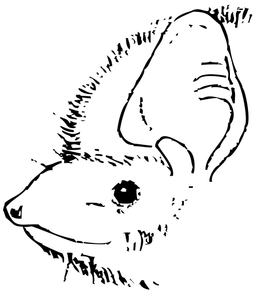
Population ecology of the pipistrelle bat (*Pipistrellus pipistrellus* Schreber, 1774): the significance of the year-round use of hibernacula for life histories



Dissertation
zur
Erlangung des Doktorgrades
der Naturwissenschaften
(Dr. rer. nat.)

dem
Fachbereich Biologie
der Philipps-Universität Marburg
vorgelegt von

Thomas Sendor
aus Starnberg

29. Mai 2002

Diese Dissertation besteht aus einer Sammlung von Manuskripten (Kapitel 2–6), von denen sich zum Zeitpunkt der Einreichung an den Promotionsausschuß des Fachbereichs Biologie der Philipps-Universität drei in verschiedenen Stadien des Veröffentlichungsprozesses befinden:

- Sendor, T., I. Roedenbeck, S. Hampl, M. Ferreri, and M. Simon (in press): Revision of morphological identification of pipistrelle bat phonic types (*Pipistrellus pipistrellus* Schreber, 1774). *Myotis* **40**.
- Sendor, T. and M. Simon (submitted): Does frost matter? Effects of sex, age, and winter severity on seasonal pipistrelle bat (*Pipistrellus pipistrellus*) survival. *Journal of Animal Ecology.*
- Sendor, T. and M. Simon (submitted): Mating behaviour or information transfer? The function of summer swarming in the pipistrelle bat (*Pipistrellus pipistrellus*). *Behavioral Ecology and Sociobiology.*

Die verbleibenden Manuskripte sind “in Vorbereitung”.

Ungeachtet der Koautorenschaft Dritter stellen sämtliche Arbeiten selbständige Leistungen meiner Person im Sinne der Promotionsordnung dar.

Vom Fachbereich Biologie
der Philipps-Universität Marburg als Dissertation am 10.07.2002
angenommen.

Erstgutachter: Prof. Dr. Roland Brandl
Zweitgutachter: Prof. Dr. Diethart Matthies
Tag der mündlichen Prüfung am 15.07.2002

Ökologie ist die Erforschung des Offensichtlichen
Ecology is the exploration of the obvious
Hermann Remmert

Contents

1. Synopsis

Low temperatures and food shortage during winter represent a major challenge for virtually all animals of the temperate latitudes. Insectivorous bats, as long-lived endothermic organisms, respond to this problem by hibernation (Davis, 1970), sometimes combined with migration (e.g. Petit and Mayer, 2000; Strelkov, 1969). Hibernation usually takes place at specific hibernacula, which are separate from the summer roosts. These sites, however, are not only used in the hibernal period: Bats may also be observed there, particularly at underground hibernacula, in considerable numbers during the summer months (Fenton, 1969; Degn *et al.*, 1995). Thus, hibernacula represent a central element in the life cycle of temperate bats. Although the almost year-round use of hibernacula has long been recognised (Fenton, 1969, and references therein), questions about the functional significance of these phenomena for the life-histories of bats have largely been ignored (but see Kretzschmar and Heinz, 1995; Thomas *et al.*, 1979). This is also reflected by the common image of a standard bat life cycle (Fig. 1.1). The present thesis deals with the all-the-year processes that are observable at a large hibernaculum of the pipistrelle bat, 45-kHz phonic type (*Pipistrellus pipistrellus*

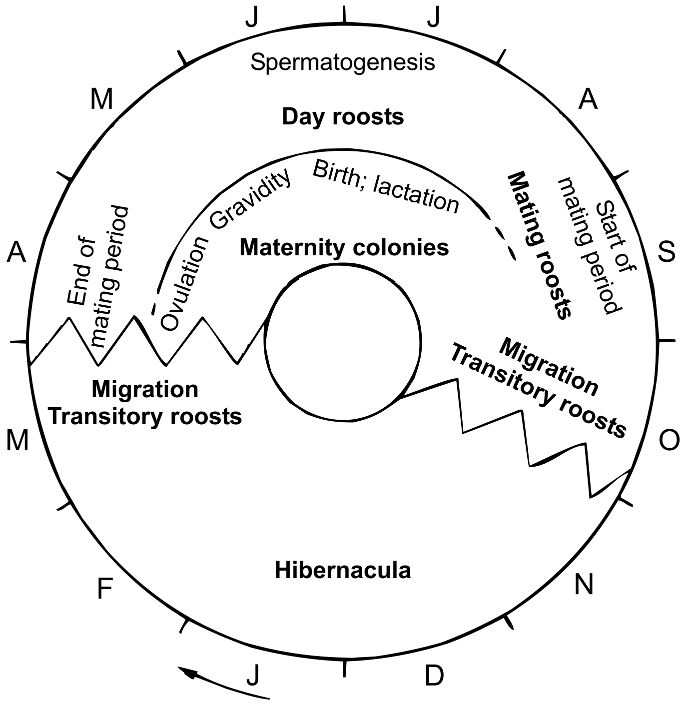


Fig. 1.1: Schematic diagram of the annual life cycle of temperate bats (after Schober and Grimmberger, 1998, modified).

Schreber, 1774), and their impact on the involved life-history components, essentially survival. The hibernaculum is free of frost, but with a median temperature of approx. 7°C and relative humidities between 60% and 93% cooler and drier than underground hibernacula used by, e.g., many *Myotis* species.

Annual and seasonal survival, estimated in a capture-recapture study, showed surprisingly little variation. In particular, winter survival was unexpectedly high, varied little across years, and was not related to winter severity. Summer and autumn survival, however could not be reliably estimated due to some minor difficulties with the data. In conclusion, winter does not seem to represent a survival bottleneck, as otherwise frequently suspected. Winter survival is independent of weather, at least in the observed range of winter conditions which were quite different. The rough estimate of annual adult survival of almost 0.8 – for both sexes – considerably exceeds values reported previously. Thus, the classification as an r-selected species seems questionable. Increased survival costs for the males due to the mating system, as suggested by a previous study, cannot be concluded from the present study.

The presence of the pipistrelle bats at the hibernaculum between late April and September is termed summer swarming – purely nocturnal flight activity without usage of the hibernaculum as a day roost. The nightly amount of swarming activity (approx. proportional to the number of individuals) is low in spring and early summer, shows a high peak in August, and is positively related to temperature and negatively to wind speed.

The swarming population in early summer consists almost exclusively of adult males, who are gradually replaced by reproductively active females after mid-July, whose presence overlaps with that of the juveniles until only juveniles form the swarming population after mid-August. This pattern is a central argument in support of the hypothesis that summer swarming has the function of an initially maternally guided exploration of hibernacula by the juveniles. Further support for the "maternal guidance hypothesis" comes from the near-equality of juvenile and adult female population sizes (adult male population size was estimated at only a third of those) and the larger amount of individual time invested in swarming by reproductive females and juveniles, in comparison to adult males and nonreproductive females. The latter finding, as well as the non-occurrence of reproductively active males and of advertisement calls is considered as evidence against the hypothesis that swarming constitutes mating behaviour – or even a mating system, as stated by (Lundberg, 1989). However, mating and summer swarming may be linked in some other bat species (Thomas *et al.*, 1979). According to current knowledge, these are species with a longer hibernation period than the pipistrelle bat; early onset of hibernation is presumed to force bats to combine swarming with mating due to a restricted time budget, while reproductive success is maximised by establishing separate mating roosts with a late start of hibernation. This is the case in the pipistrelle bat. Males are suspected to increase their fitness by swarming because this facilitates the detection and establishment of new hibernacula. Nevertheless, regular participation in swarming seems to be of less importance for the adult males, as indicated by their smaller apparent population size. It is worth noting that this could be an artifact: the pattern of a greatly reduced recapture probability in later summers found in the survival study is unique to the adult males (Fig. 3.1). Thus, they seem to have less interest to visit the well-established hibernaculum once they have explored it.

The hibernal period of the pipistrelle bat, as observable at Marburg Castle, lasts from mid-November to mid-March. Extensive hibernal roost switching occurs, which appears energetically disadvantageous at a first glance. In hibernation, pipistrelle bats lose considerably less body mass than (a) predicted from evaporative water loss alone with the given microclimate, and (b) expected from estimates of the hibernal metabolic rate reported in the literature. The hibernal energy budget is less influenced by roost switching frequency than by different levels of metabolism in hibernation: If hibernal metabolism is as low as reported for other bat species, 10 or more transfer flights between hibernacula could take place without any critical effect on the energy reserves. The observed mass loss rates suggest that metabolism in hibernation should indeed lie considerably below those reported in laboratory studies.

In conclusion, frost-free hibernacula like Marburg Castle are presumably *the* central habitat in the life-histories of pipistrelle bats. Microclimatically stable, they ensure high and constant survival probabilities, by and large independent of winter harshness. This is indicated by survival estimates from capture-recapture data as well as by assessments of energy budgets. As paradoxical it may appear – hibernal roost switching between various, presumably climatically different hibernacula, is an integral part of an energy saving strategy which attempts to use roost sites that are best suited for a variety of weather situations, respectively. The near-constancy of survival across years, the absence of a seasonal bottleneck, and the surprisingly high estimate of annual survival suggest that pipistrelle bat life histories, despite the small body size, are shaped to cope with varying environmental conditions in a very flexible way, so that high survival is ensured. The enormous significance of hibernacula like Marburg Castle is emphasised by the findings on the function of summer swarming. The supposed purpose of this behaviour is to maximise reproductive success through transfer of information on hibernacula from reproductive females to their offspring. Less obviously, but consistent with sociobiological concepts, male summer swarming can be interpreted in a similar way: As males are not constrained by breeding, they have sufficient time to detect new hibernacula. From the respective information (first transferred to the females), their (unknown) offspring could eventually benefit.

A methodological note Inspired by recent advances in capture-recapture methodology, particularly the problem how to determine the most parsimonious model (Anderson and Burnham, 1994; Burnham *et al.*, 1994, 1995a,b; Burnham and Anderson, 1992; Lebreton *et al.*, 1992), I focused part of my attention to the statistical problems of hypothesis testing, estimation and model selection. Several ecologists and statisticians have complained of the prevalence of null hypothesis testing in the ecological sciences and stressed its drawbacks (e.g. Anderson *et al.*, 2000; Cherry, 1998; Johnson, 1999; Nester, 1996; Yoccoz, 1991). These drawbacks are particularly severe in model selection processes (e.g. variable selection via stepwise regression: Anderson *et al.*, 2000; Hurvich and Tsai, 1990). As an alternative with superior performance in model selection, information-theoretic methods, in particular Akaike's information criterion (AIC) has been recommended (Anderson *et al.*, 2000; Burnham and Anderson, 2001; Buckland *et al.*, 1997; Burnham and Anderson, 1998). The use of AIC and its derivatives has reached a very sophisticated level in the analysis of capture-recapture data (Anderson *et al.*, 2000; Burnham and Anderson, 2001; Buckland *et al.*, 1997; Burnham and Anderson, 1998), but it is applicable in a much more general context (Burnham and Anderson, 1998). There are also slightly deviating opinions on the benefits of information-theoretic methods (Guthery *et al.*, 2001). Clearly, the danger of misuse is also given with this technique, but the inherent emphasis on *a priori* formulation of multiple working hypotheses (Anderson *et al.*, 2000) alleviates this problem.

The arguments against the prevalence of hypothesis testing and in favour of estimation and information-theoretic methods are very convincing so that I have adopted this philosophy and used AIC whenever appropriate. Clearly, conventional hypothesis testing will not be completely abandoned because it also has its merits and cannot be completely replaced (Burnham and Anderson, 1998). Consequently, also a small number of test results will appear in the present thesis.

References

Anderson, D. R. and K. P. Burnham (1994): AIC model selection in overdispersed capture-recapture data. *Ecology* **75**: 1780–1793.

Anderson, D. R., K. P. Burnham, and W. L. Thompson (2000): Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* **64**: 912–923.

Buckland, S. T., K. P. Burnham, and N. H. Augustin (1997): Model selection: an integral part of inference. *Biometrics* **53**: 603–618.

Burnham, K. P. and D. R. Anderson (1992): Data-based selection of an appropriate biological model: the key to modern data analysis. In D. R. McCullough and R. H. Barrett (Eds.), *Wildlife 2001: Populations*, pp. 16–30, Elsevier Applied Science, London, New York: Elsevier Science Publishers.

Burnham, K. P. and D. R. Anderson (1998): *Model Selection and Inference: A Practical Information-Theoretic Approach.* New York, Berlin, Heidelberg: Springer Verlag.

Burnham, K. P. and D. R. Anderson (2001): Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* **28**: 111–119.

Burnham, K. P., D. R. Anderson, and G. C. White (1994): Evaluation of the Kullback-Leibler discrepancy for model selection in open population capture-recapture models. *Biometrical Journal* **36**: 299–315.

Burnham, K. P., D. R. Anderson, and G. C. White (1995a): Selection among open population capture-recapture models when capture probabilities are heterogeneous. *Journal of Applied Statistics* **22**: 611–624.

Burnham, K. P., G. C. White, and D. R. Anderson (1995b): Model selection strategy in the analysis of capture-recapture data. *Biometrics* **51**: 888–898.

Cherry, S. (1998): Statistical tests in publications of The Wildlife Society. *Wildlife Society Bulletin* **26**: 947–953.

Davis, W. H. (1970): Hibernation: Ecology and physiological ecology. In W. A. Wimsatt (Ed.), *Biology of Bats*, vol. I, pp. 266–300, New York, London: Academic Press.

Degn, H. J., B. B. Andersen, and H. Baggoe (1995): Automatic registration of bat activity through the year at Mønsted Limestone Mine, Denmark. *Zeitschrift für Säugetierkunde* **60**: 129–135.

Fenton, M. B. (1969): Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology* **47**: 597–602.

Guthery, F. S., J. J. Lusk, and M. J. Peterson (2001): The fall of the null hypothesis: liabilities and opportunities. *Journal of Wildlife Management* **65**: 379–384.

Hurvich, C. M. and C.-L. Tsai (1990): The impact of model selection on inference in linear regression. *The American Statistician* **44**: 214–217.

Johnson, D. H. (1999): The insignificance of statistical significance testing. *Journal of Wildlife Management* **63**: 763–772.

Kretzschmar, F. and B. Heinz (1995): Social behaviour and hibernation of a large population of *Pipistrellus pipistrellus* (Schreber, 1774) (Chiroptera: Vespertilionidae) and some other bat species in the mining-system of a limestone quarry near Heidelberg (South West Germany). *Myotis* **32-33**: 221–231.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson (1992): Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**: 67–118.

Lundberg, K. (1989): Social organization and survival of the pipistrelle bat (*Pipistrellus pipistrellus*), and a comparison of advertisement behaviour in three polygynous bat species. Dissertation, University of Lund.

Nester, M. R. (1996): An applied statistician's creed. *Journal of the Royal Statistical Society C (Applied Statistics)* **45**: 401–410.

Petit, E. and F. Mayer (2000): A population genetic analysis of migration: the case of the noctule bat (*Nyctalus noctula*). *Molecular Ecology* **9**: 683–690.

Schober, W. and E. Grimmberger (1998): *Die Fledermäuse Europas.* 2nd edn., Kosmos Naturführer, Stuttgart: Franckh-Kosmos Verlags-GmbH & Co.

Strelkov, P. P. (1969): Migratory and stationary bats (Chiroptera) of the European part of the Soviet Union. *Acta Zoologica Cracoviensia* **14**: 393–440.

Thomas, D. W., M. B. Fenton, and R. M. R. Barclay (1979): Social behavior of the little brown bat, *Myotis lucifugus*. I. Mating behavior. *Behavioral Ecology and Sociobiology* **6**: 129–136.

Yoccoz, N. G. (1991): Use, overuse, and misuse of significance tests in evolutionary biology and ecology. *Bulletin of the Ecological Society of America* **72**: 106–111.

2. Revision of morphological identification of pipistrelle bat phonic types (*Pipistrellus pipistrellus* Schreber, 1774)

Manuscript accepted: Myotis **40** (2002, in press)

by Thomas Sendor, Inga Roedenbeck, Svenja Hampl, Miro Ferreri,
and Matthias Simon

Abstract

The recently proposed length difference of the 2nd and 3rd phalanx of the 3rd finger (ΔFTL) as a diagnostic trait for discriminating pipistrelle bat phonic types is questioned. Its validity was controlled by measuring pipistrelles sampled at the large hibernaculum “Marburg Castle”. The identity of pipistrelle bats with the 45-kHz phonic type was confirmed by sound analysis. Variation in ΔFTL among these pipistrelles was high and this characteristic turned out to be unsuitable for species discrimination: in 22.8% of the males and 17.3% of the females the terminal phalanges were of equal length, and these individuals would thus have been falsely identified as 55-kHz pipistrelles. Penis morphology, however, appears to remain a reliable diagnostic trait in the males. An internarial ridge (or hump) appears to be present in both sexes of the 55k-kHz pipistrelles only. We thus suggest to abandon ΔFTL for the identification of pipistrelle bat phonotypes. Instead, bat workers should focus on absence (45-kHz pipistrelle) or presence (55-kHz pipistrelle) of a small hump between the nostrils, a trait already mentioned but less emphasised by Häussler *et al.* (1999). However, more research on the reliability of this trait is necessary. Thus, identification of pipistrelle bat phonic types should provisionally be founded on a combination of characters, including determination of echolocation call frequency – if possible by sound analysis.

Key words: Chiroptera, cryptic species, echolocation calls, sound analysis, species identification, wing morphology.

2.1 Introduction

In the past decade convincing evidence has been found that the common pipistrelle bat (*Pipistrellus pipistrellus*) actually comprises two cryptic species (Barlow, 1997; Barlow and Jones, 1997a, 1999; Barratt *et al.*, 1997; Jones and van Parijs, 1993; Park *et al.*, 1996). As they differ in the spectral characteristics of their echolocation calls (Jones and van Parijs, 1993), they are tentatively referred to as the 45-kHz and 55-kHz phonic type. Although it is now generally accepted that these two forms correspond to separate species, we will term them as “phonic types” for the remainder of this paper, because the scientific nomenclature still needs to be clarified (Jones and Barratt, 1999). For a detailed historical review on the identification and separation of pipistrelle phonic types, including a discussion on taxonomy and scientific nomenclature, also see Häussler *et al.* (1999).

Both species reveal strong similarities in their external characters. Consequently, first attempts to find diagnostic morphological traits for field discrimination of the two sibling species have been unsuccessful (Barlow and

Jones, 1999; Barlow *et al.*, 1997; Jones and van Parijs, 1993). However recently, Häussler *et al.* (1999) have, among other less quantitative traits, proposed the length difference of the 2nd and 3rd phalanx of the 3rd finger (hereafter termed "difference of finger tip length", ΔFTL) as a valuable characteristic discriminating the two cryptic species: In the 45-kHz phonotype, the 3rd (distal) phalanx should be approx. 2 mm shorter than the 2nd, while they should be of equal length in the 55-kHz pipistrelle. This measure, after Häussler *et al.* (1999), appears as the most relevant external character for discriminating pipistrelle bat phonic types, because being objective, consistent and easily applicable.

While such a practicable trait is highly desirable, we had reasons to doubt that ΔFTL is sufficiently reliable: During a study primarily focusing on population ecology and use of hibernacula we caught large numbers of pipistrelle bats at a mass hibernaculum. From the pipistrelles that were captured we received the subjective impression that the length difference of the terminal phalanges varied considerably and a fraction of the investigated pipistrelle bats appeared to have a ΔFTL at or very close to zero. Following the suggested trait, these individuals would have been determined as 55-kHz pipistrelles. This contradicted our personal experience, as we never encountered pipistrelles echolocating at 55 kHz during detector studies in Marburg and surroundings. Thus, the question arose if the pipistrelle bat population using Marburg Castle is actually formed of a so far undetected mixture of both phonic types, or if ΔFTL is a less reliable trait for species identification than claimed by Häussler *et al.* (1999). Therefore, the aim of this study was (1) to clarify if the equality or disparity of the length of the 2nd and 3rd phalanx actually coincides with the pipistrelle bat phonic types and to evaluate the suitability of alternative characteristics. (2) A side effect with respect to further studies at Marburg Castle would be to obtain reliable information on the species composition of the pipistrelles using this specific hibernaculum.

2.2 Materials and methods

We caught pipistrelle bats using mist nets at a large hibernaculum, Marburg Castle (Hesse, Germany), during a mark-recapture study. Samples of 49 male and 66 female pipistrelles that had been individually marked with alloy bands previously, were taken in late spring and early summer 2000, during the period of summer swarming. The bats were investigated on the traits discriminating phonic types given by Häussler *et al.* (1999), with particular focus on wing morphology. The pipistrelles were also checked on the presence or absence of a small internarial ridge (hump). Identity of phonic type was examined by analysis of vocalisations (see below). All individuals tested were adults. Capture, handling and marking of the bats was done under license of the Regierungspräsidium Gießen (Upper Nature Conservation Authority).

The length of the two terminal phalanges of the 3rd finger was measured to the nearest 0.5 mm by tracing them on graph paper. Additionally, all pipistrelles caught at Marburg Castle between 10 May and 07 August 2000 were routinely checked on equality/disparity of the length of the 2nd and 3rd phalanx of the 3rd finger by rough visual assessment. Males were further investigated on characters of penis morphology and colouring as described by Häussler *et al.* (1999): colour, hair covering, shape of glans penis and presence or absence of a contrasting median stripe on the upper side of the penis.

Of the pipistrelle bats whose lengths of the terminal phalanges were measured exactly, the phonic type (i.e. species) was identified by determining the frequency of maximum energy (FMAXE) of search phase echolocation calls (Jones and van Parijs, 1993). To avoid duplicate sampling (pseudoreplication), the identity of individuals was ensured by ring numbers. The pipistrelles were released from hand in open habitat in close vicinity to the capture location. Bat calls were recorded using a ten-fold time-expansion ultrasound detector (Laar® Bridge Box) at a sampling rate of 200 kHz. The expanded calls were stored on a portable digital tape recorder (Sony® TCD-D8).

