, the probability for such losses may differ between the sexes. Our radio-tracking data indicate that male colonies use more roosts than female colonies. Therefore the destruction of a single roost, for example through the renovation of a building, would presumably have a greater impact on a female colony than on a male colony.

Despite the demographic isolation of the two female colonies, high gene diversity at the level of the nuclear micro-satellites indicates that the Swiss female parti-colored bat population is not genetically isolated. Males immigrating into Switzerland from other parts of

Europe and mating with local females presumably cause substantial gene flow. This emphasizes the importance of male colonies for the maintenance of the genetic variability of the Swiss female population of parti-colored bats. Sex-specific differences in dispersal and colonization rates are probably typical for European bats and have been used to explain the population structure and emphasize the importance of protecting female colonies in other endangered bat species (e.g. Kerth et al. 2002a; Kerth and Petit 2005; Petit and Mayer 1999, 2000). While our findings have strong implications for the conservation of the parti-colored bat in Switzerland, the number of investigated colonies and micro-satellites used in our study is too low to draw conclusions on the species over its entire range. To verify sex-specific immigration rates into peripheral areas in general, more colonies at the periphery of the species distribution must be compared with colonies in the centre of its distribution.

The sex-specific use of habitat types in parti-colored bats is another conservation relevant result of our study. The fact that females predominately foraged over large water bodies is in line with other studies that report maternity colonies of the parti-colored bat to occur in the vicinity of lakes (Baagøe 2001; Becker et al. 2001; Hermanns et al. 2001; Jaberg and Guisan 2001; Jaberg et al. 1998; Leuthold and Jaberg 2000; Liegl 2004). In fact all maternity roosts of the parti-colored bat in Switzerland and southern Germany known to be occupied after the year 2000 (N=9) are situated less than 6 km (the maximum travel distance of females in our study) from lakes or marshes (Liegl 2004).

The observed differences in habitat use and home range size of males and females probably reflect differences in parental investment of the sexes. Unlike males that provide no parental care, lactating females need to return to the roost during the night to nurse their young. This may limit the size of female foraging areas and restrict the range of foraging females more than males. Such a restriction may result in dependence on more profitable areas (such as lakes) that are in addition located in the proximity of the maternity roosts (Walsh and Harris 1996). Males, however, may be able to use less profitable areas (such as

open landscape) and avoid competition with females. Segregation of males and females into areas of different profitability has also been demonstrated in other bats. In the Daubenton's bat, males use less profitable hunting areas than females, thereby causing broad scale habitat segregation (Senior et al. 2005). A broader ecological niche and higher dispersal ability of male parti-colored bats may also explain the higher number of males at the edge of the species distribution in Western Europe.

Sex-specific habitat use has been found in a variety of animal taxa, with fundamental implications for the conservation of the species (reviewed in: Catry et al. 2005, and Rubin and Bleich 2005). For example, sex-specific habitat use explained sex-specific mortality rates and subsequent shifts in adult sex-ratios in several maritime bird species owing to incidental mortality caused by long-line and trawl fisheries (Gonzalez-Solis et al. 2000; Lewis et al. 2002; Phillips et al. 2005; Phillips et al. 2004). Our finding that the sexes in the parti-colored bats display strong “ecological dimorphism” (Shine et al. 2002) underlines the importance of including sex as a factor when studying the ecology and population genetics of a species. We suggest that such an approach will be particularly important for bats. Currently more than 50% of the over 1000 bat species are threatened worldwide (Hutson et al. 2001). Even though sexual segregation is widespread in bats (Altringham and Senior 2005), its impact on conservation remains unknown for most species. The existing evidence from other studies and our own results underline the importance of considering sexual segregation in conservation.

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Table 1: Sample sizes of animals for the different aspects of this study. The figures in brackets indicate the total number of radio tagged individuals in the colonies including those from which insufficient amount of data was obtained and therefore were excluded from the analyses.

Table 2: Details of radio-tracked animals. The percentage of body mass is the relative weight of the transmitters used in our study (0.96 g) compared with the body weight of the animals. Dependent on the outcome of a bootstrapping test, which compared the increase in home range size and number of fixes, only the data of animals which reached a satiation in home range size were included. Whether an animal was included in the analyses of habitat use and home range size, is given in the last column of the table.