Echolocation calls were transferred to an IBM-compatible computer, stored as wav-files, and analyzed using the Avisoft Sonagraph Pro software (Raimund Specht, Hauptstr. 52, D-13158 Berlin, Germany). Only search phase echolocation calls comprising a quasi constant-frequency (cf) terminal tail were included into the analysis (Jones and van Parijs, 1993). The recordings were processed by a Fast Fourier Transformation (FFT) algorithm, using a sampling frequency of $f = 22.05$ kHz, and a FFT-length of 512. For producing sonagrams we used a frame length of 50% and an overlap of 93.75%. With the help of the sonagrams we judged if calls met the requirements for inclusion in the analysis (quasi-cf tail). FMAXE was determined from logarithmic power spectra using a Hamming window. Mean FMAXE was calculated from three to five appropriate calls of each individual.

2.3 Results

FMAXE of the echolocation calls of 114 pipistrelle bats fell within the interval between 42.0 and 49.5 kHz (Fig. 2.1). A single male individual echolocated at 51.4 kHz (Fig. 2.1). This exceptionally high frequency might be an artifact

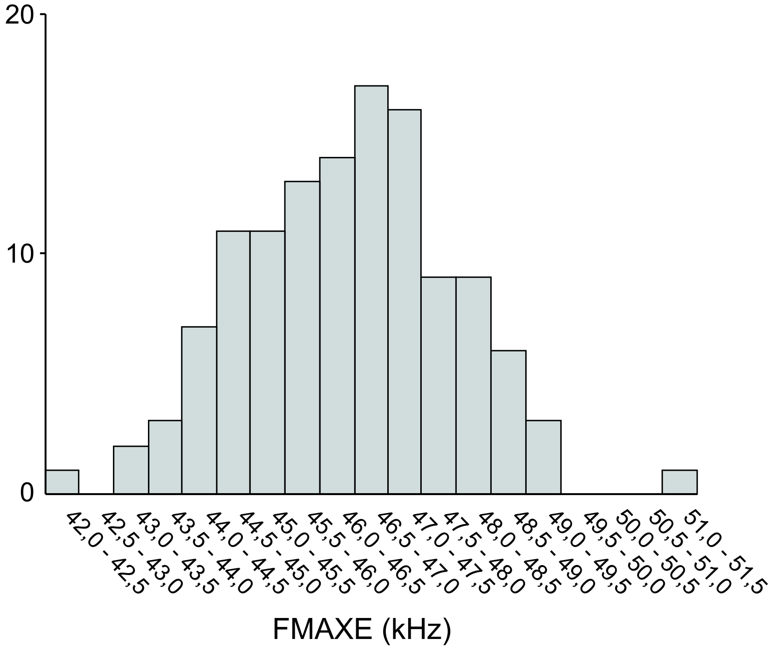


Fig. 2.1: Histogram of the distribution of frequencies of maximum energy (FMAXE) of pipistrelle bats at the hibernaculum Marburg Castle ($n = 115$).

due to unrecognised irregularities during the recording. A FMAXE of 51.4 kHz represents an unclear case that cannot be assigned to either phonic type. Accordingly, apart from the exceptional individual, all pipistrelles could unequivocally be assigned to the 45-kHz phonic type by means of their vocal characteristics.

Among these 115 pipistrelles, the length difference (ΔFTL) between the 2^{nd} (l_2) and the 3^{rd} (l_3) phalanx was zero or negative, i.e. the 3^{rd} was of equal length or even longer than the 2^{nd} (Fig. 2.2), in 35 (30.4%) individuals, irrespective of sex. In the male echolocating at 51.4 kHz, the 3^{rd} phalanx was slightly shorter than the 2^{nd} ($\Delta\text{FTL} = 0.5\,\text{mm}$). None of these individuals had an internarial hump.

A similar image emerged when ΔFTL was assessed by a rough visual check among all individuals captured between 10 May and 07 August 2000 ($n = 2,056$): In 229 male pipistrelles (22.8%), the phalanges were of equal length, while a marked difference was noted in 774 individuals (77.2 %). Among the females this ratio was 182 (17.3%) vs. 871 individuals (82.7%), respectively.

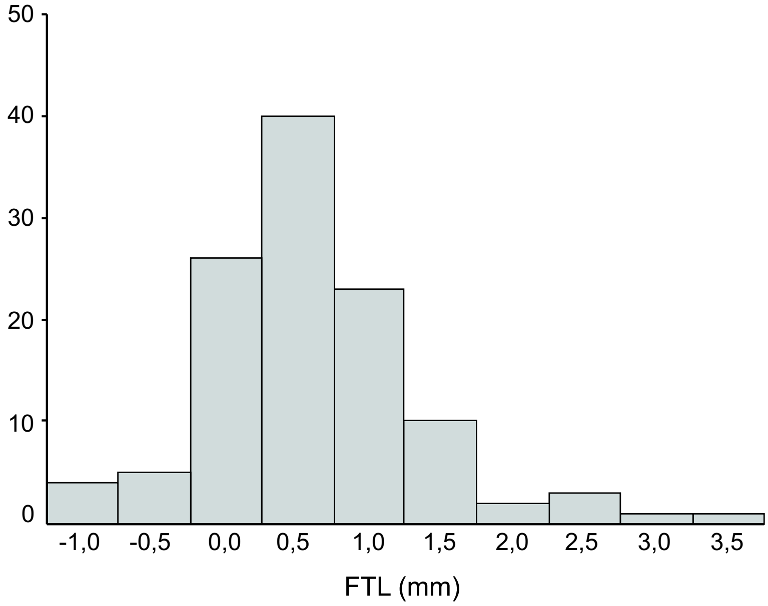


Fig. 2.2: Histogram of the distribution of length differences between the 2nd and 3rd phalanx of the 3rd finger ($\Delta\mathrm{FTL} = l_2 - l_3$) of pipistrelle bats caught at the hibernaculum Marburg Castle ($n = 115$).

In the males, penis morphology and colour were rather uniform: a large majority exhibited dark grey colouring of the skin and in all examined individuals there was a pale median stripe and a white, bristly hair covering all over the penis. While the median stripe and hair covering were present in all males, a lighter colour was observed in a small number of individuals. Also one of the sound-recorded males had a light-coloured penis (but with median stripe). It echolocated at FMAXE of 46.3 kHz and its 2nd and 3rd phalanx were of equal length.

2.4 Discussion

The questions that initiated this study can be answered as follows:

1. All sampled individuals (except one unclear case) belong to the 45-kHz phonic type. Therefore, we conclude that Marburg Castle is a hibernaculum exclusively used by the 45-kHz phonic type of *P. pipistrellus.*

2. The length difference of the 2nd and 3rd phalanx of the 3rd finger (ΔFTL) is inappropriate for the discrimination of the pipistrelle bat phonic types.

The latter issue is of general importance, especially for bat workers who rely on easily observable traits for species identification. The results of the current study demonstrate that variation in ΔFTL is too large to maintain this characteristic as a diagnostic trait for morphological discrimination of 45-kHz and 55-kHz pipistrelles: If it was applied as the main diagnostic trait, a considerable number of 45-kHz pipistrelles would falsely be determined as belonging to the 55-kHz phonic type.

As we could not examine 55-kHz pipistrelles, it is difficult to argue about the reasons for the conflicting results between our study and that of Häussler *et al.* (1999). However, already a note by Häussler *et al.* (1999) indicated problems with the validity of ΔFTL as a diagnostic trait. The authors attributed exceptions from unequal lengths of phalanges in 45-kHz pipistrelles to the identity of the respective individuals with a particular morphotype. On the other hand, most of the 45-kHz pipistrelles investigated by Häussler *et al.* (1999) were alcohol-preserved museum specimens. The 3^{rd} phalanx remains cartilaginous for a lifetime in most microchiropterans (Adams, 1998). Therefore, length differences between phalanges in alcohol-preserved bats could have resulted from differential tissue shrinkage and thus the corresponding findings of Häussler *et al.* (1999) could be artifacts. Another potential complication might arise from allometric growth of the phalanges (e.g. Swartz, 1997).

Unfortunately, the ineligibility of ΔFTL means the failure of the currently most propagated discriminative morphological trait that was potentially applicable irrespective of an individual's sex. Species identity of male pipistrelle bats can be determined by penis morphology. Our results agree with the findings of Häussler *et al.* (1999), at least with respect to the penis morphology of 45-kHz pipistrelles: all males caught during our study exhibited the characteristic median stripe. We therefore consider the differences stated by Häussler *et al.* (1999) very plausible, but suggest to focus on morphology (median stripe) rather than on colouring, because the penis may exceptionally appear light-coloured also in 45-kHz pipistrelles. Further details on the genital morphology as a discriminative trait, with particular focus on the baculum, are provided by recent work of Ziegler *et al.* (2001).

Häussler *et al.* (1999) rather parenthetically mention the presence (55 kHz) and absence (45 kHz) of a small hump between the nostrils as a discriminative trait. With respect to the 45-kHz type, this is consistent with our results. Furthermore, the first author of the present study also had the opportunity to examine a small number of 55-kHz pipistrelles (n = 3 males, 2 females; identity confirmed by vocalisations) when controlling bat boxes. All individuals showed a small hump between the nostrils. They were furthermore characterised by a yellow colouring of the skin in the genital area, as described by Häussler *et al.* (1999). ΔFTL, however, was variable among these five individuals: in one male and one female the 3^{rd} phalanx was shorter than the 2^{nd}, respectively. The sample size of the 55-kHz pipistrelles was clearly too small to make valid inferences. Nonetheless, the results obtained so far indicate the possible importance of an internarial hump as a discriminating trait, which Häussler *et al.* (1999) have recognised, but apparently underrated in favour of ΔFTL. Further research on this trait is required, as the sample sizes are still insufficient to judge on its reliability.

Based on the results of the present study, we strongly suggest to abandon the usage of ΔFTL for species discrimination. Instead, it seems more appropriate to focus on the presence or absence of an internarial hump as a discriminative character. Until more research on this topic is done, morphological determination of pipistrelle bat species should be complemented by acoustical identification, if possible by sound analysis, and a combination of further external characters.

2.5 Acknowledgements

We are grateful to the many people who assisted us in catching bats, too numerous to be named. We further thank Andreas Kiefer for the opportunity to examine 55-kHz pipistrelles. Discussions with Sandra Hüttenbügel and Roland Brandl as well as the comments of an anonymous referee helped to improve the manuscript.

References

Adams, R. A. (1998): Evolutionary implications of developmental and functional integration in bat wings. *Journal of Zoology (London)* **246**: 165–174.

Barlow, K. E. (1997): The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. *Journal of Zoology (London)* **243**: 597–609.

Barlow, K. E. and G. Jones (1997): Differences in songflight calls and social calls between two phonic types of the vespertilionid bat *Pipistrellus pipistrellus. Journal of Zoology (London)* **241**: 315–324.

Barlow, K. E. and G. Jones (1999): Roosts, echolocation calls and wing morphology of two phonic types of *Pipistrellus pipistrellus. Zeitschrift für Säugetierkunde* **64**: 257–268.

Barlow, K. E., G. Jones, and E. M. Barratt (1997): Can skull morphology be used to predict ecological relationships between bat species? A test using two cryptic species of pipistrelle. *Proceedings of the Royal Society of London, Series B – Biological Sciences* **264**: 1695–1700.

Barratt, E. M., R. Deaville, T. M. Burland, M. W. Bruford, G. Jones, P. A. Racey, and R. K. Wayne (1997): DNA answers the call of pipistrelle bat species. *Nature* **387**: 138–139.

Häussler, U., A. Nagel, M. Braun, and A. Arnold (1999): External characters discriminating species of European pipistrelles, *Pipistrellus pipistrellus* (Schreber, 1774) and *P. pygmaeus* (Leach, 1825). *Myotis* **37**: 27–40.

Jones, G. and E. M. Barratt (1999): *Vespertilio pipistrellus* Schreber, 1774 and *V. pygmaeus* Leach, 1825 (currently *Pipistrellus pipistrellus* and *P. pygmaeus*; Mammalia, Chiroptera): proposed designation of neotypes. *Bulletin of Zoological Nomenclature* **56**: 182–186.

Jones, G. and S. M. van Parijs (1993): Bimodal echolocation in pipistrelle bats: are cryptic species present? *Proceedings of the Royal Society of London, Series B – Biological Sciences* **251**: 119–125.

Park, K. J., J. D. Altringham, and G. Jones (1996): Assortative roosting in the two phonic types of *Pipistrellus pipistrellus* during the mating season. *Proceedings of the Royal Society of London, Series B – Biological Sciences* **263**: 1495–1499.

Swartz, S. M. (1997): Allometric patterning in the limb skeleton of bats: implications for the mechanics and energetics of powered flight. *Journal of Morphology* **234**: 277–294.

Ziegler, T., A. Feiler, and U. Zöphel (2001): New data on the genital morphology of the midge bat *Pipistrellus pygmaeus* (Leach, 1825) from Germany (Mammalia: Chiroptera: Vespertilionidae). *Zoologische Abhandlungen, Staatliches Museum für Tierkunde Dresden* **51**: 435–444.

3. Does frost matter? Effects of sex, age, and winter severity on seasonal pipistrelle bat (*Pipistrellus pipistrellus*) survival

Manuscript submitted to *Journal of Animal Ecology*

by Thomas Sendor and Matthias Simon

Abstract

Life history theory assumes increased mortality at certain stages like hibernation. However, seasonal variation of survival rates of hibernating mammals has rarely been estimated. In this study, apparent survival of pipistrelle bats (*Pipistrellus pipistrellus*) hibernating and performing summer swarming at a large hibernaculum, Marburg Castle (Hesse, Germany), was modelled using seasonal (summer/winter) capture-recapture data from the years 1996 to 2000. The spring survival interval includes the period of arousal at the end of hibernation and therefore validly measures survival associated with hibernation. Analysis was complicated by transience and trap-dependence. Recapture rates varied following a seasonal pattern and according to group. Survival probabilities in autumn were negatively biased due to unaccounted transience effects. Survival could be modelled using two age-classes, with reduced first-year juvenile survival. The age effect carried over first autumn and spring. There was virtually no evidence for sex-specific survival rates; male and female survival were found to be almost equal. In the best-fitting models, survival rates varied over time and differed among sexes and age-classes by a constant amount. Among years, there was only little variation in spring survival, that could not be explained by winter severity. Adult spring survival was surprisingly high, averaging at 0.892 ($\widehat{\mathrm{SE}} = 0.028$). No evidence for increased mortality during hibernation could be found. This contradicted the expectation of reduced over-winter survival due to depleted fat reserves at the end of hibernation. Thus, hibernation does apparently not entail a survival cost for the pipistrelle bat. Rough estimates of annual adult survival averaged at 0.799 ($\widehat{\mathrm{SE}} = 0.051$), which considerably exceeds previous estimates; annual juvenile survival was estimated at 0.527 ($\widehat{\mathrm{SE}} = 0.095$). Previous studies have substantially underestimated pipistrelle bat survival. Therefore, the classification of the pipistrelle as an r-selected species is questioned and the appropriateness of the $r - K$ model as well as alternative life history models are discussed.

Key Words: Chiroptera, capture-recapture, Cormack-Jolly-Seber model, hibernacula, population dynamics, life history strategy.

3.1 Introduction

Understanding factors that influence patterns of population dynamics is of fundamental importance in animal ecology and conservation biology. Among life history traits, the probability of survival, particularly adult survival, has the largest impact on population changes in long-lived species (Prévot-Juillard *et al.*, 1998), like many mammals and birds. Among mammalian species of comparable body size, bats are generally considered long-lived

(Altringham, 1996; Tuttle and Stevenson, 1982). Also first-year survival of juveniles is of importance, as this often determines recruitment to reproductive age. Therefore, knowledge of survival rates is of special interest in the study of bat population dynamics.

For endothermic animals of the temperate zones, winter represents a serious energetic challenge. Animals respond to food shortage and low temperatures during winter by either migration, by morphological or behavioural adaptation, or by reducing metabolism, i.e. hibernation (Speakman and Rowland, 1999). The overwhelming majority of temperate zone bat species hibernate to bypass the energetic bottleneck during winter (Webb *et al.*, 1996). Hibernation is clearly a strategy to promote survival under unfavourable environmental conditions. Nevertheless, bat populations are suspected to suffer from increased mortality in winter (Davis and Hitchcock, 1965). The critical period is early spring: fat reserves are depleted and hibernators experience energetic stress from the arousal process. Consequently, it is plausible to hypothesize seasonal patterns in survival probabilities of temperate bats, with reduced over-winter survival rates compared to summer/autumn.

Survival rates often differ between sexes and age-classes (Lebreton *et al.*, 1992) and are influenced by environmental variables like temperature (North and Morgan, 1979). Sex-specific variation of survival is often considered as a consequence of the mating system (Greenwood, 1980). Generally, little is known on sex-specific survival in temperate bats, but a variety of patterns are suspected depending on the mating system (Davis, 1966; Stevenson and Tuttle, 1981). Gerell and Lundberg (1990) have explained low male survival rates in the pipistrelle bat by its mating system, a resource defence polygyny (Clutton-Brock, 1989). Juvenile survival in mammals and birds generally is assumed to be low during some period following fledging or weaning, and to approach constancy after becoming adult (Loery *et al.*, 1987). To our knowledge, neither studies that address age-specific variation of bat survival, nor detailed investigations of seasonal survival patterns related to hibernation and weather conditions exist.

Population studies are usually confined to female bats, who form easily observable maternity colonies, whereas males roost solitarily during summer and are therefore difficult to sample (Kurta and Kunz, 1988; Speakman *et al.*, 1991). At hibernacula, however, sexes are mixed and thus can be studied comparatively. As outlined above, the hibernation period may significantly influence population dynamics, consequently may generate seasonal survival patterns, of which sexes and age classes may be differentially affected. Winter severity is also likely to have an effect on over-winter survival.

Survival processes are usually not directly observable in wild animals. This applies particularly to bats. Therefore, survival studies frequently employ mark-recapture methods. Recent advances in capture-recapture methodology have enabled researchers to address specific biological hypotheses concerning variation of population parameters (Lebreton *et al.*, 1992). Only a limited number of studies have applied this sophisticated modelling approach to test specific hypotheses of bat population dynamics (e.g. Hoyle *et al.*, 2001). However, some earlier studies, using rather ad hoc approaches, provided rough ideas on annual survival rates and sex-specific survival patterns (Boyd and Stebbings, 1989; Davis, 1966; Elder and Gunier, 1981; Gerell and Lundberg, 1990; Hitchcock *et al.*, 1984; Keen and Hitchcock, 1980).

The pipistrelle bat (*Pipistrellus pipistrellus* Schreber, 1774), with a body mass of about 5.5 g, is probably the smallest hibernating mammal of the northern hemisphere (Geiser and Ruf, 1995). It is widely distributed and one of the most common bat species in Europe (Schober and Grimmberger, 1998). So-called mass hibernacula of *P. pipistrellus*, comprising up to several thousand individuals, are known to occur (Dumitresco and Orghidan, 1963; Grimmberger and Bork, 1978; Lustrat and Julien, 1997). Recent findings suggest that *P. pipistrellus* should be split into two sibling species (Barratt *et al.*, 1997; Jones and van Parijs, 1993). According to spectral characteristics of their echolocation calls, they are tentatively referred to as the 45- and 55-kHz phonic type, respectively. The 45-kHz type will retain the name *Pipistrellus pipistrellus* (Jones and Barratt, 1999). The discovery of this "new" species complicates the interpretation of previous studies and calls for further research.

In this study, we present a survival analysis based on live-recapture data of *Pipistrellus pipistrellus*, 45-kHz phonic type, sampled at a mass hibernaculum where about 5,000 pipistrelles hibernate (Sendor *et al.*, 2000). Summer swarming, defined as mere nocturnal flight activity at hibernacula (Fenton, 1969; Degn *et al.*, 1995; Sendor *et al.*, 2000), is a regular phenomenon at this location. The bats arrive at and leave the site on the same night, without using it as a day roost. Due to the almost year-round presence of bats, hibernacula are ideal locations to study population dynamics, permitting a study design that aims at the examination of seasonal patterns. The aims of our study were to examine variation in pipistrelle bat survival by addressing the following working hypotheses:

1. Male survival probabilities are expected to be reduced compared to females (Gerell and Lundberg, 1990)

2. First-year survival of juveniles is expected to be lower than adult survival

3. Autumnal survival rates are expected to exceed spring survival

4. Cold winters should reduce, mild winters should enhance spring survival probabilities.

We will discuss the obtained results in the context of mortality-related aspects of life history theory (Stearns, 1992) and their consequences for population dynamics.

3.2 Materials and methods

3.2.1 Study site

We caught pipistrelle bats at a large bat hibernaculum, Marburg Castle (Hesse, Germany). The castle is situated on top of a hill at about 290 m a.s.l., in the centre of the city of Marburg, on the western side of the Lahn valley. The pipistrelle hibernaculum is located in a vaulted cellar of this building, partially situated at ground level. The cellar measures about 32.5 × 12.5 × 6 m ($l \times w \times h$). The bats roost in narrow crevices in the walls (3.5 to 4.5 m thick) and the ceiling. The inside of the cellar is accessible for the bats via an embrasure. The hibernaculum is almost exclusively used by pipistrelle bats. Occasionally, also few individuals of other species as the grey long-eared bat (*Plecotus austriacus*), the barbastelle (*Barbastella barbastellus*), and the serotine bat (*Eptesicus serotinus*) may be encountered, but make up less than one per cent of the observations. About 5,000 pipistrelle bats use this location for hibernation (Sendor *et al.*, 2000), and substantially larger numbers participate in summer swarming between June and September.

3.2.2 Field methods and data sources

Bats were usually caught with a mist-net placed close to the embrasure, so that capture happened immediately after the bats had entered the hibernaculum. Alternatively, we sometimes placed a mist-net further inside the cellar, covering its entire cross-sectional area, likewise ensuring high success of capture. The capture sessions took place in the years 1996 to 2000. They covered the periods of summer swarming between mid-May and mid-September, and the hibernation periods between late November and early March. In the latter case the pipistrelles were mainly caught when they were immigrating for hibernation. Each primary capture period (season) consisted of approximately 20–30 separate nights. We attempted a capture frequency of two nights per week in summer. In winter, the timing of the capture nights was highly dependent on changes in ambient temperature between frost and mild weather. Changing weather conditions caused substantial bat movements into and out of the hibernaculum (Sendor *et al.*, 2000). Thus, bats were caught only when they were active (flying), to keep disturbance at a minimum.

The pipistrelles were marked with uniquely coded alloy bands of sizes H and M (2.4–2.9 mm diameter), attached to the forearm. The bats were released immediately after each capture session. Bat bands were provided by the Museum Alexander Koenig, Bonn. Individuals were sexed, aged according to the degree of epiphyseal fusion (Anthony, 1988; Racey, 1974a), and weighed to the nearest 0.1 g. Reproductive status was assessed according to the size of the testes and distension of the epididymis in the males, as well as size and hair covering of the nipples in the females (Racey, 1974a, 1988). Individuals with unfused epiphyses were classified as juveniles, those with fused epiphyses as adults (unknown age). During winter, discrimination of newly captured young of the year was often impossible due to the advanced ossification of the epiphyses. Male young of the year still could be distinguished by the black pigmentation of the *tunica vaginalis*, which covers the epididymis (Racey, 1974a). Apart from a few exceptions where the epiphyses were still unfused, we had no means to determine the age of unmarked females in winter and hence classified them all as adults, which introduced some heterogeneity to the data.

Capture, handling and marking of the bats was done under license of the Regierungspräsidium Gießen (Upper Nature Conservation Authority).

Weather data were obtained from a weather station located within the municipal area of Marburg, about 4.5 km from the study site, that is operated by the Technical University of Darmstadt.

3.2.3 Data analysis

The pipistrelle bat data were divided into four groups, according to sex and age: juvenile males, adult males, juvenile females, and adult females. Data from within a summer or winter were pooled into one capture occasion, respectively. We constructed capture histories representing an alternating sequence of summer and winter samples, according to the seasonal design of our study. This resulted in a data set with 9 capture occasions (5 summers, 4 winters). The respective survival intervals are spring and autumn. Spring validly measures winter survival as it includes the critical period of arousal from hibernation (see introduction).

We used capture-recapture models of the Cormack-Jolly-Seber (CJS) type (Lebreton *et al.*, 1992) to estimate apparent survival probabilities (ϕ). The fully time-dependent CJS-model makes some fundamental assumptions (Pollock *et al.*, 1990): (1) the individuals of the ith sample have the same probability of recapture, (2) the individuals of the ith sample have the same probability of surviving to $i+1$, (3) marks are not lost or overlooked, and (4) samples are instantaneous and the individuals are released immediately after the sample. Unknown mark loss (assumption 3) was unlikely to occur in this study because the bands are securely fastened to the forearm and pipistrelle bats are not capable of removing the bands. Of 13 individuals recaptured at subsequent occasions, the bands had to be removed due to injuries. We treated these removals as losses on capture, as well as 24 individuals reported dead from the public. Assumption 4, however, was not well met: the sampling periods (see above) were long relative to the inter-sample intervals. This problem was less serious in summer, because individuals out of a certain group (e.g. adult males) were predominantly caught during restricted periods of approximately four to six weeks. According to Smith and Anderson (1987), lengthy ringing periods have merely a negligible effect on survival estimates if there is no great variation in the shapes of the temporal distribution of ringing effort (TDR) and if survival within the periods is high. In our study, variation in TDR within the groups was low because the phenology of summer swarming was similar among years. Noteworthy mortality was unlikely to occur during the summer marking periods. This was probably also the case in the winter samples, because capture efficiency was highest in the first half of the winters, during the immigration period (approx. 6 weeks). Accordingly, we expect only negligible bias resulting from the lengthy sampling periods.

Departures of the data from assumptions (1) and (2) were tested by a χ^2 goodness-of-fit (GOF) test using a modified version of program RELEASE (Burnham *et al.*, 1987; Pradel, 1993). The RELEASE test consists of four test components, the first two of them (3.SR, 3.Sm) being sensitive to violations of assumption (1), while the other two components (2.Ct, 2.Cm) are sensitive to departures from assumption (2). Common sources of violations of model assumptions may be (a) permanent emigration from the study area after first capture, also termed the transience effect (Pradel *et al.*, 1997), (b) positive or negative trap-response (Pollock *et al.*, 1990), or (c) additional heterogeneity in survival and recapture probabilities, which may include temporary emigration, individually varying recapture probabilities, etc. The GOF of a model accounting for transience can be tested by leaving aside the RELEASE component 3.SR (Pradel *et al.*, 1997), and trap-dependence by leaving aside Test 2.Ct (Pradel, 1993). The goodness-of-fit of a model combining effects (a) and (b) was tested by the procedure outlined by Viallefont *et al.* (1995).

To allow modelling of possible trap-dependence, capture histories were rewritten, replacing each real individual by as many imaginary animals recaptured at most once as there were recapture events (Pradel, 1993), with the help of program U-CARE (available from ftp://ftp.cefe.cnrs-mop.fr/pub/

biom/Soft-CR). The sources of additional heterogeneity are frequently not testable because of the required splitting of capture histories, leading to low cell probabilities in the contingency tables (little recaptures). This was also the case in the present study. If no adequate model fit can be achieved at this point, it is convenient to assume that the data are overdispersed, i.e. contain extra-binomial variation (Anderson and Burnham, 1994; Lebreton, 1995). Overdispersed data frequently result in underestimated sampling variances and selection of an overparameterized model. We corrected for overdispersion – if detected – in variance estimation and model selection (see below) by the inclusion of a variance inflation factor c; its estimate, $\hat{c}$, was obtained by dividing the goodness-of-fit statistic (χ^2) of the highest-dimensioned acceptable model by its degrees of freedom (Anderson and Burnham, 1994, 1999a).

After identification of a satisfactory general model, we fitted progressively simpler models using the maximum likelihood methods of program MARK (White and Burnham, 1999). Modelling strategy and model notation generally followed the approach of Lebreton *et al.* (1992), introducing the flexibility and power of generalized linear models to capture-recapture analysis. We modelled the effects of the factors sex, age class (initially expressed as a single factor "group"), and time on recapture and survival probabilities. Time was also expressed as a seasonal effect, i.e. parameters were allowed to differ between summer and winter, but were constrained to be constant among all summers or winters, respectively. In contrast to fully time-dependent models, all parameters are individually identifiable in seasonal models, because there are no final β-terms in the probability statements (Lebreton *et al.*, 1992). We hypothesized an age effect with two age classes, lasting for two sampling periods ($a2'$). This type of effect accounts for the seasonal study design, in contrast to the bats' annual life cycle. Transience and trap-dependence were included if required according to the GOF test. The symbols used for model notation and their biological meaning are summarized in Table 3.1. Note that transience or trap-dependence are structurally equivalent to an age-effect and hence cannot be distinguished from the latter within a group. The problem of modelling an age-effect in the presence of transience can partly be bypassed by comparing adults and juveniles, but confounding of both effects will remain also with such a construction. The logit link-function was preferred in the modelling process (Lebreton *et al.*, 1992).

We also hypothesized that the above effects could have affected autumnal and spring survival rates differentially. This requires separate model structures for autumn and spring survival; thus, deviating from the usual notation (e.g. ϕ_t, p_t), we will denote such models as, e.g. (ϕ_t^A, ϕ^S, p_t), following Prévot-Juillard *et al.* (1998). The superscripts denote autumnal (A) and spring (S) survival rates, respectively.

Tab. 3.1: Subscripts used for model notation in CJS survival analysis.

Notation	Meaning	Applies to
$trans$	Transience effect	ϕ
$a2$	Age effect (two age classes) lasting for one survival interval	ϕ, (p)
$a2'$	Age effect carrying over two survival intervals	ϕ, (p)
sex	Sex effect	ϕ, p
g	Group effect	(ϕ), p
t	Time effect	ϕ, p
$season$	Parameters vary between, but are constant within summers and winters	ϕ, p
m	Trap-effect lasting until the first recapture period	p
m'	Trap-effect lasting until the second recapture period	p
Covariates		
T_w	Temperature sum November–March	ϕ
FD	Number of frost days November–March	ϕ
E	Capture effort: number of capture hours within a capture period	p

We also modelled the effect of capture effort (E) as an external covariate (North and Morgan, 1979), measured as hours of sampling within a capture period, on recapture probabilities (p). We further hypothesized that winter severity had an effect on subsequent spring survival: Temperature sums, calculated from the daily mean temperatures, and the number of days with a mean temperature below 0°C (frost days) from November to March, were used as external covariates to model spring survival. The months November to March correspond to the period when pipistrelle bats are predominantly torpid. The covariates were rescaled to fit in the interval [0,1] and included into the models as linear, quadratic, or logarithmic functions. Predictions for these models were that a covariate effect changed at a constant rate (linear), achieved a maximum or minimum at an intermediate effect (quadratic), or approached an asymptote (logarithmic). The quadratic function was used only for capture effort as we did not assume an optimum effect with respect to survival within the usual range of Central European winter temperatures.

Model selection (i.e. finding the most parsimonious model) was performed by minimizing AICc, the small-sample version of Akaike's information criterion (Anderson and Burnham, 1999b). For comparison among models we further report the difference in AICc between the best fitting and alternative models (ΔAICc) and the relative Akaike weights (Buckland *et al.*, 1997), computed for each candidate model as

$$w_i = \frac{\exp -\frac{1}{2}\Delta_i}{\sum_{r=1}^{R} \exp -\frac{1}{2}\Delta_r}$$

where $\Delta_i = \Delta\text{AICc}$. The weight w_i is considered as a measure of evidence for the plausibility of a model, given the data (Burnham and Anderson, 1998).

If overdispersion was identified in the data, we accounted for it by employing quasi-likelihood methods (Anderson and Burnham, 1994): inclusion of $\hat{c}$ then leads to QAICc instead of AICc and inflated variances of the parameter estimates.

3.3 Results

3.3.1 Global model

Between summer 1996 and winter 1999/2000, 15,839 pipistrelle bats were captured and released (3,311 juv. ♂♂, 3,263 ad. ♂♂, 4,408 juv. ♀♀, 4,857 ad. ♀♀), comprising 13,082 individuals. In subsequent sampling periods, 3,403 recaptures were recorded (750 juv. ♂♂, 648 ad. ♂♂, 883 juv. ♀♀, 1,122 ad. ♀♀). The numbers of captures varied between summers and winters:

Tab. 3.2: Results of the goodness-of-fit tests of various models accounting for departures from the assumptions of the standard CJS model.

	χ^2	*df*	*p*
juv. males			
CJS	102.55	32	< 0.001
transience	83.90	25	< 0.001
trap-dependence	79.43	26	< 0.001
combined	89.29	38	< 0.001
ad. males			
CJS	131.89	39	< 0.001
transience	109.82	32	< 0.001
trap-dependence	73.92	23	< 0.001
combined	79.56	38	< 0.001
juv. females			
CJS	102.00	37	< 0.001
transience	33.59	30	0.298
trap-dependence	93.61	31	< 0.001
combined		—	
ad. females			
CJS	106.76	32	< 0.001
transience	87.48	25	< 0.001
trap-dependence	82.70	26	< 0.001
combined	76.74	42	0.001

we regularly caught approximately the triple number of bats in summer, compared to winter.

The CJS-model (ϕ_t, p_t) clearly did not fit the data in either group (Table 3.2). In the juvenile females, the lack of fit could largely be attributed to TEST 3.SR, indicating a transience effect, and actually the transience model was acceptable (Table 3.2). In the other groups, the lack of fit was largely concentrated in the components 3.SR and 2.Ct, indicating an impact of transience plus trap-dependence. Generally, about every second release cohort was affected by severe departures from expectations, thus indicating a seasonal pattern in the violations of model assumptions. The spring intervals were affected by transience and the winter occasions by trap-dependence. However, additional model structure did not lead to satisfactory model fit:

neither a transience effect, nor trap-dependence, nor a model combining both effects was acceptable (Table 3.2). Thus, we assumed that the remaining lack of fit was caused by individual heterogeneity in survival and recapture probabilities, which should be considered as overdispersion. Actually, when accepting transience for the juvenile females and a combination of transience and trap-dependence for the other groups, overdispersion was moderate ($\hat{c} = 1.89; \chi^2_{148} = 279.2$). Thus, an appropriate global model included group, time, and transience as factors affecting survival and group, time and trap-dependence (except for the juvenile females, i.e. group 3, denoted by $m - g124$) affecting recapture. We specified trap-dependence and time as additive effects, because full trap-dependence models have still unexplored parameter identifiability problems (Pradel, 1993). The resulting initial model is denoted as $\phi_{trans \times g \times t}, p_{(m-g124+t) \times g}$.

3.3.2 Modelling recapture

Despite the obvious presence of transience and trap-dependence revealed by the GOF test, the data were apparently insufficient (too little recaptures) to support such a complex model structure: Only 62 out of 87 parameters were estimable in the global model. To simplify model structure, we decided to remove the transience effect for modelling recapture rates, leading to model $\phi_{g \times t}, p_{(m-g124+g) \times t}$, and to reintroduce transience after the most parsimonious recapture model was determined; $\hat{c}$ was left at 1.89.

A trap-effect lasting for two capture periods (m') turned out to describe the data better than a simple one or a model ignoring it (Table 3.3, models 1–4 vs. 5–7). A seasonal effect (models 2, 3, 6, 7) described recapture rates better than full time dependence. This is not surprising considering the consistent threefold difference between summer and winter captures. Models that eliminated the group effect completely or introduced a sex effect (models 8–12) had very large QAICc values and were therefore inadequate. Models that restricted the trap-effect to the winter were not well supported, although this could have been plausible in view of the seasonal variation of numbers of bats captured. In the best-fitting recapture model, p varies by season and group, and is affected by a two-period trap-effect, except for the juvenile females ($\phi_{g \times t}, p_{m'-g124 \times season \times g}$, no. 6). Competing models were far less supported and are therefore not useful to describe patterns of recapture rates. Models with an age-specific trap-effect had severe problems with parameter estimatibility and are therefore not reported.

The attempts to model p as linear, quadratic, or logarithmic functions of capture effort did not lead to improved model fit (Table 3.4). The reason for this was probably that groups were differentially affected by capture effort

Tab. 3.3: Modelling recapture probabilities of *Pipistrellus pipistrellus* marked at Marburg Castle, as functions of trap-dependence (m and m'), time (t), season, group or sex, starting from model $\phi_{g\times t}, p_{(m-g124+t)\times g}$; QAICc = Akaike's information criterion, quasi-likelihood corrected; ΔQAICc = QAICc-based difference to the best model; w_i = normalized Akaike weight of model i; np = number of estimated parameters.

No.	Model name	QAICc	ΔQAICc	w_i	np
Modelling group-specific time and trap effects					
1	$\phi_{g\times t}, p_{(m-g124+t)\times g}$	13611.92	42.38	0.000	63
2	$\phi_{g\times t}, p_{m-g124\times season\times g}$	13588.63	19.09	0.000	46
3	$\phi_{g\times t}, p_{(m-g124+season)\times g}$	13596.39	26.85	0.000	43
4	$\phi_{g\times t}, p_{g\times t}$	13628.36	58.81	0.000	60
5	$\phi_{g\times t}, p_{(m'-g124+t)\times g}$	13607.28	37.74	0.000	63
6	$\boldsymbol{\phi_{g\times t}, p_{m'-g124\times season\times g}}$	**13569.54**	**0.00**	**0.999**	**46**
7	$\phi_{g\times t}, p_{(m'-g124+season)\times g}$	13586.40	16.86	0.000	34
Modelling p sex-specific and common across all groups					
8	$\phi_{g\times t}, p_{(m'+t)\times sex}$	13663.45	93.91	0.000	42
9	$\phi_{g\times t}, p_{m'\times season\times sex}$	13637.82	68.28	0.000	30
10	$\phi_{g\times t}, p_{(m'+season)\times sex}$	13685.01	115.47	0.000	27
11	$\phi_{g\times t}, p_{m'+t}$	13701.29	131.75	0.000	34
12	$\phi_{g\times t}, p_{m'\times season}$	13702.58	133.04	0.000	28
Modelling trap-effect restricted to winter captures ($m(wi)$)					
13	$\phi_{g\times t}, p_{(m(wi)+t)\times g}$	13601.00	31.46	0.000	61
14	$\phi_{g\times t}, p_{m(wi)-g124\times season\times g}$	13584.67	15.13	0.001	43

among years. Also the capture effort models had considerable problems with parameter estimatibility (Table 3.4).

The magnitude of the trap-effect was very different among the four groups (Fig. 3.1), being most pronounced in the juvenile males and least obvious in the adult females, while modelling trap-dependence had not been necessary in the juvenile females. Recapture probabilities were generally rather low (Fig. 3.1). While in both male age-classes there appeared to be a negative trap-effect after the first two capture periods, in the adult females no consistent pattern was apparent.

Tab. 3.4: Modelling the effect of capture effort (E), expressed as functions of the number of capture hours within capture periods, and two-period trap-dependence (m') on recapture probabilities of *Pipistrellus pipistrellus* marked at Marburg Castle; QAICc = Akaike's information criterion, quasi-likelihood corrected; ΔQAICc = QAICc-based difference to the best model; np = number of estimated parameters, (the number of potentially estimable parameters is given in parentheses).

No.	Model name	QAICc	ΔQAICc	w_i	np
6	$\boldsymbol{\phi_{g\times t}, p_{m'-g124\times season\times g}}$	**13569.54**	**0.00**	**0.999**	**46 (46)**
15	$\phi_{g\times t}, p_{m'-g124\times g\times E}$	13645.26	75.72	0.000	35 (46)
16	$\phi_{g\times t}, p_{(m'-g124+E)\times g}$	13659.97	90.43	0.000	32 (42)
17	$\phi_{g\times t}, p_{m'-g124\times g\times E^2}$	13643.13	73.59	0.000	40 (53)
18	$\phi_{g\times t}, p_{(m'-g124+E^2)\times g}$	13654.95	85.41	0.000	36 (47)
19	$\phi_{g\times t}, p_{m'-g124\times g\times \ln E}$	13653.82	84.28	0.000	35 (46)
20	$\phi_{g\times t}, p_{(m'-g124+\ln E)\times g}$	13667.32	97.78	0.000	32 (42)

3.3.3 Modelling survival

Transience

Reintroduction of group-specific transience lead to a worse model fit (models 21–23 in Table 3.5), compared to the best recapture model. Restricting transience to autumn was more appropriate than global transience, but still less useful than simple time-dependence. This seems surprising, considering the GOF results, but may be caused by the partial confounding of an age-effect and transience. Furthermore the failure to model transience indicates that a general one-period age-effect would be inappropriate to describe survival patterns.

Effects of sex, age, and time

Several models that included an age-effect with two age-classes carrying over two survival intervals were highly ranked. Models omitting the age-effect were not well supported (Table 3.5, model 29). Considerable progress in model fit was achieved by formulating age, sex, and time as additive effects (Table 3.5, models 24–28). Accordingly, we proceeded with building additive models for the remainder of the model selection process. Specifying time-dependence as a seasonal effect was not appropriate (no. 28; further

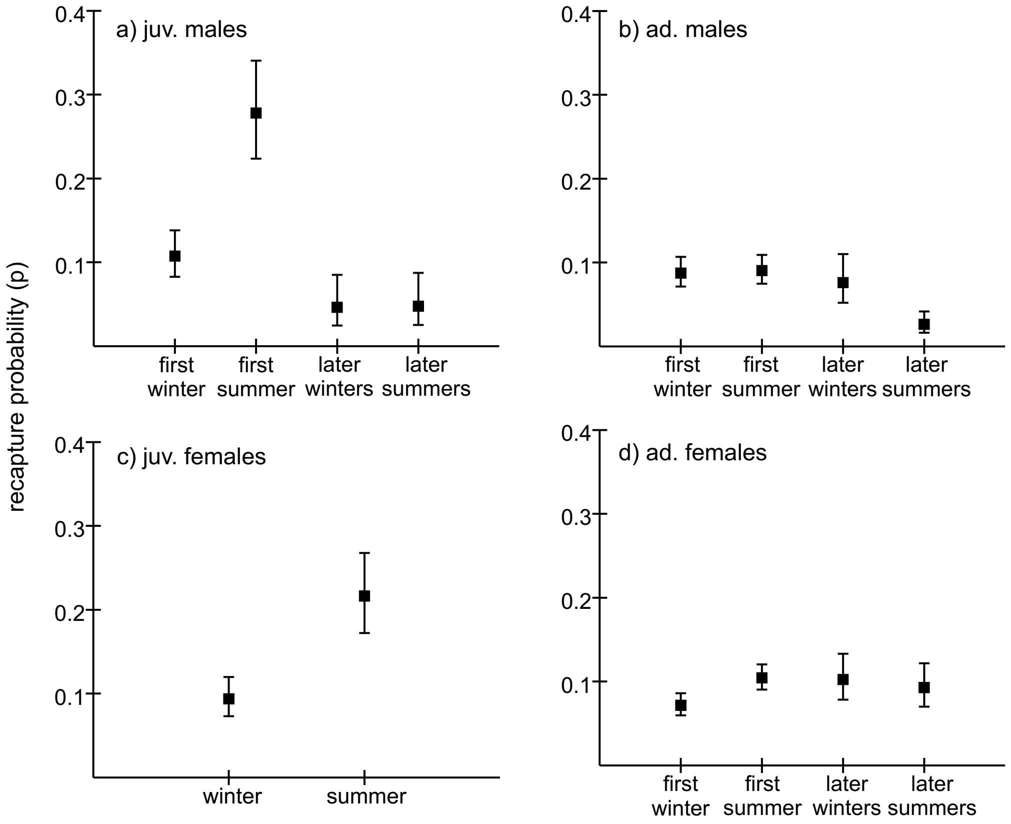


Fig. 3.1: Recapture probabilities of the pipistrelle bats marked at the mass hibernaculum Marburg Castle, estimated from model $\phi_{a2'+t+sex}, p_{m'-g124\times g\times season}$; vertical bars represent 95% confidence intervals; a) juvenile males, b) adult males, c) juvenile females, d) adult females.

seasonal models are not presented: they fit even less). However, already the comparison of the transience models 22 vs. 23 revealed some evidence for approximate constancy among spring survival rates. This tendency was confirmed after incorporation of an age-structure: models 30 and 31 were ranked only slightly below fully time-dependent models (26 and 27, Table 3.5). As a general tendency, there was relatively good support for models where the sex effect was omitted, indicating little importance of sex differences.