Table 3: Mean±S.D home range sizes (in km^2) of the male (N=11) and female (N=8) parti-colored bats. Wilcoxon rank sum test statistics for differences between the two sexes for all three contrasts: $Z=3.4$, d.f.=1, $p<0.001$.

Figure 1: Regression of body mass vs. forearm length. Post-hoc adjusted Bonferroni p-values for inter-group differences in body mass were for all pair wise contrasts <0.0001. Each animal was measured once.

Figure 2: Minimum spanning tree of the colonies M1, M2, and F3. The numbers depict different haplotypes. The distances between sequences are symbolized by either the length of the lines or in case of the dotted lines, which represent alternative branches, by the number of cross lines. The radius of the circles depicts the absolute frequencies of the haplotypes in the colonies.

Figure 3: Habitat types (log ratio with the habitat type “rest” as the denominator (Aebischer et al. 1993)) that underlie the 95% KHR of the radio tracked individuals separated by sex. The p*-values are Bonferroni adjusted for inter-sex contrasts, error bars depict standard deviation.

Figure 4: The distribution patterns of nightly passes through roost entrances monitored by automatic transponder readers for the female colony F1 and the male colony M2 for the years 2003 and 2004 (Kolmogorov-Smirnov: N_{F1}=3133, N_{M2}=835, Z=8.3, $p<0.0001$).

Table 1:

Colony	Years	No. of females caught (adults)	No. of males caught (adults)	No. of tissue samples analyzed	No. fitted with transponders	No. of radio tagged individuals	No. measured
F1	2003-04	141	2	48	140	7 (8)	140
F2	2000			10	0	0	0
F3	2001,04	25	0	24	0	0	0
M1	2002-04	2	126	69	126	4 (5)	112
M2	2002-04	0	138	72	138	7 (10)	138

Table 2:

Colony	Sex	Body mass [g]	% Body mass	Tagging date	No. of days	No. of fixes	Included in analysis
F1	F	14.5	6.6	16.05.2003	9	145	Yes
F1	F	14.0	6.9	17.06.2003	5	97	Yes
F1	F	14.5	6.6	16.05.2003	10	152	Yes
F1	F	14.0	6.9	17.06.2003	5	78	Yes
F1	F	14.5	6.6	16.05.2003	9	104	Yes
F1	F	13.5	7.1	17.06.2003	5	89	Yes
F1	F	14.5	6.6	16.05.2003	9	131	Yes
F1	F	15.0	6.4	17.06.2003	5	88	No
M1	M	13.5	7.1	31.05.2002	11	141	Yes
M1	M	13.5	7.1	07.06.2002	9	127	Yes
M1	M	13.0	7.4	31.05.2002	14	179	Yes
M1	F	14.0	6.9	07.06.2002	0	0	No
M1	M	14.0	6.9	07.06.2002	10	106	Yes
M2	M	14.0	6.9	27.06.2002	3	29	No
M2	M	14.0	6.9	04.06.2003	5	100	Yes
M2	M	14.0	6.9	27.06.2002	3	37	No
M2	M	13.5	7.1	07.07.2002	9	183	Yes
M2	M	13.0	7.4	04.06.2003	6	111	Yes
M2	M	13.5	7.1	07.07.2002	2	31	No
M2	M	13.0	7.4	04.06.2003	5	113	Yes
M2	M	14.0	6.9	04.06.2003	6	144	Yes
M2	M	14.0	6.9	07.07.2002	7	115	Yes
M2	M	14.0	6.9	07.07.2002	9	159	Yes

Table 3:

	Males	Females
90% MCP	83.6±40.7	15.9±6.1
95% KHR	61.5±16.5	18.6±8.0
50% KHR	10.5±3.9	2.4±1.1

Figure 1:

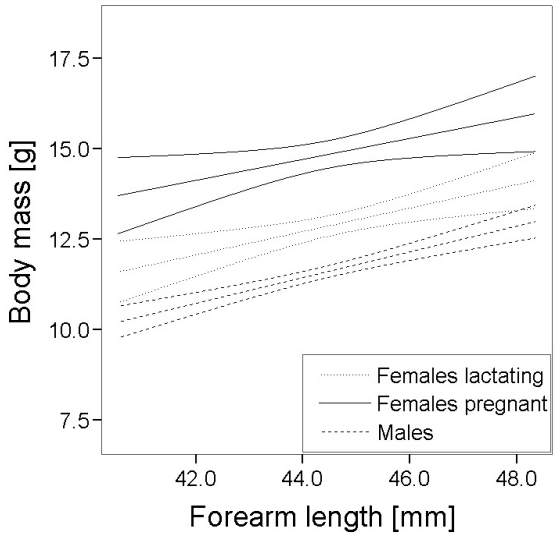
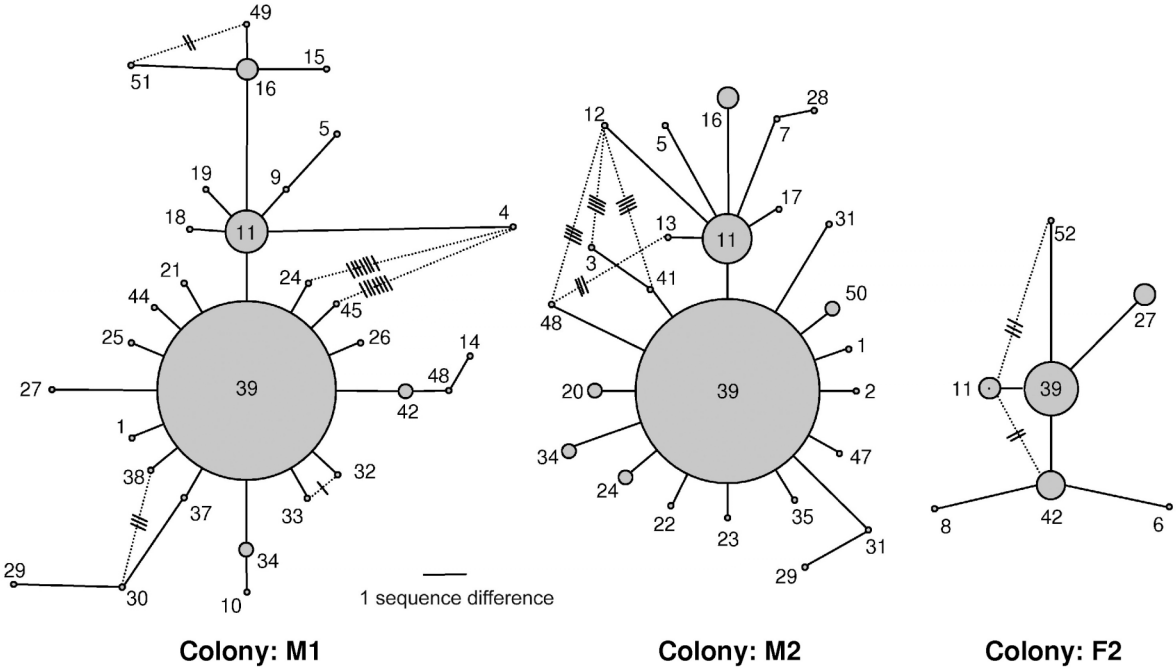

17.5
15.0
12.5
10.0
7.5
Body mass [g]
42.0
44.0
46.0
48.0
Forearm length [mm]
Females lactating
Females pregnant
Males

Figure 2:



Colony: M1 **Colony: M2** **Colony: F2**

Figure 3:

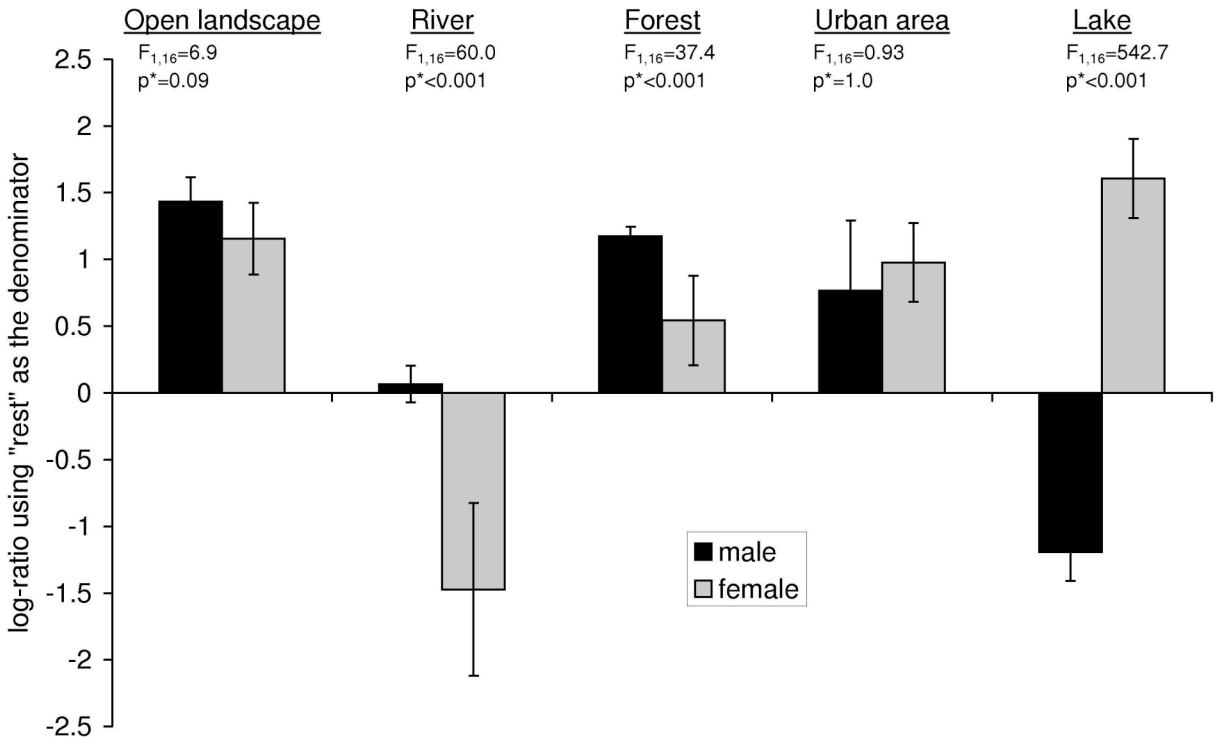
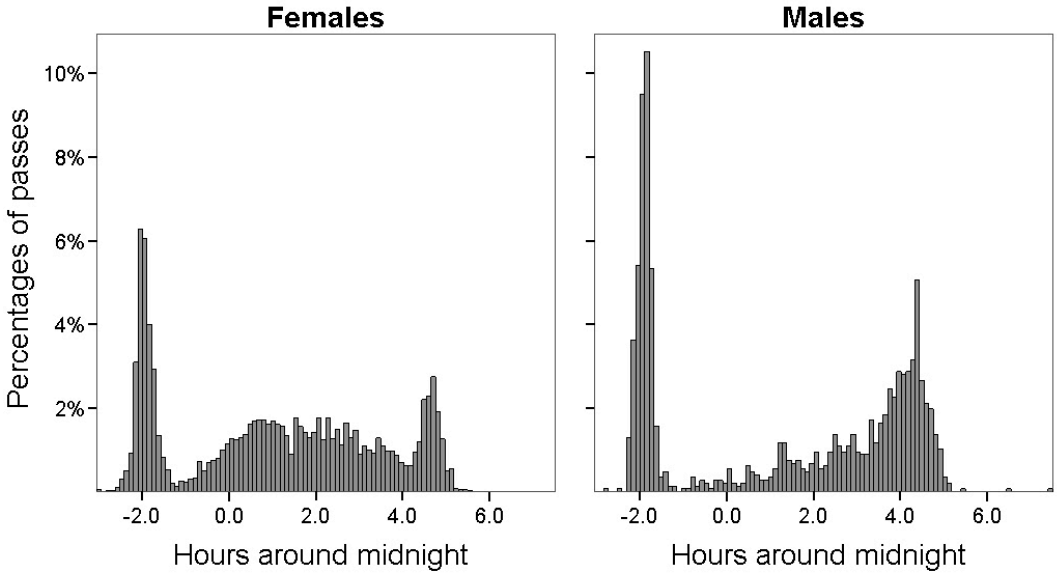

Open landscape
River
Forest
Urban area
Lake
$F_{1,16}$=6.9
p*=0.09
$F_{1,16}$=60.0
p*<0.001
$F_{1,16}$=37.4
p*<0.001
$F_{1,16}$=0.93
p*=1.0
$F_{1,16}$=542.7
p*<0.001
log-ratio using "rest" as the denominator
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
male
female

Figure 4:


Females
Males
Percentages of passes
10%
8%
6%
4%
2%
-2.0
0.0
2.0
4.0
6.0
Hours around midnight
Hours around midnight