We introduced a biologically realistic age effect by specifying a two-period age-structure in autumn and a simple age-structure in spring ($\phi^{A}_{a2'+sex+t}$, $\phi^{S}_{a2+sex+t}$), i.e. the age effect was constrained to last until the end of an individual's first year (models no. 32–35, Table 3.5), leading to further im-

Tab. 3.5: Modelling survival probabilities of *Pipistrellus pipistrellus* marked at Marburg Castle, as functions of transience (*trans*), time (t), season, sex and age (a), and differentially affected autumn and spring survival intervals (ϕ^A, ϕ^S); the recapture part ($p_{m'-g124\times season\times g}$) is held constant across all models; QAICc = Akaike's information criterion, quasi-likelihood corrected; ΔQAICc = QAICc-based difference to the best model; w_i = normalized Akaike weight of model i; np = number of estimated parameters. The best supported models are highlighted in boldface. Note that not all tested models are presented.

No.	Model name	QAICc	ΔQAICc	w_i	np
Best recapture model					
6	$\phi_{g\times t}, p_{m'-g124\times season\times g}$	13563.69	16.35	0.000	46
Reintroduction of the transience effect					
21	$\phi_{trans\times g\times t}$	13597.86	50.53	0.000	72
22	$\phi^A_{trans\times g\times t}, \phi^S_{g\times t}$	13580.60	33.27	0.000	57
23	$\phi^A_{trans\times g\times t}, \phi^S_{g}$	13570.38	23.04	0.000	45
Significance of a two-period age-effect					
24	$\phi_{a2'\times t\times sex}$	13571.69	24.35	0.000	46
25	$\phi_{a2'\times(sex+t)}$	13554.80	7.47	0.006	30
26	$\phi_{a2'+sex+t}$	13550.18	2.84	0.057	24
27	$\phi_{a2'+t}$	13550.28	2.94	0.054	23
28	$\phi_{a2'+season+sex}$	13575.70	28.37	0.000	18
29	ϕ_{sex+t}	13573.41	26.07	0.000	22
Separating autumn and spring survival					
30	$\phi^A_{a2'+sex+t}, \phi^S_{a2'+sex}$	13551.46	4.13	0.030	21
31	$\phi^A_{a2'+t}, \phi^S_{a2'}$	13552.09	4.75	0.038	20
Age-effect constrained to last over first spring					
32	$\boldsymbol{\phi^A_{a2'+sex+t}, \phi^S_{a2+sex+t}}$	**13547.75**	**0.42**	**0.191**	**24**
33	$\phi^A_{a2'+sex+t}, \phi^S_{a2+sex}$	13550.44	3.11	0.050	21
34	$\boldsymbol{\phi^A_{a2'+t}, \phi^S_{a2+t}}$	**13547.33**	**0.00**	**0.236**	**23**
35	$\phi^A_{a2'+t}, \phi^S_{a2}$	13549.94	2.61	0.064	20

provement of model fit. The two top-ranked models (no. 32 and 34) were almost equally supported. As they differ by inclusion/exlusion of a sex effect, there is considerable uncertainty about the importance of sex differences in survival. Also constancy of spring survival (no. 33 and 35) remained fairly

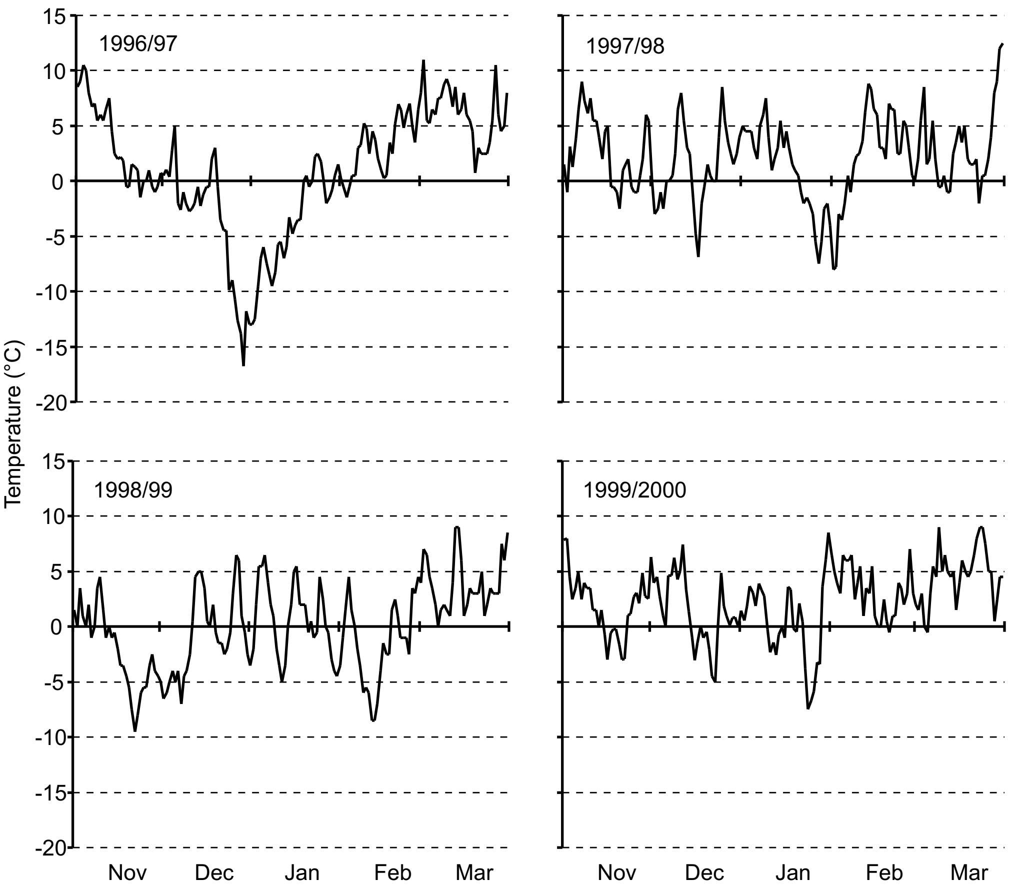


Fig. 3.2: Course of daily mean winter temperatures in Marburg in the four successive winters of the study period.

plausible, but the fully time-dependent models fit approx. 3.7 times better.

Effect of winter severity

The winter 1996/97 was rather harsh from a human viewpoint, with daily mean temperatures down to –17°C (Fig. 3.2). The subsequent winters had higher minimum temperatures and were rather characterized by short-term fluctuations of temperature. Nonetheless, there were also marked periods of frost, e.g. in Nov/Dec 1998. The numbers of days with frost were, in chronological order, 60, 45, 78, and 40, and the temperature sums 145.1, 321.0, 5.5, and 353.5°C, respectively.

The apparently relatively small residual variation of spring survival might be explained by winter conditions. Therefore, we modelled spring survival

Tab. 3.6: Modelling the effect of winter severity, expressed as functions of temperature sums from November to March (T_w) and number of frost days (FD) on spring survival probabilities of *Pipistrellus pipistrellus* marked at Marburg Castle; the recapture part ($p_{m'-g124\times season\times g}$) as well as the autumnal survival part were held constant across all models; QAICc = Akaike's information criterion, quasi-likelihood corrected; ΔQAICc = QAICc-based difference to the best model; np = number of estimated parameters.

No.	Model name	QAICc	ΔQAICc	w_i	np
36	$\phi^A_{a2'+t+sex}, \phi^S_{a2+sex+Tw}$	13549.88	2.54	0.066	21
37	$\phi^A_{a2'+t+sex}, \phi^S_{a2+sex+FD}$	13550.13	2.79	0.058	21
38	$\phi^A_{a2'+t+sex}, \phi^S_{a2+sex+\ln Tw}$	13550.20	2.87	0.056	21
39	$\phi^A_{a2'+t+sex}, \phi^S_{a2+sex+\ln FD}$	13550.38	3.05	0.051	21
40	$\phi^A_{a2'+t+sex}, \phi^S_{(a2+sex)\times FD}$	13552.40	5.06	0.019	23
41	$\phi^A_{a2'+t+sex}, \phi^S_{(a2+sex)\times \ln FD}$	13552.92	5.59	0.014	23
42	$\phi^A_{a2'+t+sex}, \phi^S_{(a2+sex)\times Tw}$	13553.22	5.88	0.013	23
43	$\phi^A_{a2'+t+sex}, \phi^S_{(a2+sex)\times \ln Tw}$	13553.95	6.61	0.009	23

based on the so far top-ranked time-dependent model ($\phi^A_{a2'+sex+t}, \phi^S_{a2+sex+t}$). We held the autumnal part constant and modelled residual variation of spring survival using the weather covariates.

The best temperature-dependent models, expressing either the number of frost days (FD) or winter temperature sums (T_w) as additive effects (Table 3.6) lead to slight improvement compared to constant spring survival ($\phi^A_{a2'+t+sex}, \phi^S_{a2+sex}$), but were ranked below the models with full time dependence (no. 35 and 37). Neither (T_w) nor (FD) was clearly preferred as explanatory weather variable, as the corresponding models were ranked close to each other (Table 3.6). The slope estimates for the weather variables from these two models ($\hat{\beta}_1 = 0.0008, \widehat{\mathrm{SE}} = 0.0011$ for T_w; $\hat{\beta}_1 = -0.0031, \widehat{\mathrm{SE}} = 0.0054$ for FD) also indicated at most a weak relationship between winter conditions and survival, that could not satisfactorily explain residual variation.

Survival estimates

We present survival estimates derived from model ($\phi^A_{a2'+sex+t}, \phi^S_{a2+sex+t}, p_{m'-g124\times g\times season}$) to illustrate the magnitude of sex-specific differences. Cor-

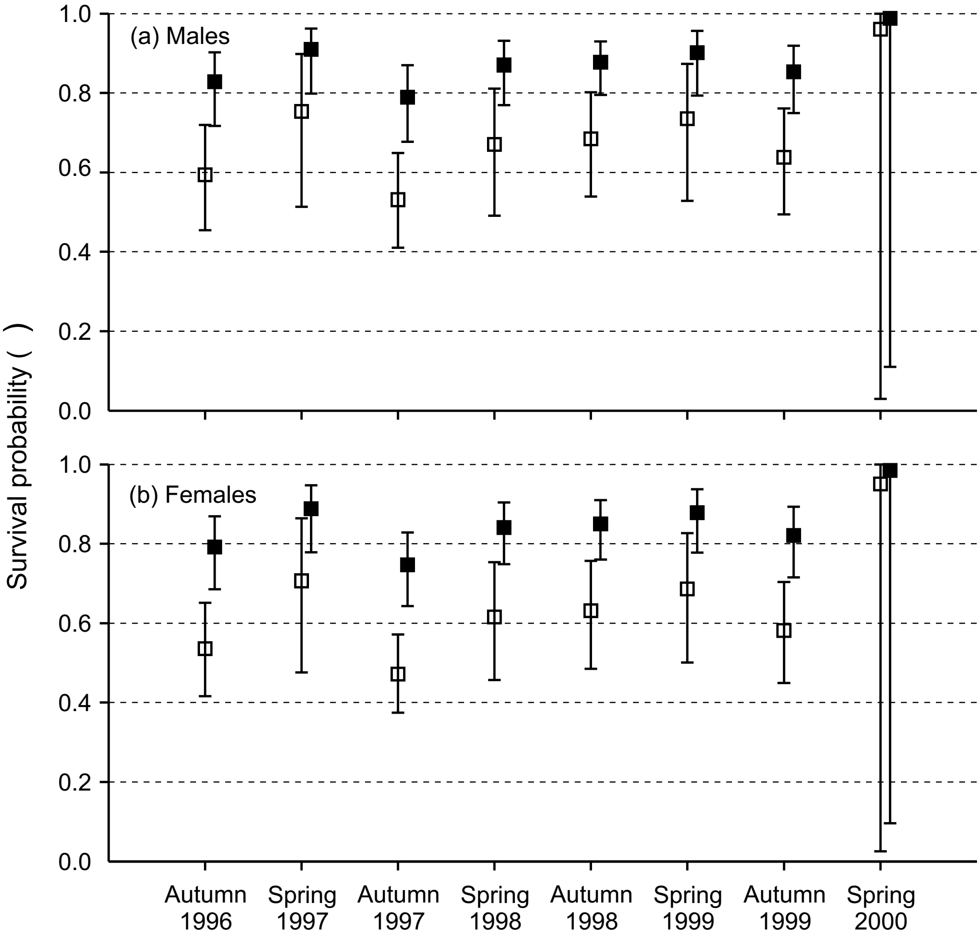


Fig. 3.3: Estimates of seasonal survival probabilities of the pipistrelle bats marked at the mass hibernaculum Marburg Castle, estimated from model $\phi^{A}_{a2'+sex+t}, \phi^{S}_{a2+sex+t}, p_{m'-g124\times g\times season}$; error bars represent 95% confidence intervals; black squares represent adults, open squares juveniles, respectively.

responding to the model selection results, differences in survival estimates between the sexes were small (Fig. 3.3). Acceptance of sex differences provided, the male survival estimates slightly exceeded the female ones. Juvenile survival was approximately 20–25% lower than adult survival. Differences between sexes and age classes were constant (on a logit scale), according to the additive model structure.

In contrast to our expectations, the autumnal survival estimates were consistently lower than in spring. However, this can be explained by the unaccounted transience effect in all groups: According to the GOF tests, transience predominantly affected the autumnal survival interval. Consequently the respective parameter estimates are biased low, while the estimates for spring are approximately unbiased. There was only little variation in spring survival, although constancy was not justified (see above). Average adult spring survival, conditional on model $(\phi^{A}_{a2'+t}, \phi^{S}_{a2+t})$, was 0.892 ($\widehat{\mathrm{SE}} = 0.028$). Variation in apparent autumnal survival was considerably higher (Fig. 3.3).

Mean life span

Annual survival probabilities and average life expectancy in the literature usually refer to unknown-aged adults (Loery *et al.*, 1987). Due to the biased autumnal survival estimates obtained in the present study, we cannot simply calculate annual survival by multiplying spring and autumn estimates. For convenience, we will ignore the biased autumnal survival rates. Instead, we assume that they will be approximately as high as in spring, so that squared spring survival can be regarded as a rough approximation of annual survival. Averaging the squared adult spring survival probabilities obtained under the best-fitting model $\phi^{A}_{a2'+t}, \phi^{S}_{a2+t}, p_{m'-g124\times g\times season}$, we get a mean annual survival rate of 0.799 ($\widehat{\mathrm{SE}} = 0.051$). This estimate results in an expected mean life span (MLS) for unknown-aged adults of

$$MLS = \frac{-1}{\ln\hat{\phi}} = \frac{-1}{\ln 0.836} = 4.5\,\text{years}$$

for both sexes (95%CI $= 2.04 - 6.96$years).

Under the same assumptions of approximately unbiased spring estimates as the basis for annual survival, mean first-year survival of juveniles is estimated as $\hat{\hat{\phi}} = 0.527$ ($\widehat{\mathrm{SE}} = 0.095$).

3.4 Discussion

In the present study we modelled seasonal survival of *Pipistrellus pipistrellus* as functions of various population characteristics and weather variables, based on capture-recapture data collected at a large hibernaculum. The results suggest that pipistrelle bat survival follows an age-structure with two age-classes and does not, or only marginally, differ between sexes. Winter severity had no significant effect on spring survival.

3.4.1 Impact of transience and trap-dependence

The most serious problem in our study was the confounding of age- and transience-effect, which are structurally equivalent. This is one reason why we did not specify models with a simple (i.e. lasting only one survival interval) age effect, in which first-interval juvenile survival would have been completely confounded with transience (Pradel *et al.*, 1997). Although transience was clearly detected by the goodness-of-fit test, models incorporating group-specific transience were not supported by the data. This already indicated that a one-period age-effect would hardly be justified. The inability to appropriately model transience is a matter of sample size. Unaccounted transience was always confounded with age-effects to some degree in our analysis. However, this problem is alleviated in models with an age-effect carrying over two survival periods ($a2'$), because transience is, by definition, permanent emigration after first capture (Pradel *et al.*, 1997). Particularly in a "realistic", biologically more meaningful formulation of an age-effect constrained to end after first spring (models no. 35–38, Table 3.5), confounding of age-effect and transience was largely restricted to autumn because the GOF test did not detect transience in spring. Hence, spring survival estimates should be approximately unbiased in adults as well as in juveniles.

The combination of transience and trap-dependence can partly be viewed as an artifact due to the study design: Between summer and winter temporary emigration takes place, as indicated by the consistent threefold discrepancy in the numbers of individuals that were catchable. Temporary emigration interacting with natural mortality may have caused a quasi-trap-response. Transience is a rather plausible effect, as it occurred predominantly in autumn: It is likely that a considerable fraction of the individuals that are catchable during summer swarming choose alternative sites for hibernation and for swarming in subsequent summers, which corresponds to permanent emigration. In contrast, individuals caught during winter might have an increased probability to return to the hibernaculum and thus to be recaptured.

The unaccounted transience effect produced negative bias in the autumnal survival estimates. This explains the unexpected seasonal survival pattern with higher apparent spring survival. As the fraction of transient individuals is unknown, bias cannot be quantified and therefore the autumnal survival cannot be assessed realistically. Transience can be best explained by dispersal processes, predominantly taking place in autumn (Davis and Hitchcock, 1965). Regarding this, there is no serious evidence for seasonally differing survival rates.

3.4.2 Differences between sexes

The model selection results are equivocal with respect to sex-specific survival: We may or may not accept the existence of sex differences (Table 3.5). However, the differences between estimates from the best sex-specific model ($\phi^A_{a2'+sex+t}, \phi^S_{a2+sex+t}$) are only marginal (Fig. 3.3), so that rejection of the hypothesis of sex-specific survival seems appropriate. This finding contrasts the results of Gerell and Lundberg (1990), who estimated consistently lower male survival probabilities in southern Sweden. They discuss this difference as a consequence of energetic constraints imposed on the males by the mating system, a resource defence polygyny. One should be aware of several issues in this respect:

1. Gerell and Lundberg (1990) probably investigated the 55-kHz phonic type, while our study refers to the 45-kHz pipistrelle.
2. The study site of Gerell and Lundberg (1990) was composed of mating roosts (bat boxes) defended by territorial males.
3. The sample size in the Swedish study was rather small (501 individuals marked in 7 years) and the authors estimated survival using a rather ad hoc approach.

We consider the first point to be of little importance when discussing sex-specific survival because both, the 45- and the 55-kHz pipistrelle, have the same mating system (Park *et al.*, 1996). Thus, they should share general survival patterns. The question which species was examined could possibly be of interest with respect to absolute survival rates, as they might vary by species or by geographical area. Nevertheless, parameter estimates are not directly comparable here because the data were collected under different conditions.

The two latter points, however, appear more relevant: It is easily conceivable that larger sample sizes improve statistical inference. Furthermore, proper modelling and selection of a parsimonious model is a prerequisite for insight in the biological process of interest (Burnham and Anderson, 1992). Models accounting for transience or trap-dependence had not yet been developed when Gerell and Lundberg (1990) conducted their study. Their conclusion that sex-specific survival is caused by energetic constraints imposed on the males due to territorial defence and mate attraction is contradicted by our study. There may be mainly two reasons for the conflicting results:

1. Differential bias in survival estimates between the sexes: Gerell and Lundberg (1990) report high turnover of individuals (i.e. transience,

and possibly also trap-dependence like in our study), and thus their estimates are heavily biased. We suspect turnover of male individuals to be higher at mating grounds than at hibernacula due to competition for territories, causing a more severe transience effect in the males and hence differences in apparent survival estimates. Clearly, also the estimates from our study are still negatively biased due to the unaccounted transience effect.

2. Geographic variation of energetic constraints due to climatic factors: The mating season in pipistrelle bats extends until November (Gerell and Lundberg, 1985). This is also valid for Marburg, where hibernal immigration starts in late November (Sendor *et al.*, 2000). Autumnal temperatures, however, are lower in southern Sweden than in Central Europe. Consequently, territorial males in Sweden could suffer from more severe energetic stress than Central European ones. This might explain geographically varying survival patterns.

In conclusion, a resource defence polygyny does not appear to generally induce reduced male survival in temperate bats, but sex-specific variation of mortality may be a result of the interaction of courtship behaviour with environmental factors like ambient temperature during the mating season.

3.4.3 Age-structure

Although partly confounded with transience, an age-effect constrained to last until the end of the first year of life described variation in the data appropriately. According to the best-fitting models, there was a constant difference between adult and first-year juvenile survival over time (additive effects on a logit scale). This corresponds to prior expectations about age-specific survival in long-lived species (Begon *et al.*, 1990; Loery *et al.*, 1987). The additive model structure further demonstrates that variation in juvenile survival is not greater than in adult survival. This conforms with the statement that species generally tend to have either high or low mortality throughout their lifetime (Promislov and Harvey, 1990). The low variation in juvenile survival leads to the conclusion that pipistrelle bat life histories are shaped in order to maintain approximately constant recruitment rates across years. However, as data on pre-weaning survival are scarce (see below) the question of recruitment to reproductive age should be treated with caution. To our knowledge, this is the first study to demonstrate age-effects on the mortality regime of both sexes in temperate bats (but see Thompson, 1987, for age-structured female pipistrelle populations, based on cohort life tables).

3.4.4 Seasonal, annual, and weather-related survival

Life history theory attempts to identify factors that shape aspects of life histories (e.g. mortality regimes, Stearns, 1992). A usual assumption is that natural mortality risk varies in an animal's annual life cycle (Gauthier *et al.*, 2001). Hibernation, like reproduction or migration, is a stage in the life cycle to which response of mortality risk should be expected. However, we found little evidence for seasonal variation of pipistrelle bat survival (the observed seasonal patterns are most likely results of unaccounted seasonal transience). Furthermore, winter survival was unexpectedly high. Thus, it appears that hibernation does not entail an increased survival cost for the pipistrelle bat.

The factors that influence mortality still remain unknown even after the present study: variability of over-winter survival was low and could not be explained satisfactorily by winter severity. This finding is also emphasized by some – yet weak – support for models constraining spring survival to be constant (Table 3.5). Accordingly, although a number of pipistrelle bats obviously freezed to death in close proximity to the hibernaculum in the harsh winter 1996/97 (T. Sendor, personal observation), our analysis allows the conclusion that low winter temperatures had no significant effect on survival probability associated with hibernation. Residual variation of spring survival remains unexplained. The reason for this might be that (1) variation in winter severity during our study was too low to have a detectable effect on pipistrelle survival. However, this should be unimportant because winter weather in the four years of our study covered the usual range of Central European conditions. More plausible is that (2) sites like Marburg Castle can be viewed as high-quality hibernacula, which provide a predictably stable microclimate and hence maintain high survival under otherwise adverse environmental conditions. Indeed, temperatures in roost crevices in Marburg Castle never fell below 4°C during the study period (T. Sendor, unpublished).

Studies on non-hibernating birds have found markedly decreased survival after harsh winters (Barbraud *et al.*, 2000; Lebreton *et al.*, 1992; North and Morgan, 1979). This underpins, in contrast to previous expectations (Davis and Hitchcock, 1965), the importance of hibernation as a stage with an advantageous effect on survival in an animal's annual life cycle. Nevertheless, there are conflicting results on over-winter survival of hibernating small mammals (e.g. Arnold, 1990; Fleming, 1979; Juškaitis, 1999; Schaub and Vaterlaus-Schlegel, 2001). Schaub and Vaterlaus-Schlegel (2001), in their study on garden dormice, argue that these animals are sufficiently well adapted to typical European winter conditions to survive the hibernal period with a high probability. Mammalian species with reduced winter survival, in contrast, were usually studied in extreme habitats with a prolonged winter and/or unpredictable environmental conditions. Hibernators actively seek sites with predictably stable microclimate for hibernation. In a temperate environment, microclimates of bat hibernacula are apparently stable enough to have a positive effect on hibernal survival probability. Hibernacula situated in colder climates (Davis and Hitchcock, 1965) could possibly bear less stable conditions, so that increased hibernal mortality risk cannot be compensated. We expect, however, that over-winter survival should be generally high in temperate bats to counterbalance their low reproductive output of usually one young per female per year (Tuttle and Stevenson, 1982). Otherwise lifetime reproductive success would be too low to maintain stable populations.

Pipistrelle bats tend to immigrate to climatically stable hibernacula not until the occurrence of frost and to leave them again when ambient temperatures rise above 0°C (Avery, 1985; Sendor *et al.*, 2000). Presumably, they spend the frost-free periods in less predictable but colder roosts to save energy. This hibernal roost switching can be regarded as a behavioural component of life history strategy in order to avoid the risks associated with a fluctuating environment. This strategy seems to be favoured by natural selection because pipistrelle bats, with their small body size, are supposedly not able to accumulate enough fat to survive the winter in a predictable, and thus warm, roost. Thus, habitat stability of hibernacula seems to be a crucial factor to influence the mortality regime, but the behavioural component is equally important because it partly compensates the particular disadvantages of stable vs. unstable habitats. Consequently, with the hibernal roost switching strategy, pipistrelle bats are apparently very successful in selecting hibernation sites that maximize survival.

Variation in apparent autumnal survival, in contrast to spring survival, could for instance be caused by varying impact of transience and thus is difficult to interpret biologically.

Pipistrelle bats are commonly considered r-selected (Gaisler, 1987), primarily because of their body size and assumed survival rates and fecundity. Stearns (1992) points out some serious shortcomings of the $r-K$ selection concept, mainly that it was not developed for age-structured populations, its focus on density dependence, and its deterministic nature. Thus, application of the $r-K$ model seems particularly problematic in temperate bats. Gaisler (1987), although he applies the $r-K$ model, also provides a good discussion of the problems associated with classifying bat life histories within this concept. The results of the present study indicate that pipistrelle bat survival rates have been considerably underestimated previously and that the classification as an r-selected species should be reassessed: Estimates like 0.44 for males and 0.54 for females by Gerell and Lundberg (1990) or in the range of 0.60 to 0.64 (von Helversen *et al.*, 1987; Thompson, 1987) probably result from methodological drawbacks. The latter two estimates were obtained with simple regression or cohort life table methods and are somewhat questionable because these methods, unlike CJS-models, do not estimate survival and recapture separately and because the underlying models make unrealistic assumptions about age distribution, population stability etc. (Anderson *et al.*, 1985; Clobert, 1995; Promislov and Harvey, 1990). Potential difficulties of the Swedish estimates were already discussed above.

Information on other life history traits of the pipistrelle bat is more uncertain, as only rough estimates are available. Reproductive age is assumed to be reached at the end of the first year, and an unknown and geographically variable fraction of the female pipistrelles gives birth to twins (Tuttle and Stevenson, 1982). We think that this information is insufficient to reliably assess the life histories of pipistrelle bats. Considering *P. pipistrellus* an r-selected species therefore seems somewhat questionable, even if some of the life history traits can be characterized accordingly. Not even the stochastic life history model (Stearns, 1977) is very useful here: It assumes that either juvenile or adult mortality rates fluctuate, but according to our results both show only little variation. Alternatively, the model assumes that birth rates or pre-weaning mortality fluctuate, as it is known from other bat species like *Myotis myotis* (Güttinger *et al.*, 2001), but corresponding data are not available for the pipistrelle.

Generally, too little is known on seasonal survival, the role of hibernacula, and consequently the factors that influence population dynamics and life histories in temperate bats. We suspect a variety of patterns depending on the species and the geographical region considered. For instance, winter conditions in Central Europe are usually much milder than in Canada, where Davis and Hitchcock (1965) conducted their study. Thus, their conclusion of reduced survival during winter and spring in *Myotis lucifugus* might be correct under the local conditions. Conversely, the climatic conditions in Marburg are quite representative for Central Europe. We therefore believe that the survival patterns found in the present study can be generalized for pipistrelle bats in large parts of Europe.

3.5 Acknowledgements

We are grateful to the many people who assisted us in catching bats, too numerous to be named. We further thank Markus Kaempf and Tilman Holfelder for providing weather data. This work is a part of T. Sendor's doctorate, supported by a grant of the "Hessische Graduiertenförderung" and further assistance by an “E&E-Project” by the German Federal Agency for Nature Conservation (Bundesamt für Naturschutz). Fruitful discussions with Janna Smit, Sandra Hüttenbügel and Roland Brandl helped to improve the manuscript.

References

Altringham, J. D. (1996): *Bats: Biology and Behaviour.* Oxford, New York, Tokyo: Oxford University Press.

Anderson, D. R. and K. P. Burnham (1994): AIC model selection in overdispersed capture-recapture data. *Ecology* **75**: 1780–1793.

Anderson, D. R. and K. P. Burnham (1999a): General strategies for the analysis of ringing data. *Bird Study* **46 Supplement**: 261–270.

Anderson, D. R. and K. P. Burnham (1999b): Understanding information criteria for selection among capture-recapture or ring recovery models. *Bird Study* **46 Supplement**: 14–21.

Anderson, D. R., K. P. Burnham, and G. C. White (1985): Problems in estimating age-specific survival rates from recovery data of birds ringed as young. *Journal of Animal Ecology* **54**: 89–98.

Anthony, E. L. P. (1988): Age determination in bats. In T. H. Kunz (Ed.), *Ecological and Behavioural Methods for the Study of Bats*, pp. 47–58, Washington D.C. & London: Smithsonian Institution Press.

Arnold, W. (1990): The evolution of marmot sociality: II. Costs and benefits of joint hibernation. *Behavioral Ecology and Sociobiology* **27**: 239–246.

Avery, M. I. (1985): Winter activity of pipistrelle bats. *Journal of Animal Ecology* **54**: 721–738.

Barbraud, C., H. Weimerskirch, C. Guinet, and P. Jouventin (2000): Effect of sea-ice extent on adult survival of an Antarctic top predator: the snow petrel *Pagodroma nivea. Oecologia* **125**: 483–488.

Barratt, E. M., R. Deaville, T. M. Burland, M. W. Bruford, G. Jones, P. A. Racey, and R. K. Wayne (1997): DNA answers the call of pipistrelle bat species. *Nature* **387**: 138–139.

Begon, M., J. L. Harper, and C. R. Townsend (1990): *Ecology: Individuals, Populations and Communities.* 2nd edn., Boston, Oxford, London, Edinburgh, Melbourne: Blackwell Scientific Publications.

Boyd, I. and R. E. Stebbings (1989): Population changes of brown long-eared bats (*Plecotus auritus*) in bat boxes at Thetford Forest. *Journal of Applied Ecology* **26**: 101–112.

Buckland, S. T., K. P. Burnham, and N. H. Augustin (1997): Model selection: an integral part of inference. *Biometrics* **53**: 603–618.

Burnham, K. P. and D. R. Anderson (1992): Data-based selection of an appropriate biological model: the key to modern data analysis. In D. R. McCullough and R. H. Barrett (Eds.), *Wildlife 2001: Populations*, pp. 16–30, Elsevier Applied Science, London, New York: Elsevier Science Publishers.

Burnham, K. P. and D. R. Anderson (1998): *Model Selection and Inference: A Practical Information-Theoretic Approach.* New York, Berlin, Heidelberg: Springer Verlag.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock (1987): *Design and analysis methods for fish survival experiments based on release-recapture*, vol. 5 of *American Fisheries Society Monographs.* Bethesda, Maryland: American Fisheries Society.

Clobert, J. (1995): Capture-recapture and evolutionary ecology: a difficult wedding? *Journal of Applied Statistics* **22**: 989–1008.

Clutton-Brock, T. H. (1989): Mammalian mating systems. *Proceedings of the Royal Society of London, Series B – Biological Sciences* **236**: 339–372.

Davis, W. H. (1966): Population dynamics of the bat *Pipistrellus subflavus. Journal of Mammalogy* **47**: 383–396.

Davis, W. H. and H. B. Hitchcock (1965): Biology and migration of the bat, *Myotis lucifugus*, in New England. *Journal of Mammalogy* **46**: 296–313.

Degn, H. J., B. B. Andersen, and H. Baggoe (1995): Automatic registration of bat activity through the year at Mønsted Limestone Mine, Denmark. *Zeitschrift für Säugetierkunde* **60**: 129–135.

Dumitresco, M. and T. Orghidan (1963): Contribution à la connaissance de la biologie de *Pipistrellus pipistrellus* Schreber. *Annales de Spéléologie* **18**: 511–517.

Elder, W. H. and W. J. Gunier (1981): Dynamics of a gray bat population (*Myotis grisescens*) in Missouri. *The American Midland Naturalist* **105**: 193–195.

Fenton, M. B. (1969): Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology* **47**: 597–602.

Fleming, T. H. (1979): Life-history strategies. In D. M. Stoddart (Ed.), *Ecology of small mammals*, pp. 1–61, London: Chapman and Hall.

Gaisler, J. (1987): The r-K selection model and life-history strategies in bats. In V. Hanák, I. Horáček, and J. Gaisler (Eds.), *European Bat Research*, pp. 117–124, Praha: Charles University Press.

Gauthier, G., R. Pradel, S. Menu, and J.-D. Lebreton (2001): Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. *Ecology* **82**: 3105–3119.

Geiser, F. and T. Ruf (1995): Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiological Zoology* **68**: 935–966.

Gerell, R. and K. Lundberg (1985): Social organization in the bat *Pipistrellus pipistrellus*. *Behavioral Ecology and Sociobiology* **16**: 177–184.

Gerell, R. and K. Lundberg (1990): Sexual differences in survival rates of adult pipistrelle bats (*Pipistrellus pipistrellus*) in South Sweden. *Oecologia* **83**: 401–404.

Greenwood, P. J. (1980): Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28**: 1140–1162.

Grimmberger, E. and H. Bork (1978): Untersuchungen zur Biologie, Ökologie und Populationsdynamik der Zwergfledermaus, *Pipistrellus p. pipistrellus* (Schreber 1774), in einer großen Population im Norden der DDR, Teil 1. *Nyctalus (N.F.)* **1**: 55–73.

Güttinger, R., A. Zahn, F. Krapp, and W. Schober (2001): *Myotis myotis* (Borkhausen, 1797) - Großes Mausohr, Großmausohr. In F. Krapp (Ed.), *Handbuch der Säugetiere Europas, Band 4: Fledertiere, Teil I: Chiroptera I*, pp. 123–207, Wiebelsheim: Aula-Verlag.

von Helversen, O., M. Esche, F. Kretzschmar, and M. Boschert (1987): Die Fledermäuse Südbadens. *Mitteilungen des Badischen Landesvereins für Naturkunde und Naturschutz, N.F.* **14**: 409–475.

Hitchcock, H. B., R. Keen, and A. Kurta (1984): Survival rates of *Myotis leibii* and *Eptesicus fuscus* in southeastern Ontario. *Journal of Mammalogy* **65**: 126–130.

Hoyle, S. D., A. R. Pople, and G. J. Toop (2001): Mark-recapture may reveal more about ecology than about population trends: Demography of a threatened ghost bat (*Macroderma gigas*) population. *Austral Ecology* **26**: 80–92.

Jones, G. and E. M. Barratt (1999): *Vespertilio pipistrellus* Schreber, 1774 and *V. pygmaeus* Leach, 1825 (currently *Pipistrellus pipistrellus* and *P. pygmaeus*; Mammalia, Chiroptera): proposed designation of neotypes. *Bulletin of Zoological Nomenclature* **56**: 182–186.

Jones, G. and S. M. van Parijs (1993): Bimodal echolocation in pipistrelle bats: are cryptic species present? *Proceedings of the Royal Society of London, Series B – Biological Sciences* **251**: 119–125.

Juškaitis, R. (1999): Winter mortality of the common dormouse (*Muscardinus avellanarius*) in Lithuania. *Folia Zoologica (Brno)* **48**: 11–16.

Keen, R. and H. B. Hitchcock (1980): Survival and longevity of the little brown bat (*Myotis lucifugus*) in southeastern Ontario. *Journal of Mammalogy* **61**: 1–7.

Kurta, A. and T. H. Kunz (1988): Roosting metabolic rate and body temperature of male little brown bats (*Myotis lucifugus*) in summer. *Journal of Mammalogy* **69**: 645–651.

Lebreton, J.-D. (1995): The future of population dynamic studies using marked individuals: a statistician's perspective. *Journal of Applied Statistics* **22**: 1009–1030.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson (1992): Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**: 67–118.

Loery, G., K. H. Pollock, J. E. Nichols, and J. E. Hines (1987): Age-specificity of Black-capped Chickadee survival rates: Analysis of capture-recapture data. *Ecology* **68**: 1038–1044.

Lustrat, P. and J.-F. Julien (1997): Monitoring of an important hibernaculum in Paris (France). *Myotis* **35**: 109–110.

North, P. M. and B. J. T. Morgan (1979): Modelling heron survival using weather data. *Biometrics* **35**: 667–681.

Park, K. J., J. D. Altringham, and G. Jones (1996): Assortative roosting in the two phonic types of *Pipistrellus pipistrellus* during the mating season. *Proceedings of the Royal Society of London, Series B – Biological Sciences* **263**: 1495–1499.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines (1990): Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**: 1–97.

Pradel, R. (1993): Flexibility in survival analysis from recapture data: handling trap-dependence. In J.-D. Lebreton and P. M. North (Eds.), *Marked Individuals in the Study of Bird Population*, pp. 29–37, Advances in Life Sciences, Basel, Boston, Berlin: Birkhäuser.

Pradel, R., J. E. Hines, J.-D. Lebreton, and J. E. Nichols (1997): Capture-recapture survival models taking account of transients. *Biometrics* **53**: 60–72.

Prévot-Juillard, A.-C., J.-D. Lebreton, and R. Pradel (1998): Re-evaluation of adult survival of black-headed gulls (*Larus ridibundus*) in presence of recapture heterogeneity. *The Auk* **115**: 85–95.

Promislov, D. E. L. and P. H. Harvey (1990): Living fast and dying young: a comparative analysis of life-history variation among mammals. *Journal of Zoology (London)* **220**: 417–437.

Racey, P. A. (1974): Ageing and assessment of reproductive status of pipistrelle bats, *Pipistrellus pipistrellus. Journal of Zoology (London)* **173**: 264–271.

Racey, P. A. (1988): Reproductive assessment in bats. In T. H. Kunz (Ed.), *Ecological and Behavioural Methods for the Study of Bats*, pp. 31–45, Washington D.C. & London: Smithsonian Institution Press.

Schaub, M. and C. Vaterlaus-Schlegel (2001): Annual and seasonal variation of survival rates in the garden dormouse (*Eliomys quercinus*). *Journal of Zoology (London)* **255**: 89–96.

Schober, W. and E. Grimmberger (1998): *Die Fledermäuse Europas.* 2nd edn., Kosmos Naturführer, Stuttgart: Franckh-Kosmos Verlags-GmbH & Co.

Sendor, T., K. Kugelschafter, and M. Simon (2000): Seasonal variation of activity patterns at a pipistrelle (*Pipistrellus pipistrellus*) hibernaculum. *Myotis* **38**: 91–109.

Smith, D. R. and D. R. Anderson (1987): Effects of lengthy ringing periods on estimators of annual survival. *Acta Ornithologica* **23**: 69–76.

Speakman, J. R., P. A. Racey, C. M. C. Catto, P. I. Webb, S. M. Swift, and A. M. Burnett (1991): Minimum summer populations and densities of bats in N.E. Scotland, near the northern borders of their distribution. *Journal of Zoology (London)* **225**: 327–345.

Speakman, J. R. and A. Rowland (1999): Preparing for inactivity: how insectivorous bats deposit a fat store for hibernation. *Proceedings of the Nutrition Society* **58**: 123–131.

Stearns, S. C. (1977): The evolution of life history traits: A critique of the theory and a review of the data. *Annual Review of Ecology and Systematics* **8**: 145–171.

Stearns, S. C. (1992): *The Evolution of Life Histories.* Oxford, New York, Tokyo: Oxford University Press.

Stevenson, D. E. and M. D. Tuttle (1981): Survivorship in the endangered gray bat (*Myotis grisescens*). *Journal of Mammalogy* **62**: 244–257.

Thompson, M. J. A. (1987): Longevity and survival of female pipistrelle bats (*Pipistrellus pipistrellus*) on the Vale of York, England. *Journal of Zoology (London)* **211**: 209–214.

Tuttle, M. D. and D. E. Stevenson (1982): Growth and survival of bats. In T. H. Kunz (Ed.), *Ecology of Bats*, pp. 105–150, New York: Plenum Press.

Viallefont, A., F. Cooke, and J.-D. Lebreton (1995): Age-specific costs of first time breeding. *The Auk* **112**: 67–76.

Webb, P. I., J. R. Speakman, and P. A. Racey (1996): How hot is a hibernaculum? A review of the temperatures at which bats hibernate. *Canadian Journal of Zoology* **74**: 761–765.

White, G. C. and K. P. Burnham (1999): Program MARK: survival estimation from populations of marked animals. *Bird Study* **46 Supplement**: 120–139.

4. Mating behaviour or information transfer? The function of summer swarming in the pipistrelle bat (*Pipistrellus pipistrellus*)

Manuscript submitted to *Behavioral Ecology and Sociobiology*

by Thomas Sendor and Matthias Simon

Abstract

Summer swarming in temperate bats is mere nocturnal flight activity at hibernacula, not related to day roosting. The validity of several functional hypotheses, in particular maternally guided exploration of hibernacula by juveniles vs. mating behaviour, was assessed for the European pipistrelle bat (*Pipistrellus pipistrellus*) in the present study. The swarming period lasted from mid-May to late September. The phenology of swarming was characterised by a unidirectional sequence of different groups, starting with adult males early in summer, superseded by adult females, and finally by juveniles of both sexes in August and September. Reproductively active males played no significant role. The sizes of adult female and juvenile swarming populations were similar. Juveniles and reproductive females spent longer times swarming during a given night than adult males and nonreproductive females. No observations indicating mating behaviour were made. The results indicated that maternally assisted exploration of hibernacula by the juveniles is likely to be the primary function, while mating is functionally not related to summer swarming in the pipistrelle bat. The relationships between hibernal ecology, mating systems, and functions of summer swarming, as well as the potential significance of male swarming, are discussed in an ecological and evolutionary context.

Key words: Chiroptera, hibernacula, mating systems, information transfer, life history evolution

4.1 Introduction

Bats of the temperate zones hibernate to survive the cold season (e.g. Webb *et al.*, 1996). For hibernation, bats visit hibernacula, which usually represent locations that are different from the summer roosts (e.g. Kunz, 1982; Neuweiler, 1993). Despite the fact that hibernacula are, by definition, used for hibernation, particularly high bat activity may be observed during the summer (June to September). This phenomenon is referred to as "summer swarming" or "fall swarming" (Degn, 1987; Fenton, 1969; Thomas *et al.*, 1979; Whitaker and Rissler, 1992), sometimes simply "summer activity" (Bauerová and Zima, 1988; Horáček and Zima, 1978; Klawitter, 1980). Summer swarming is defined as nocturnal flight activity, usually not related to day roosting (Hall and Brenner, 1965; Sendor *et al.*, 2000).

The function of summer swarming is still subject of considerable debate. The following mutually non-exclusive hypotheses have emerged in the literature:

Tab. 4.1: Predictions derived from hypotheses about the function of summer swarming at hibernacula in temperate bats.

Hypothesis	Predictions
Mating hypothesis	• Increasing numbers and proportions of reproductively active males (distended epididymis) in the course of the summer • Swarming of adult males on individual nights lasts at least as long as in other groups (mate attraction) • Occurrence of songflight calls in the hibernaculum
Maternal guidance hypothesis	• Reproductive females occur together with juveniles; increasing proportions of juveniles over the course of the summer • Similar numbers (population sizes) of adult females and juveniles • Swarming of juveniles and reproductive females on individual nights takes a longer time than in adult males and nonreproductive adult females
Feeding hypothesis	• Occurrence of insects at the swarming site • Emission of feeding buzzes by swarming bats

- The mating hypothesis: Thomas *et al.* (1979) convincingly demonstrated that mate attraction and mating play a significant role in the swarming activity at hibernacula of *Myotis lucifugus.* This has been transferred to other bat species (Schober and Grimmberger, 1998), although the function of summer swarming may vary across species.

- The maternal guidance hypothesis: Davis and Hitchcock (1965), in a study on *M. lucifugus*, suggested that swarming may familiarise bats with hibernation sites. Like most vertebrates, bats gather information about their environment by learning. Therefore, familiarisation with hibernacula should be particularly relevant for juveniles. In a study on "invasions" of *Pipistrellus pipistrellus*, Sachteleben (1991), extending Davis and Hitchcock, hypothesised that hibernacula are in effect "shown" to juveniles by their mothers.

- The feeding hypothesis: Whitaker and Mumford (1971) discussed the possibility that feeding at cave entrances could be associated with summer swarming.

- The social interaction hypothesis: Kretzschmar and Heinz (1995) described "social interactions" in a hibernaculum used, among other species, by *P. pipistrellus.* Social interactions may include mate attraction, mating, agonistic behaviour, and mother-infant relationships. Accordingly, the social interaction hypothesis subsumes other hypotheses, is rather diffuse and does not make specific predictions. Consequently, we will ignore this hypothesis for the remainder of this paper.

From the above hypotheses, we derived a set of predictions concerning phenology, population sizes, and swarming behaviour of various groups of individuals (Table 4.1). The hypotheses and predictions are not necessarily mutually exclusive, but more or less likely depending on the biology of the species considered. For instance, mating and familiarisation with hibernacula may occur at the same time and at the same locations. On the other hand, establishment of special mating roosts, separate from hibernacula, has been reported for *Nyctalus noctula*, *P. pipistrellus* and *P. nathusii.* The mating system of these species can be characterised as a resource defence polygyny (Barlow and Jones, 1996; Gerell and Lundberg, 1985; Gerell-Lundberg and Gerell, 1994; Sluiter and van Heerdt, 1966), while *M. lucifugus*, for which there is evidence in favour of the mating hypothesis, is promiscuous. The proposed functional relationship of mating and summer swarming in species with different mating systems is still unexplored. Mating is still generally discussed as the primary function of summer swarming (Schober and Grimmberger, 1998). In the present study, we address the function of summer swarming at hibernacula in a species whose mating system is described as a resource defence polygyny, the common European pipistrelle bat (*P. pipistrellus*).

Recent findings suggest that *P. pipistrellus* should be split into two sibling species (Barratt *et al.*, 1997; Jones and van Parijs, 1993). According to spectral characteristics of their echolocation calls, they are tentatively referred to as the 45- and 55-kHz phonic type, respectively. The 45-kHz type will presumably retain the name *Pipistrellus pipistrellus* (Jones and Barratt, 1999). Here we present results obtained at a large hibernaculum used by the 45-kHz pipistrelle.

Guided by the predictions listed in Table 4.1, the objectives of our study were (1) to describe and characterise the phenology of the participation of various groups of pipistrelles (individuals of different sex, age, and reproductive status); (2) to estimate the size of the swarming population, with particular emphasis on the ratio of adult females and juveniles; and (3) to estimate the effect of sex and age on swarming time. We will discuss how species-specific variation in hibernal ecology may have acted as an ultimate factor in the evolution of summer swarming and mating systems.

4.2 Materials and methods

4.2.1 Study site

We conducted this study between 1996 and 2000 at a large bat hibernaculum, Marburg Castle (Hesse, Germany). The castle is situated on top of a hill at about 290 m a.s.l., in the centre of the city of Marburg, on the western side of the Lahn valley. The pipistrelle hibernaculum is located in a vaulted cellar of this building, partially situated at ground level, measuring about $32.5 \times 12.5 \times 6$ m ($l \times w \times h$). During winter, the bats roost in narrow crevices in the walls (3.5 to 4.5 m thick) and the ceiling, built of coarse sandstone pieces. The inside of the cellar is accessible to the bats via an embrasure; two other openings play no major role as flight paths. The hibernaculum is almost exclusively used by pipistrelle bats (45-kHz phonic type).

4.2.2 Phenology

We caught bats using a mist-net, usually placed close to the embrasure, so that capture happened immediately after the bats had entered the hibernaculum. Alternatively, we sometimes placed a mist-net further inside the

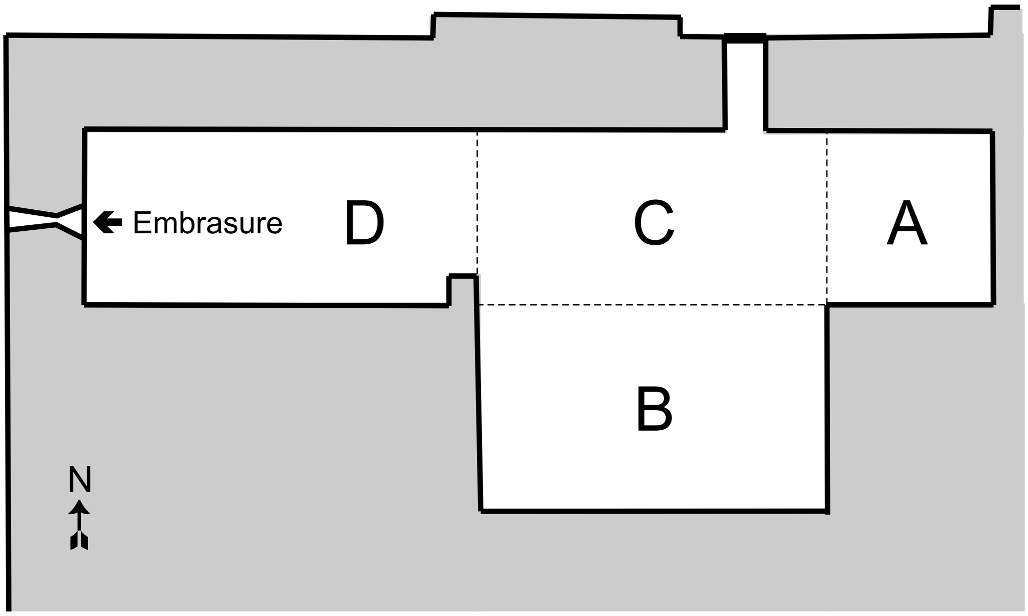


Fig. 4.1: Map of the cellar at Marburg Castle used as a hibernaculum by pipistrelle bats. Letters A–D denote sections of the cellar used to describe aspects of behaviour. Shaded areas symbolise walls; shaded areas that are not bordered by black lines indicate adjacent parts of the building.

cellar, covering its entire cross-sectional area (Fig. 4.1), likewise ensuring high success of capture.

After capture, the bats were sexed, and their age (adult, juvenile) was determined according to the degree of epiphyseal fusion (Anthony, 1988; Racey, 1974a). Reproductive status was assessed according to the size of the testes and distension of the epididymis in the males, and size and hair covering of the nipples in the females (Racey, 1974a). We distinguished reproductively active (i.e. ready to mate, recognisable by distended epididymis) vs. inactive adult males and nonreproductive (nipples without signs of lactation) vs. reproductive adult females (lactating or post-lactating).

To describe the phenology, we divided each month into quarters of approximately equal length of seven to eight days (e.g. Jun1–Jun4). For each of these periods, we estimated the proportions ($\hat{p}$) of adult males, nonreproductive and reproductive females, and juveniles participating in summer swarming. Likewise, we estimated the proportions of reproductively active individuals among adult males (with distended epididymis). Due to weather-dependent year to year variation of the timing of swarming intensity, samples for some time periods were not available from all years (Table 4.2).

Tab. 4.2: Sample sizes, numbers of samples (years) and total number of capture occasions (nights) in which capture data could be obtained with respect to the phenological time periods.

Period	No. of samples	Capture occasions	n
May3	1	1	133
May4	1	1	98
Jun1	3	4	92
Jun2	3	5	446
Jun3	2	4	30
Jun4	4	4	146
Jul1	4	5	163
Jul2	3	4	349
Jul3	4	7	893
Jul4	4	8	1753
Aug1	4	8	1393
Aug2	4	9	1605
Aug3	4	9	1999
Aug4	3	7	1409
Sep1	4	5	898
Sep2	3	4	361
Sep3	1	1	18
Sep4	1	1	47

4.2.3 Estimating population size

We estimated population sizes using capture-recapture methods. The pipistrelles were marked with uniquely coded alloy bands of sizes H and M (2.4–2.9 mm diameter). The bands were attached to the forearm and the bats were released immediately at the end of a capture session. Bat bands were provided by the Museum Alexander Koenig, Bonn. Capture, handling and marking of the bats was done under license of the Regierungspräsidium Gießen (Upper Nature Conservation Authority).

Regarding the expectation of similar numbers of adult females and juveniles derived from the maternal guidance hypothesis, we attempted to estimate the numbers of individuals (population sizes) of these groups that participate in summer swarming. We could estimate population sizes with the data from 1996, when numbers of recaptures were sufficiently large to apply capture-recapture methods (a total of 4,238 individuals), while we caught smaller numbers of bats in subsequent summers. Population sizes are preferably estimated under models that assume population closure (Otis *et al.*, 1978), i.e. no individuals leave and enter the population during the study. Additions or deletions can take place by birth, immigration, death or emigration. Clearly, no natural population is closed. The concept of closure is useful, however, when violations of the closure assumption are only moderate. This is the case when the study period is short relative to the life span of the organism, when recruitment from births can be excluded, and when migration processes are of little importance.

There is a finite number of bats that participate in swarming during a given summer. The population sizes of adult males, adult females, and juveniles are the parameters of interest. Within the swarming period, these groups are closed to additions from birth. The swarming (i.e. study) period is short relative to the life span of a bat, so that mortality is also negligible. We could actually demonstrate that mortality is close to zero during the period of summer swarming and even remains low until winter immigration (T. Sendor, unpublished data). The pipistrelle bat is a non-migrating species. The individuals visiting a hibernaculum come from a restricted area (Grimmberger and Bork, 1978, M. Simon, unpublished data). Hence, geographical closure was fairly met. The bats from the catchment area can be viewed as a closed superpopulation (Kendall, 1999), i.e. a population whose individuals randomly immigrate to and emigrate from the study area (here: the hibernaculum). The size of the superpopulation can be validly estimated with little bias but at the cost of reduced precision under closed models (Kendall, 1999).

In conclusion, we assume that violations of the closure assumption are only moderate and application of closed models is justified. Moreover, we were less interested in accurate estimates of absolute population size rather than in estimates of the ratio of juveniles and adult females, and the number of adult males as a by-product. Violations of the closure assumption are probably similar in all groups, so that this ratio should be approximately unbiased. The group “adult females”, however, represents a mixture of reproductive and nonreproductive individuals of at least one year of age. Pooling of these groups was necessary for statistical reasons (sample size) and furthermore because they could not always be distinguished sufficiently reliable in the field. Consequently, the number of potential mothers will be overestimated by approx. 20%.

We used the closed models of program CAPTURE (Otis *et al.*, 1978; Rexstad and Burnham, 1991; White *et al.*, 1982) to estimate population sizes. Unequal capture probabilities may occur even under the assumption of closure. Sources of varying capture probabilities are accounted for by models allowing temporal variation (model $\mathrm{M_t}$), individual heterogeneity (model $\mathrm{M_h}$), behavioural response (model $\mathrm{M_b}$), and combinations of these three factors. The most recent version of CAPTURE (Rexstad and Burnham, 1991) provides estimators derived from each of these models except the most complex model $\mathrm{M_{tbh}}$. The program conducts a variety of goodness-of-fit tests of assumptions of particular models and takes their results for model selection using a linear discriminant function (Otis *et al.*, 1978).

The numbers of bats captured varied considerably across capture sessions. Therefore, capture occasions were pooled within each group in order to reduce temporal variation in capture probabilities as far as possible (White *et al.*, 1982). We pooled as many successive capture occasions as necessary to approximate the occasion with the highest number of captures. This way of pooling was limited by the occurrence of recaptures between unpooled capture occasions. We included the captures from the approx. 6-week long winter immigration period (10 Nov–22 Dec) into the analysis because of improved precision resulting from the higher proportion of recaptures during that period. Captures from winter were merged into a single occasion. This does not invalidate the closure assumption, because with respect to immigration and emigration processes the pooled winter captures are equivalent to any of the summer capture occasions. Rather, fulfillment of model assumptions is stabilised due to increased recapture rates during that period. Starting from 24 unpooled occasions, this procedure resulted in capture histories consisting of 12 occasions in adult females and 11 occasions in adult males and juveniles, respectively. The exact pooling procedure is given in Sendor and Simon (2000). A comprehensive overview of the capture statistics is given in the appendix.

4.2.4 Modelling and estimating swarming time

To study group-specific swarming duration, a sample of 107 pipistrelle bats (28 adult males, 25 adult nonreproductive females, 22 reproductive females, 14 juvenile males, and 18 juvenile females) were tagged with chemiluminescent light sticks (size “mini”, various manufacturers). Only individuals that have been caught immediately after entering the hibernaculum were used, so that minimal bias with respect to swarming time was ensured. At a given night, a small number (up to 10) of randomly selected individuals out of a homogeneous group (e.g. only adult males) were fitted with light tags. The light sticks were loosely glued to the fur of the back with Skin Bond® surgical adhesive (Smith & Nephew Inc., Largo, FL, USA). The individuals of each light-tagged sample were released simultaneously in the hibernaculum, close to the embrasure (section D in Figure 4.1). Their flight behaviour was observed and their times of leaving the cellar (passage through the embrasure) recorded.

We analysed the two factors (age-class and sex) suspected to influence swarming time by general linear models using program SPSS for Windows. We used AICc, the small sample version of Akaike's information criterion (Burnham and Anderson, 1998) for model selection. The most parsimonious model was selected by minimizing AICc. Furthermore, to allow assessment of model ranking and relative support, ΔAICc, the simple difference to the best fitting model, and w_i, the relative Akaike weights for each model (Buckland *et al.*, 1997), are reported.

Because the raw data were not normally distributed we used $\log_e$-transformed swarming times as the response variable. After transformation, the distribution of the data was approximately normal and variances were homogeneous.

4.2.5 Behavioural observations

During the capture sessions we further payed attention to conspicuous bat behaviour: We noted if songflight calls or agonistic calls occurred. Both types of calls are, in the lower part of their frequency range, audible to and clearly distinguishable by the naked human ear (Barlow and Jones, 1997a,b; Racey and Swift, 1985). Furthermore, we regularly controlled if feeding buzzes were emitted by the bats, using bat detectors tuned to 45 kHz.

4.3 Results

4.3.1 Phenology

The onset of summer swarming varied from mid-May to early June among years, apparently dependent on the occurrence of warm weather. In early summer, i.e. until mid-July, approx. 30–140 individuals per night could be caught. The main swarming period lasted from mid-July to mid-September, with expected values (means) of more than 200 captured individuals per night (Figure 4.2).

The samples from the early phases of the swarming period (May to mid-July) were heavily dominated by adult males. Their proportion steadily declined during July and stabilised below 10% from the first week of August onwards (Figure 4.3a). Nulliparous females were less abundant, reaching a maximum of approx. 20% in late July (Figure 4.3b). Proportions of reproductive females increased from close to zero during May and June to

Fig. 4.2: Expected values (means) of the numbers of individuals per capture session in the course of summer swarming for all individuals (solid line) and adult males (dashed line).

a maximum of approximately 50% in early August (Figure 4.3c), declining again close to zero in late August and September. Juveniles first occurred in late July, initially parallel to the reproductive females, exceeding them by mid-August and finally approaching proportions close to 100% for the rest of the swarming period from late August onwards (Figure 4.3d). The wide confidence intervals in the central parts of the curves come from weather-related among-year displacements of group-specific swarming phases, thus reflecting temporal variation. The sex ratio in the juveniles varied little and no clear trend of deviations from the average ratio of 0.65:1 (males:females) was identifiable (Figure 4.4). Both the decline of adult males as well as the increase of juveniles are real effects, not just compensatory effects caused by increasing absolute numbers (compare Figs. 4.2 and 4.3, where the vertical dashed lines mark the onset of juvenile swarming).

Among adult males, proportions of reproductively active individuals increased from late July onwards to a maximum of approximately 60% in mid-August, declining again afterwards (Figure 4.5). Note, however, that numbers of adult males as a whole were very small during August and September (Figure 4.2). Thus, males became ready to mate around late July / early August, but quantities of reproductively active males in the swarming population were negligible.

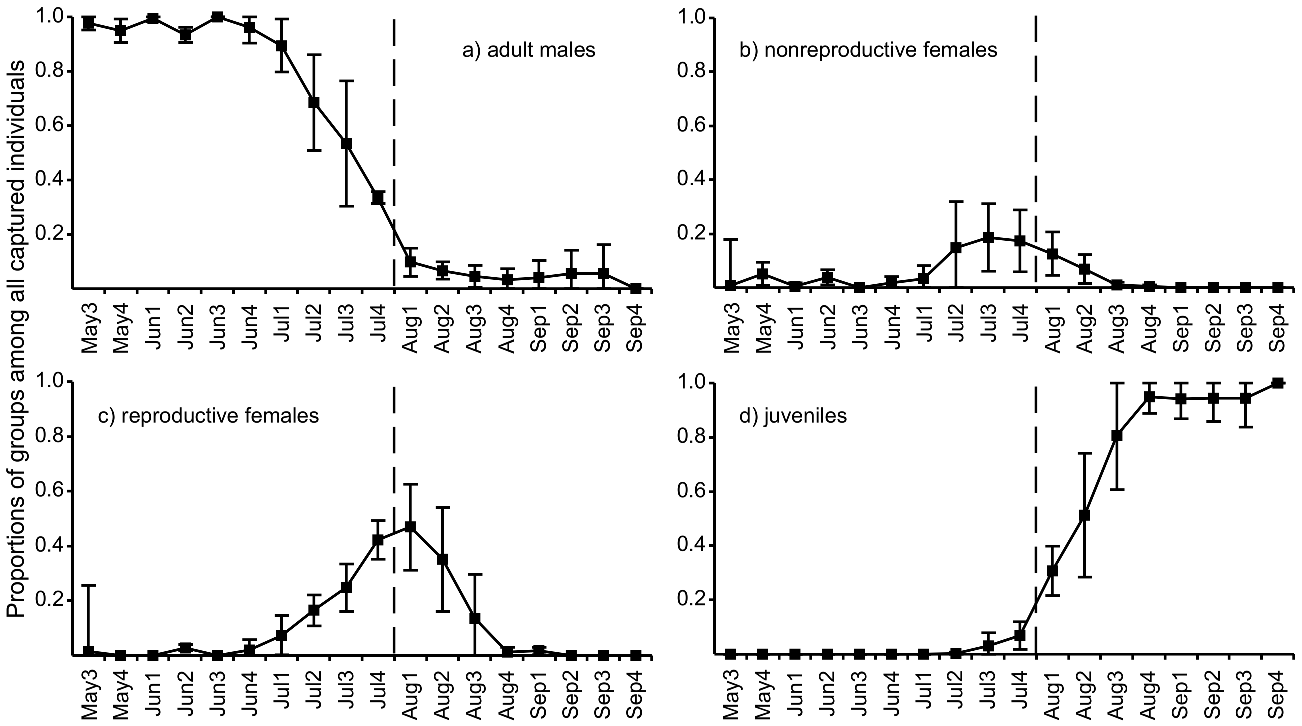


Fig. 4.3: Phenology of summer swarming: Estimated proportions (with 95% confidence intervals) and temporal sequence of various groups of pipistrelle bats catchable during the swarming period; a) adult males, b) nulliparous adult females, c) reproductive females, d) juveniles.

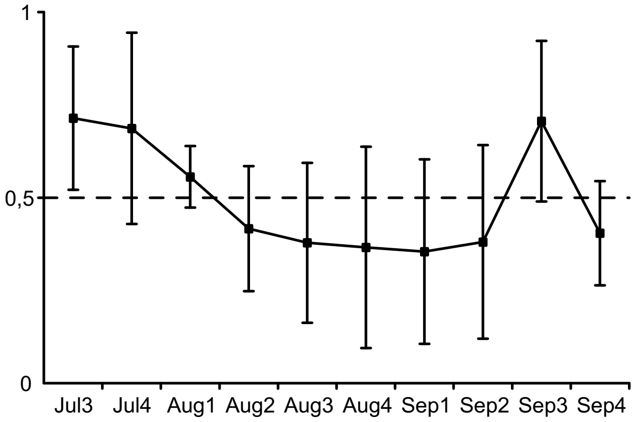


Fig. 4.4: Juvenile sex ratio, expressed as proportions of males (with 95% confidence intervals), in summer swarming pipistrelle bats.

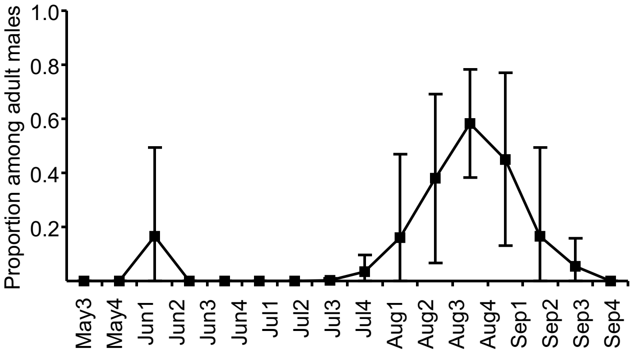


Fig. 4.5: Phenology of reproductively active males participating in summer swarming: Estimated proportions (with 95% confidence intervals) and temporal sequence of individuals with distended epididymis among adult males.

4.3.2 Population sizes

Temporal variation of capture probabilities remained an important factor in the estimation of population sizes, although we had attempted to reduce it by the pooling of capture occasions. Capture probabilities were generally low (Table 4.3), varying from 0.005 to 0.050 among occasions. The model selection procedure of program CAPTURE detected individual heterogeneity as a further source of unequal capture probabilities and thus selected the model combining temporal variation and heterogeneity (M_{th}) in all groups (Table 4.3). Despite the low and variable capture probabilities, coefficients of

Tab. 4.3: Estimates of population size of the pipistrelle bat population at risk of capture at the hibernaculum Marburg Castle under the closed models of program CAPTURE. $\hat{\mathrm{N}}$ = estimated population size, $\widehat{\mathrm{SE}}(\hat{\mathrm{N}})$ = estimated standard error of $\hat{\mathrm{N}}$, 95%CI = 95%-confidence interval limits, cv = coefficient of variation, $\bar{\hat{p}}$ = mean capture probabilities over all capture occasions.

	model/estimator	$\hat{\mathrm{N}}$	$\widehat{\mathrm{SE}}(\hat{\mathrm{N}})$	95%CI	cv	$\bar{\hat{p}}$
ad. males	Chao's $\mathrm{M_{th}}$	3,970	383.98	3,306-4,819	0.097	0.025
ad. females	Chao's $\mathrm{M_{th}}$	11,185	1,100.31	9,260–13,594	0.098	0.013
juveniles	Chao's $\mathrm{M_{th}}$	8,565	671.94	7,369–10,012	0.078	0.022
Total	–	23,720	1,320.59	20,797–25,974	–	–

variation of the population estimates were below 10%, indicating acceptable precision of the estimates. The large sample sizes apparently counterbalanced the above deficiencies of the data.

Estimates for adult female (including nonreproductive females) and juvenile population sizes differed by approx. 2,500 individuals (23%), but their confidence intervals overlapped (Table 4.3). The ratio of female and juvenile population sizes, $\frac{\hat{\mathrm{N}}_{\mathrm{juv}}}{\hat{\mathrm{N}}_{\mathrm{fem}}}$ is estimated as 0.766 (95%CI = 0.547–0.984). Contrasting this, the estimate for the adult males was only about a third, with non-overlapping confidence intervals (Table 4.3).

4.3.3 Swarming time

There was high individual variation of swarming time among the light-tagged bats: the period from release until emergence ranged from 40 seconds to 93 minutes. Consequently, individual variation explained 93.9% of the variance of swarming time in the highest-dimensioned model (see r^2-values in Table 4.4).

Despite this large amount of "noise", variation in swarming time could be adequately modelled by the factors SEX and AGE. The model selection results indicated that the factor AGE best explained the residual variation (Table 4.4), whereas SEX had little influence on swarming time. The relatively good support for the additive (AGE + SEX) model can be explained by the phenomenon that females swarmed slightly shorter both in adults and juveniles (Figure 4.6). We could not include the reproductive females

Tab. 4.4: Modelling the effect of sex and age on swarming time. AICc = Akaike's information criterion, small sample corrected; Δ_i = difference of AICc to the best-fitting model; w_i = normalised Akaike weight; np = number of estimated parameters; $n = 85$.

Model	r^2	AICc	Δ_i	w_i	np
AGE	0.055	19.474	0.000	0.517	3
SEX + AGE	0.061	21.192	1.718	0.219	4
NULL	0.000	22.073	2.599	0.141	2
SEX × AGE	0.061	23.405	3.931	0.072	5
SEX	0.003	24.090	4.616	0.051	3

in this analysis because their group coding does not fit into the factorial design. Estimated mean swarming times, however, were almost equal between juveniles and reproductive females (Figure 4.6). Juveniles and reproductive females spent considerably longer periods in the hibernaculum than adult males and nonreproductive females: Figure 4.6 presents unconditional estimates to demonstrate group-specific differences. Conditional on model AGE, mean swarming times, back-transformed from the logarithmic scale, were 6.3 min (95% CI = 3.2–9.3) for adults and 10.8 min (7.7–13.8) for juveniles. Reproductive females swarmed, on average, for 10.4 (7.9–12.9) min.

4.3.4 Behavioural observations

Songflight calls were never observed among swarming pipistrelles. Apart from echolocation calls, the only other call type we noticed were agonistic calls, occurring very infrequently. Likewise, feeding buzzes were never observed. Insects occur only exceptionally in small numbers in the cellar.

Light-tagged bats, after a period of a few seconds following release they needed to orientate themselves, quickly headed for sections A and B of the cellar (Figure 4.1). There, they repeatedly approached and occasionally entered crevices in the walls and subsequently extended this behaviour to the sections C and D. Sections A and B contain the largest numbers of crevices. Prior to leaving the hibernaculum, adult pipistrelles (irrespective of sex or reproductive status) directly approached the embrasure and circulated in front of it for a few seconds before emerging. Contrasting this, juveniles switched approximately 20–25 times between the embrasure and sections A or B in straight flight before they finally left the cellar. From a human viewpoint,

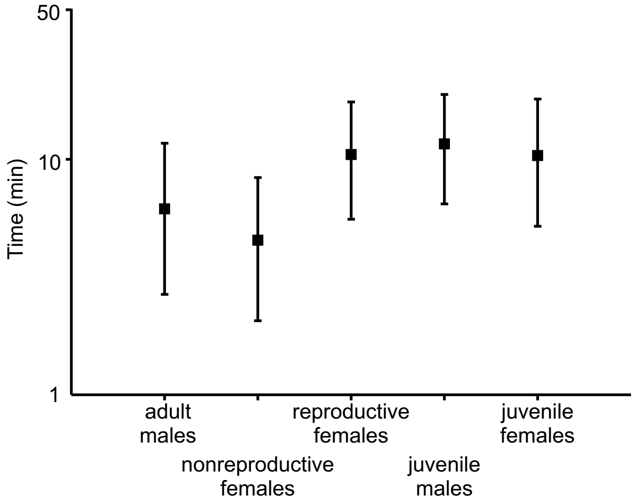


Fig. 4.6: Comparison of $\log_e$-scaled swarming times among groups of light-tagged pipistrelle bats. Error bars represent 95% confidence intervals.

this behaviour appeared as if they attempted to measure distances and to assess the dimensions of the cellar.

4.4 Discussion

The results of the present study support the maternal guidance hypothesis and contradict the mating and the feeding hypothesis: Phenology of summer swarming can be described as a unidirectional sequence of varying group dominance: adult males followed by adult females followed by juveniles. Reproductively active males played no significant role among swarming pipistrelles. The ratio of adult female and juvenile population sizes was close to unity. Mean individual swarming duration was longer in juveniles and reproductive females than in the other groups.

We found no evidence for foraging behaviour or the presence of potential prey at the swarming site. Therefore, the feeding hypothesis (Whitaker and Mumford, 1971) can be dropped; it is obviously false. The possibility that a site like the cellar in Marburg Castle could produce or attract sufficient numbers of insects to serve as a food resource appeared implausible from scratch.

4.4.1 Swarming and mating behaviour

The mating hypothesis predicted large numbers of reproductively active males to participate in summer swarming. Furthermore, it predicted longer nightly swarming times for adult males than for other groups, because prolonged presence would increase the probability to attract mates. The results from the present study contradict these predictions: Generally, adult males were increasingly absent from the hibernaculum as the mating season approached. In particular, reproductively active males were heavily underrepresented and were encountered only during a short period. These patterns were consistent across several years. Likewise, adult males swarmed for shorter periods during individual nights. Songflight calls, which are a clear indication of mate attraction (Lundberg and Gerell, 1986), were not observed. Accordingly, there is no evidence that mating plays a significant role in summer swarming of the pipistrelle bat.

4.4.2 Swarming and familiarisation with potential hibernacula

Virtually all vertebrates gain information on their environment by learning. Frequently, juveniles are assisted by their parents, a special case of social learning (Heyes and Galef, 1996). In hibernating bats, juveniles are dependent on information from conspecifics to find suitable hibernacula. Bats are highly social animals with close mother-infant relationships. On this background, Sachteleben's maternal guidance hypothesis (Sachteleben, 1991), extending Davis and Hitchcock (1965), appears plausible. Exploring unknown locations like hibernacula is time-consuming for juveniles. If mothers assist their offspring in the exploration of hibernacula, they should devote similar amounts of time to swarming like the juveniles. Other groups of individuals are not required to explore hibernacula as extensively as juveniles and therefore should spend shorter times swarming. The importance of the learning process is illustrated by the conspicuous juvenile behaviour of repeated switching between apart regions of the cellar.

Indeed, the predictions derived from the maternal guidance hypothesis were corroborated by our data: A phase of mixed occurrence of reproductive females and juveniles was followed by almost exclusive presence of the latter in August and September. The mothers-juveniles ratio (derived from estimated population sizes) is likely to be close to unity. Considering the group composition of the "adult females" (see methods section), it is likely that the mothers-juveniles ratio is closer to unity than the estimates suggest. Duration of swarming was nearly equal between juveniles and reproductive females and exceeded the swarming times of other groups. This near-equality of swarming durations and population sizes between reproductive females and juveniles represents good support for maternal guidance. Moreover, the phenological patterns suggest that this assistance is just initial and juveniles rely on themselves later on.

A potential objection to our conclusions in favour of maternally guided exploration of hibernacula might be that direct evidence for mother-infant relationships is missing. While this would be the most compelling evidence, such direct observations are hardly possible in such a complex situation like summer swarming. However, our results comply with all predictions of the maternal guidance hypothesis, of which the near-equality of swarming durations between juveniles and reproductive females represents an indirect, yet convincing evidence in favour of maternal guidance.

Maternal guidance can be interpreted as a behavioural mechanism to maximise female reproductive fitness. Generally, bats are long-lived organisms with little annual reproductive output (Kunz, 1982). Thus, females can increase their fitness by assisting their offspring in gaining information on sites that are suitable to survive the winter, the energetically most critical period in a bat's life cycle. Life histories of organisms are shaped in order to maximise reproductive success. Survival probability is the most important life history trait in long lived species, like bats (Stearns, 1992). Thus, a behaviour that increases offspring survival such as maternally assisted exploration of hibernacula will be favoured in the evolution of life histories.

4.4.3 Ecological and evolutionary implications

The results of the present study reject the mating hypothesis and suggest that maternally guided exploration of hibernacula by juveniles is the primary function of summer swarming in *Pipistrellus pipistrellus.* The two major hypotheses are not mutually exclusive, i.e. a combination of both functions could have been possible. Such a combined function actually seems to be effective in *Myotis lucifugus* (Thomas *et al.*, 1979) and *M. daubentonii* (Klawitter, 1980). These species show a promiscuous mating system. Reproductive success under promiscuity is maximised when mating takes place in large aggregations of individuals, thus providing high numbers of potential mates (Clutton-Brock, 1989). This is given in the situation of summer swarming, and consequently familiarisation with hibernacula combined with mating appears a plausible explanation.

In contrast, under a resource defence polygyny like in *P. pipistrellus*, reproductive success is maximised when males monopolise larger numbers of females in a harem. As the resource defended by male pipistrelle bats is a small territory around a mating roost (Gerell and Lundberg, 1985), summer swarming does not appear to be a suitable situation for mate attraction. Moreover, our data show that adult females participate in swarming for a relatively short period, so that potential mates are not present at the swarming site when the mating season approaches.

However, these considerations do not explain what might be the ultimate factors in the evolution of mating systems and functions of swarming. Following Clutton-Brock (1989), mating systems are outcomes of reproductive strategies of individuals rather than evolved characteristics of species. Reproductive strategies are shaped by environmental constraints. Consequently, mating systems are subject to externally induced evolutionary changes instead of acting themselves as an evolutionary factor. Thus, we need to discuss ecological factors as ultimate causes in the evolution of swarming behaviour and mating systems. *Myotis daubentonii* and *M. lucifugus* enter hibernation very early: summer swarming seamlessly turns into autumnal immigration and onset of hibernation in September (Davis and Hitchcock, 1965; Degn *et al.*, 1995; Klawitter, 1980), which restricts the length of the summerly activity period and accordingly of the mating season. The timing of the hibernal period is a result of physiological constraints and could thus be an ultimate factor to shape life histories: When time for courtship and mating is limited by a prolonged hibernal period, reproductive success in both males and females should be maximised by promiscuously mating during summer swarming.

Contrasting this, the summerly activity period of *P. pipistrellus* extends far into autumn: Immigration to hibernacula starts in November, preceded by an approx. 2-monthly gap after the swarming period (Grimmberger and Bork, 1978; Sendor *et al.*, 2000). Moreover, it is known that the mating season in the pipistrelle bat lasts until November (Gerell and Lundberg, 1985). Thus, there is no environmental or physiological constraint to force male pipistrelle bats to attract mates by participating in summer swarming. Due to the prolonged mating season, the resource defence polygyny seems to be a more effective mechanism to maximise fitness.

From the above, it seems plausible that even in species with a promiscuous mating system, mating at swarming sites has evolved on the basis of the more primordial function "familiarisation with hibernacula through maternal guidance". Mating as a primary function of summer swarming, in contrast, seems unlikely: Performance of mating at hibernacula in summer would hardly be advantageous if not based on predictable aggregations of females that have been generated by a behaviour that automatically entails such aggregations. In *M. daubentonii* and *M. lucifugus*, the temporally restricted mating season forces males to visit sites with a predictably high density of potential mates – the hibernacula where swarming is performed. As territories cannot be effectively defended in a swarming situation, evolution of promiscuity is favoured (Clutton-Brock, 1989).

Swarming of adult males early in summer is more difficult to explain. There are no obvious advantages that males might experience from summer swarming. However, participation in swarming is apparently less important for males than for the other groups, as indicated by lower numbers of captured individuals (Figure 4.2) and the smaller estimate of population size (Table 4.3). The lower male population size is not an effect of reduced survival, but of reduced recapture probabilities of males of more than one year of age (T. Sendor and M. Simon, unpublished). Hence, male swarming at established hibernacula is functionally not related to the juvenile exploratory behaviour. At this point, we should take into account that hibernacula are temporary structures on an evolutionary scale: Pipistrelle bats frequently hibernate in buildings. Buildings are raised and finally deteriorate. Even caves and mining systems, the preferred hibernation sites for many *Myotis* species, are unstable structures in the long run. Thus, as a prerequisite for the following reasoning, we assume that it is important for bats to detect and establish new hibernacula. One might suspect a pioneering function of the males in this respect. Swarming of adult males and females overlapped to a certain degree (Figure 4.3). Thus, we suppose an indicative function of male swarming with respect to newly detected hibernacula. Females are attracted by swarming males in this period and learn of potentially new hibernacula. Two ways how males benefit from swarming are imaginable: (1) Such an indicatory mechanism could serve to increase male fitness, because it can be imagined as an indirect form of parental investment (Krebs and Davies, 1993). Information of newly detected hibernacula is transferred to their potential offspring via the adult females. This would be a very diffuse form of parental investment, as it is not restricted to an individual male's offspring. However, even via this indirect way male reproductive fitness may be increased, as it is likely that eventually their offspring benefits (in terms of survival) from this information transfer. Male swarming could be an evolutionarily stable strategy (Krebs and Davies, 1993): an alternative "non-swarming" strategy is probably not stable because fitness would be reduced if hibernacula deteriorate and information on new sites is missing. (2) If females learn of new hibernacula from swarming males, they need to invest less time in searching new sites themselves. Hence, they can utilise the saved time to extend the mating period (and for accumulation of fat for hibernation). An extended female mating period (induced by male swarming) could increase male reproductive success due to an enhanced resource of mates. Admittedly, these interpretations are quite speculative at present, because our study was conducted at a well-established hibernaculum and the establishment of new hibernacula has not yet been observed. Nevertheless, they appear relatively plausible and fit into concepts of behavioural ecology.

There are too little data on further bat species with contrasting mating systems to generalise the concept we introduced with this study. Therefore, it is a future task to analyse timing of hibernation, mating systems, and patterns of summer swarming in a larger number of temperate bat species.

To summarise our discussion of the functions of summer swarming: Maternally guided exploration of hibernacula by juvenile bats is the primary function of swarming behaviour. Swarming results in predictable aggregations of adult females. Individuals of species with a temporally restricted mating period maximise their fitness by promiscuous mating in these aggregations of potential mates. In species with an extended mating season, fitness is maximised under a resource defence polygyny, which is the reason why mating does not occur during summer swarming.

4.5 Acknowledgements

We are grateful to the many people who assisted us in catching bats, too numerous to be named. The manuscript benefitted from constructive discussions with Sandra Hüttenbügel, Janna Smit, and Roland Brandl. The experiments conducted in this study comply with German conservation legislation. Capture, handling and marking of the bats was done under license of the Regierungspraesidium Giessen (Upper Nature Conservation Authority).

References

Anthony, E. L. P. (1988): Age determination in bats. In T. H. Kunz (Ed.), *Ecological and Behavioural Methods for the Study of Bats*, pp. 47–58, Washington D.C. & London: Smithsonian Institution Press.

Barlow, K. E. and G. Jones (1996): *Pipistrellus nathusii* (Chiroptera: Vespertilionidae) in Britain in the mating season. *Journal of Zoology (London)* **240**: 767–773.

Barlow, K. E. and G. Jones (1997a): Differences in songflight calls and social calls between two phonic types of the vespertilionid bat *Pipistrellus pipistrellus*. *Journal of Zoology (London)* **241**: 315–324.

Barlow, K. E. and G. Jones (1997b): Function of pipistrelle social calls: field data and a playback experiment. *Animal Behaviour* **53**: 991–999.

Barratt, E. M., R. Deaville, T. M. Burland, M. W. Bruford, G. Jones, P. A. Racey, and R. K. Wayne (1997): DNA answers the call of pipistrelle bat species. *Nature* **387**: 138–139.

Bauerová, Z. and J. Zima (1988): Seasonal changes in visits to a cave by bats. *Folia Zoologica (Brno)* **37**: 97–111.

Buckland, S. T., K. P. Burnham, and N. H. Augustin (1997): Model selection: an integral part of inference. *Biometrics* **53**: 603–618.

Burnham, K. P. and D. R. Anderson (1998): *Model Selection and Inference: A Practical Information-Theoretic Approach.* New York, Berlin, Heidelberg: Springer Verlag.

Clutton-Brock, T. H. (1989): Mammalian mating systems. *Proceedings of the Royal Society of London, Series B – Biological Sciences* **236**: 339–372.

Davis, W. H. and H. B. Hitchcock (1965): Biology and migration of the bat, *Myotis lucifugus*, in New England. *Journal of Mammalogy* **46**: 296–313.

Degn, H. J. (1987): Summer activity of bats at a large hibernaculum. In V. Hanák, I. Horáček, and J. Gaisler (Eds.), *European Bat Research*, pp. 523–526, Praha: Charles University Press.

Degn, H. J., B. B. Andersen, and H. Baggoe (1995): Automatic registration of bat activity through the year at Mønsted Limestone Mine, Denmark. *Zeitschrift für Säugetierkunde* **60**: 129–135.

Fenton, M. B. (1969): Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology* **47**: 597–602.

Gerell, R. and K. Lundberg (1985): Social organization in the bat *Pipistrellus pipistrellus. Behavioral Ecology and Sociobiology* **16**: 177–184.

Gerell-Lundberg, K. and R. Gerell (1994): The mating behaviour of the pipistrelle and the Nathusius' pipistrelle (Chiroptera) – a comparison. *Folia Zoologica (Brno)* **43**: 315–324.

Grimmberger, E. and H. Bork (1978): Untersuchungen zur Biologie, Ökologie und Populationsdynamik der Zwergfledermaus, *Pipistrellus p. pipistrellus* (Schreber 1774), in einer großen Population im Norden der DDR, Teil 1. *Nyctalus (N.F.)* **1**: 55–73.

Hall, J. S. and F. J. Brenner (1965): A behavior of bats, not related to roosting, in the use of caves in summer. *The American Zoologist* **5**: 225.

Heyes, C. M. and B. G. Galef (1996): *Social Learning in Animals: The Roots of Culture*. San Diego: Academic Press.

Horáček, I. and J. Zima (1978): Net-revealed cave visitation and cave dwelling in European bats. *Folia Zoologica (Brno)* **27**: 135–148.

Jones, G. and E. M. Barratt (1999): *Vespertilio pipistrellus* Schreber, 1774 and *V. pygmaeus* Leach, 1825 (currently *Pipistrellus pipistrellus* and *P. pygmaeus*; Mammalia, Chiroptera): proposed designation of neotypes. *Bulletin of Zoological Nomenclature* **56**: 182–186.

Jones, G. and S. M. van Parijs (1993): Bimodal echolocation in pipistrelle bats: are cryptic species present? *Proceedings of the Royal Society of London, Series B – Biological Sciences* **251**: 119–125.

Kendall, W. L. (1999): Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology* **80**: 2517–2525.

Klawitter, J. (1980): Spätsommerliche Einflüge und Überwinterungsbeginn der Wasserfledermaus (*Myotis daubentoni*) in der Spandauer Zitadelle. *Nyctalus (N.F.)* **1**: 227–234.

Krebs, J. R. and N. B. Davies (1993): *An Introduction to Behavioural Ecology*. 3rd edn., London, Edinburgh, Boston: Blackwell Scientific Publications.

Kretzschmar, F. and B. Heinz (1995): Social behaviour and hibernation of a large population of *Pipistrellus pipistrellus* (Schreber, 1774) (Chiroptera: Vespertilionidae) and some other bat species in the mining-system of a limestone quarry near Heidelberg (South West Germany). *Myotis* **32-33**: 221–231.

Kunz, T. H. (1982): *Ecology of Bats*. New York: Plenum.

Lundberg, K. and R. Gerell (1986): Territorial advertisement and mate attraction in the bat *Pipistrellus pipistrellus*. *Ethology* **71**: 115–124.

Neuweiler, G. (1993): *Biologie der Fledermäuse*. Stuttgart, New York: Georg Thieme Verlag.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson (1978): Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**: 1–135.

Racey, P. A. (1974): Ageing and assessment of reproductive status of pipistrelle bats, *Pipistrellus pipistrellus*. *Journal of Zoology (London)* **173**: 264–271.

Racey, P. A. and S. M. Swift (1985): Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *Journal of Animal Ecology* **54**: 205–215.

Rexstad, E. and K. P. Burnham (1991): Users' guide for interactive program CAPTURE. Tech. rep., Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University.

Sachteleben, J. (1991): Zum "Invasions"verhalten der Zwergfledermaus (*Pipistrellus pipistrellus*). *Nyctalus (N.F.)* **4**: 51–66.

Schober, W. and E. Grimmberger (1998): *Die Fledermäuse Europas*. 2nd edn., Kosmos Naturführer, Stuttgart: Franckh-Kosmos Verlags-GmbH & Co.

Sendor, T., K. Kugelschafter, and M. Simon (2000): Seasonal variation of activity patterns at a pipistrelle (*Pipistrellus pipistrellus*) hibernaculum. *Myotis* **38**: 91–109.

Sendor, T. and M. Simon (2000): Schätzung der Populationsgröße am Winterquartier schwärmender Zwergfledermäuse (*Pipistrellus pipistrellus*): ein Methodenvergleich. *Beiträge zur Ökologie* **4**: 43–52.

Sluiter, J. W. and P. F. van Heerdt (1966): Seasonal habits of the noctule bat (*Nyctalus noctula*). *Archives Néerlandaises de Zoologie* **16**: 423–439.

Stearns, S. C. (1992): *The Evolution of Life Histories*. Oxford, New York, Tokyo: Oxford University Press.

Thomas, D. W., M. B. Fenton, and R. M. R. Barclay (1979): Social behavior of the little brown bat, *Myotis lucifugus*. I. Mating behavior. *Behavioral Ecology and Sociobiology* **6**: 129–136.

Webb, P. I., J. R. Speakman, and P. A. Racey (1996): How hot is a hibernaculum? A review of the temperatures at which bats hibernate. *Canadian Journal of Zoology* **74**: 761–765.

Whitaker, J. O. and R. E. Mumford (1971): Notes on a collection of bats taken by mist-netting at an Indiana cave. *The American Midland Naturalist* **85**: 277–279.

Whitaker, J. O. and L. J. Rissler (1992): Seasonal activity of bats at Copperhead Cave. *Proceedings of the Indiana Academy of Science* **101**: 127–134.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis (1982): Capture-recapture and removal methods for sampling closed populations. Scientific Report LA-8787-NERP, Los Alamos National Laboratory.

5. A quantitative phenological model of summer swarming in the pipistrelle bat (*Pipistrellus pipistrellus*)

Manuscript, unpublished

Abstract

Temperate bats perform summer swarming at their hibernacula, a behaviour mainly made up of pure nocturnal flight activity that is not related to day roosting. The present study quantitatively measured swarming activity by means of a light barrier at a large hibernaculum of the European pipistrelle bat. The influence of time, temperature, and wind speed on swarming activity was estimated. Summer swarming, although reaching the expected peak levels in August, extended to times as early as April and was finished by late September. Until mid-July, swarming activity ranged at a constantly low level. The temporal course was appropriately described by fourth-order polynomial regression. Based on the polynomial function, the number of swarming bats increased with raising daily mean temperature and vice versa and was depressed by high wind speeds. Swarming at early times of the year occurred at high ambient temperatures and is explained by the flexibility of males in their decision to or not to swarm. The results conform with the hypothesis that the decision to swarm is governed by energy uptake and represents a trade-off between immediate survival and reproductive fitness.

Key Words: Automatic registration, Chiroptera, hibernacula, phenology.

5.1 Introduction

Hibernating bats of the temperate zones can be encountered at their hibernacula almost year-round (Degn *et al.*, 1995; Sendor *et al.*, 2000). In summer, pure nocturnal flight activity at the hibernacula occurs, a behaviour that is termed summer swarming (e.g. Degn, 1987; Fenton, 1969; Thomas *et al.*, 1979; Whitaker and Rissler, 1992). Also the term “fall swarming” appears in the literature (see references in Fenton, 1969), which indicates that flight activity is most frequently observed at the end of summer and in early autumn.

To study summer swarming is a difficult task. Quantification of swarming activity is usually complicated by the large number of bats chaotically flying around in a more or less cluttered environment (e.g. Kretzschmar and Heinz, 1995). Such a situation requires data recording by automatic devices (Degn *et al.*, 1995), but hibernacula are only rarely suitable for the installation of such equipment in a way that meaningful data can be obtained. Furthermore, many hibernacula are used by an assemblage of several of bat species (e.g. Bauerová and Zima, 1988; Degn *et al.*, 1995; Horáček and Zima, 1978), each with a slightly different annual life cycle and showing different behaviour, so that the resulting mixture of information severely complicates proper interpretation of the results. In the present study, I investigated the phenology of summer swarming in the pipistrelle bat, 45-kHz phonic type (*Pipistrellus pipistrellus*), at a hibernaculum almost exclusively used by this species. The unique architecture of the study site ensured sufficiently accurate monitoring of bat activity by automatic devices.

The aims of this study were to describe the intensity of summer swarming in dependence of time and to identify environmental factors that influence swarming activity. Based on more or less anecdotal results of an earlier study (Sendor *et al.*, 2000), I hypothesised temperature-dependence of swarming intensity. Furthermore, a negative effect of wind on swarming activity was suspected. Sendor *et al.* (2000) speculated that varying insect availability could determine fluctuations in swarming activity (insect availability hypothesis). I will evaluate this hypothesis and discuss the potential trade-offs involved in the bats' decision to participate in swarming.

5.2 Material and methods

5.2.1 Study site

This study was conducted between 1996 and 2000 at a large bat hibernaculum, Marburg Castle (Hesse, Germany). The castle is situated on top of a hill at about 290 m a.s.l., in the centre of the city of Marburg, on the western side of the Lahn valley. The pipistrelle bat hibernaculum is located in a vaulted cellar of this building, partially situated at ground level, measuring about 32.5 × 12.5 × 6 m ($l \times w \times h$). During winter, approx. 5000 bats hibernate in narrow crevices in the walls (3.5 to 4.5 m thick) and the ceiling, built of coarse sandstone pieces. The inside of the cellar is accessible to the bats via an embrasure. As this embrasure is the only opening that allows substantial bat movements into and out of the cellar, they can easily be monitored by automatic devices. The hibernaculum is almost exclusively used by pipistrelle bats (45-kHz phonic type).

5.2.2 Monitoring of bat activity

Bat movements were counted by a double-beam light barrier placed in the embrasure, and directly logged to an IBM-compatible computer using the software FM (Kugelschafter *et al.*, 1995). Due to its bidirectional design, the light barrier is capable of distinguishing the direction (in/out) of passes of flying objects. For a more detailed description of the equipment, refer to Kugelschafter *et al.* (1995) and Sendor *et al.* (2000). Because of the lack of other openings that would allow for significant bat movements, the light barrier counts provide a sufficiently accurate and meaningful measure of swarming activity.

5.2.3 Meteorological data

Weather data, namely temperature and wind speed, were obtained from a meteorological station located approx. 4 km south-east from the study site, that is operated by the Technical University of Darmstadt. The geographical situation of the weather station is similar to that of the castle: close to the top of a hill, at approx. 350 m a.s.l. Thus, correspondence of exposition to wind between weather station and study site was ensured. Wind data were read in hourly intervals from a Thies® anemometer. We calculated the nightly arithmetic mean of wind speeds and its variance (as a measure of the gustiness of the wind) between 22:00 h and 4:00 h, the primary swarming time.

5.2.4 Data analysis

Based on previous experience, the presumed nonlinear time-dependence of swarming activity was modelled using polynomial regression. Time was coded as integer numbers assigned to the days of the swarming period, beginning with “1” on 1^{st} May. A set of *a priori* models was specified following the hypotheses that time (t), temperature (T), wind speed (W), and variance of wind speed ($Var(W)$)influence swarming activity. With respect to wind speed, I hypothesised that the effect of this parameter could either be linear or following a pseudothreshold, i.e. that the effect changed at a constant rate to some point and then approached an asymptote. The pseudothreshold form was specified as

$$\theta = \beta_0 + \beta_1 \log_e(x + 0.5)$$

where θ is a placeholder for the parameter of interest, here the expected swarming activity. This kind of model is termed pseudothreshold because an asymptote is approached, but never reached, using the log transform. However, this can be considered a convenient approximation to a true threshold model. Zero values were accounted for by the $x+0.5$ transformation, because a discrete distribution (the light barrier counts) is appropriately described by a continuous distribution defined in $[0, \infty]$ if 0.5 is added (Yamamura, 1999). The pseudothreshold model for wind speed was considered because it seems plausible that bat activity shows an approximately linear relationship to wind speed until it is largely depressed beyond certain speeds. The expectations were that activity should increase with temperature ($\beta_T > 0$) and decrease with growing wind speed ($\beta_W < 0$).

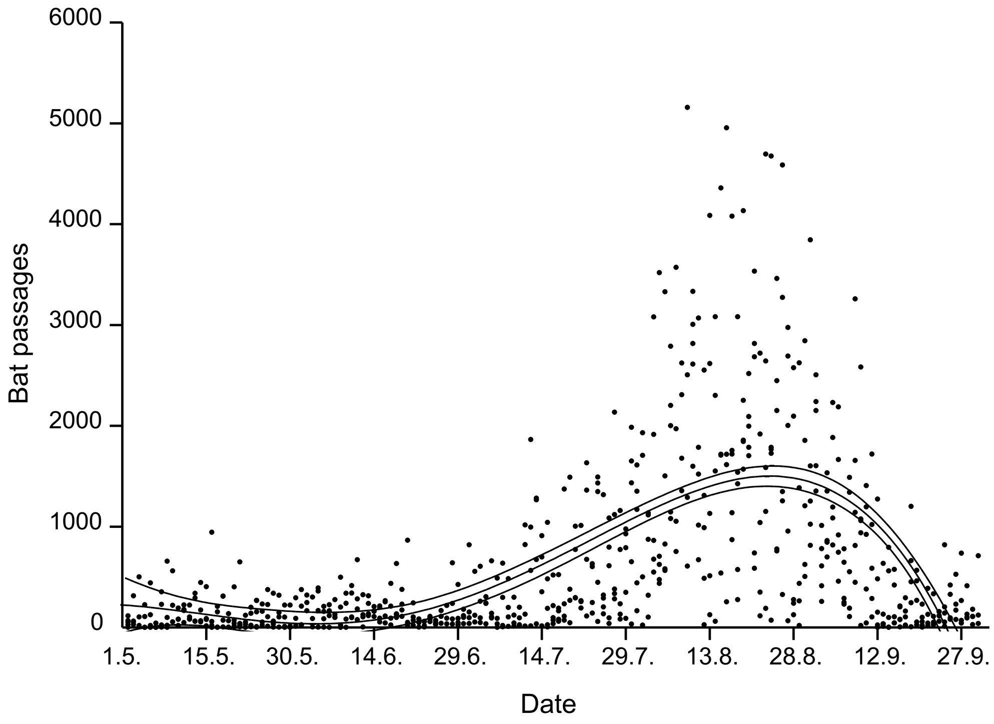


Fig. 5.1: Phenology of summer swarming: Bat passes (entries) through the embrasure at the hibernaculum "Marburg Castle" counted by a light barrier (years 1996–2000 pooled) and the fitted fourth-order polynomial with 95% confidence bands; $r^2 = 0.408$.

For model selection I used AICc, a small-sample corrected version of Akaike's information criterion (AIC Burnham and Anderson, 1998). The most parsimonious model was selected by minimizing AICc. Also ΔAICc, the difference to the model with the lowest AICc-value, and the normalised Akaike weights w_i are reported, which allow assessment of relative support among the candidate models (Buckland *et al.*, 1997).

5.3 Results

As a general pattern across all years, swarming activity remained at a relatively low level (occasionally up to 1000 entries per night) in May and June. Activity continuously increased during July until it reached maximum values in August, and then quickly declined during September. A fourth-order polynomial to describe time-dependence of swarming activity was fitted to the data. Figure 5.1 shows the observed activity values and the least-squares

Tab. 5.1: Selection and ranking of regression models relating time (fourth-order polynomial, t^4), daily mean (T_{mean}) and minimum (T_{min}) temperature, wind speed (W), and variance of wind speed ($Var(W)$) to the number of bat entries as a measure of swarming activity; AICc = Akaike's information criterion, small-sample corrected; ΔAICc = AICc difference to the best model; w_i = normalised Akaike weight of model i; K = number of estimated parameters; $n = 634$.

No.	Model	AICc	ΔAICc	w_i	K	r^2
1	$t^4 + T_{mean} + \ln(W + 0.5)$	8182.05	0.00	0.527	8	0.514
2	$t^4 + T_{mean} + W$	8182.47	0.42	0.427	8	0.513
3	$t^4 + T_{mean}$	8187.60	5.55	0.033	7	0.508
4	$t^4 + T_{mean} + Var(W)$	8189.45	7.41	0.013	8	0.508
5	$t^4 + T_{min} + W$	8207.71	25.67	0.000	8	0.490
6	$t^4 + T_{min} + \ln(W + 0.5)$	8208.83	26.79	0.000	8	0.493
7	$t^4 + T_{min}$	8219.83	37.79	0.000	7	0.482
8	$t^4 + T_{min} + Var(W)$	8221.17	39.12	0.000	8	0.483
9	t^4	8302.26	120.22	0.000	6	0.408

fitted polynomial, which appeared visually and statistically ($r^2 = 0.408$) satisfactory fit. Although a fifth-order polynomial would formally fit better to the data (lower AICc, not shown), I decided to use the former because the fifth-order function predicted negative values of swarming activity in mid-June, which is biologically meaningless (graph not shown).

The model selection results indicated that addition of temperature and wind speed variables improved model fit (Table 5.1). Daily mean temperatures (T_{mean}) provided a better description of the data than minimum (i.e. nightly) temperatures (T_{min}). Wind speed (W) was a better predictor of swarming activity than the corresponding variance, i.e. gustiness of wind played apparently no significant role. Although the gain in explained variance (r^2-values) was small after temperature dependence had been included, incorporation of wind speed resulted in clear further improvement of model fit. Formulating wind speed as pseudothreshold effect was slightly preferred: The corresponding model ($t^4 + T_{mean} + \ln(W + 0.5)$) fits approx. 1.23 times better than the linear wind speed model ($t^4 + T_{mean} + W$, Table 5.1). The corresponding regression equation is

$$\begin{aligned} E &= -517.741 - 11.027 \times t - 0.266 \times t^2 + 0.009 \times t^3 - 0.000046 \times t^4 \\ &\quad + 75.665 \times T_{mean} - 176.585 \times \ln(W + 0.5) \end{aligned}$$

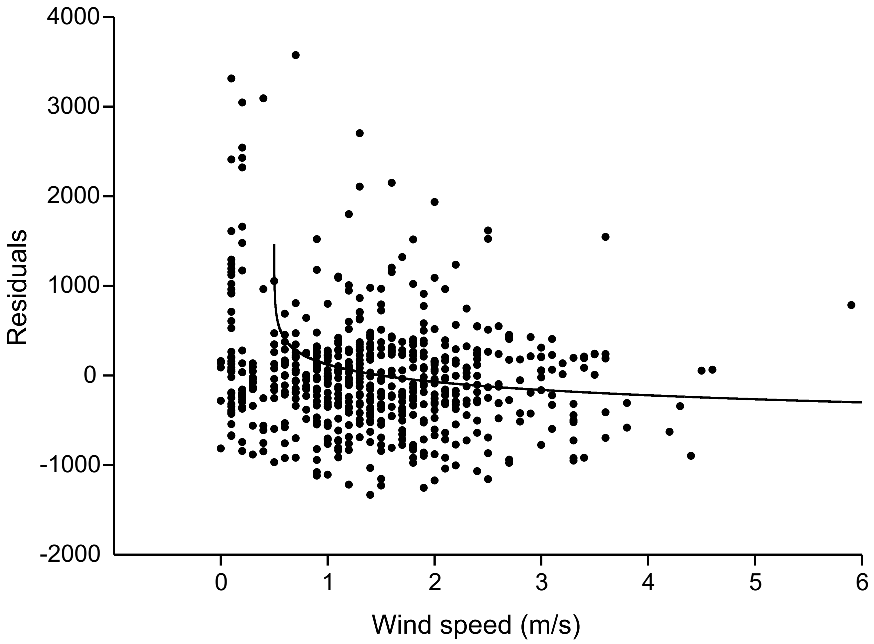


Fig. 5.2: Analysis of the residuals after fitting model t^4+T_{mean} against wind speed. The line represents the fitted pseudothreshold function from model $t^4 + T_{mean} + \ln(W + 0.5)$.

The model selection results and the estimated regression coefficients corroborated the expectations that swarming activity increased with raising temperature and was depressed by high wind speeds, with the strongest effect at speeds up to approx. 2 m × s^{-1}.

A residual analysis revealed that that wind speed did explain only a fraction of the residual variance after fitting temperature dependence (Figure 5.2). Nonetheless, wind speeds between 1 m × s^{-1} and 3 m × s^{-1} account for the majority of the negative deviations from expectations (data points below the curve). On the other hand, there were some unexpectedly high activity values (large positive residuals) at medium and low wind speeds which are consequently not related to wind and temperature. The residual variation is unevenly distributed, indicating further unexplained nonlinearities.

The predictive power of the regression model was tested by comparing model-based predictions and observed swarming activity at data points not included in the analysis: In the year 2000, late April was unusually warm, with daily mean temperatures as high as 18°C on 27th and 28th April. The complete weather data for this period are given in Table 5.2. Swarming activity varied between approx. 100 and 500 entries per night (Figure 5.3). The

Tab. 5.2: Meteorological data from late April 2000 used to predict swarming activity.

Date	T_{mean} (°C)	Wind speed ($\text{m} \times \text{s}^{-1}$)
20th Apr	12.5	2.4
21st Apr	14.0	2.6
22nd Apr	18.0	2.3
23th Apr	17.0	1.8
24th Apr	9.0	1.7
25th Apr	9.5	3.7
26th Apr	15.5	7.5
27th Apr	18.0	7.8
28th Apr	18.0	4.6
29th Apr	14.5	0.8
30th Apr	15.0	0.8

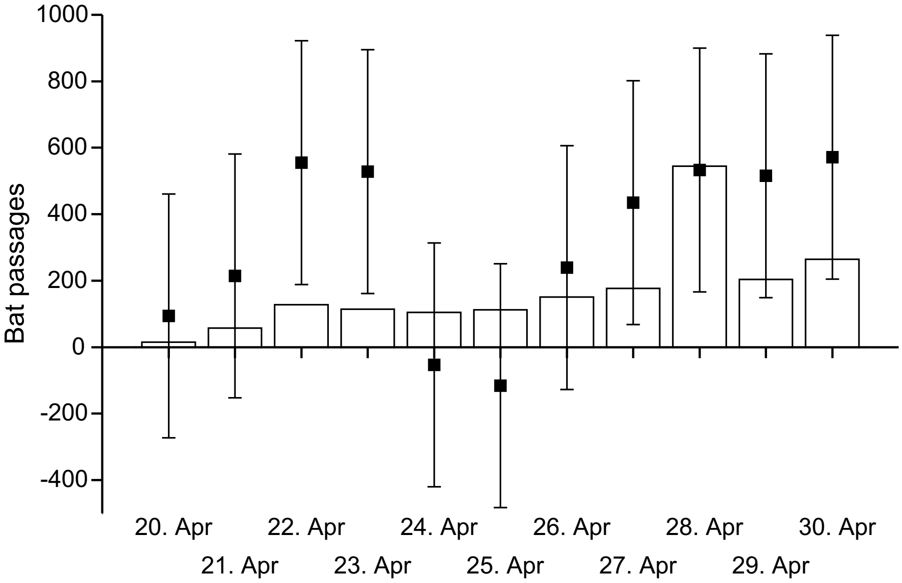


Fig. 5.3: Test of the predictive power of the summer swarming model: predicted (squares, with 95% confidence intervals) and observed (columns) values of bat entries in late April 2000.

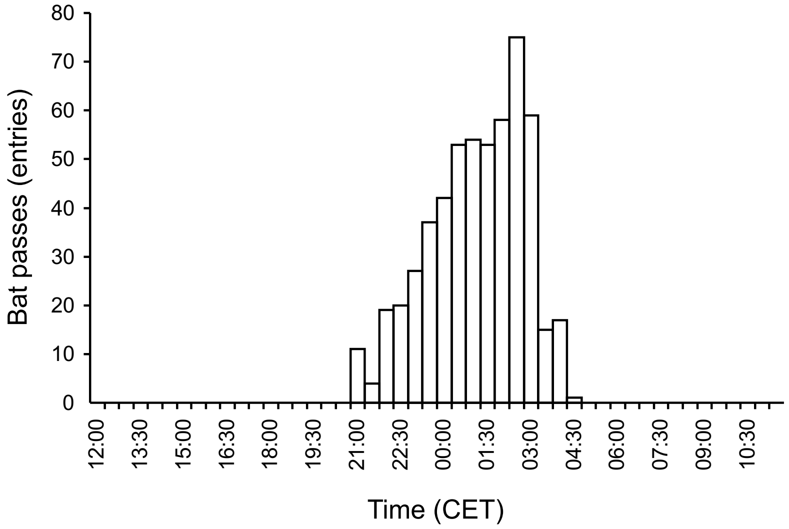


Fig. 5.4: Temporal distribution of bat activity at the hibernaculum Marburg Castle on 28th April 2000.

predictions consistently overestimated the daily bat entries (apart from two negative estimates which are biologically meaningless), but in some cases the confidence intervals covered the observed values and on 28th Apr the prediction accurately matched the observation (Figure 5.3). Both, overestimation and negative predictions can be attributed to two sources: (1) the large residual model variance, and (2) the fact that the predictions were made beyond the time scale used in the original analysis. Such extrapolations are usually not valid in regression analysis. Nevertheless, these results demonstrate that our swarming model is useful and – within certain limits – reasonably well suited to predict swarming activity at times when only meteorological data exist.

The type of activity in late April 2000 indeed can be classified as summer swarming and not, as might be supposed, delayed emergence following hibernation. The numbers of entries and exits were approximately balanced (e.g. 545 vs. 499 on 28th April; the difference is a result of counting errors). Furthermore, Sendor *et al.* (2000) demonstrated that the temporal activity distribution on a given night is symmetrical (sometimes right-skewed), centered around midnight and flat for summer swarming, while it is peaked and left-skewed (peak at dusk) for the hibernation period. The distributions from April 2000 followed the typical summer swarming pattern (Figure 5.4).

5.4 Discussion

In the present study we modelled the phenology of summer swarming at a large pipistrelle bat hibernaculum using a fourth-order polynomial regression on time. Based on this function, further analyses demonstrated that swarming activity increases with higher temperatures and is depressed at high wind speeds. With some limitation, the level of swarming activity is predictable using time and meteorological data.

A note on terminology: The number of bat passes as a measure of activity level does not directly reflect the number of individuals, as there are no means to assess the number of entries and exits per individual. Nevertheless, larger numbers of bats will inevitably lead to higher activity levels and, reversely, high activity reflects large numbers of individuals. I will not explicitly separate "activity" and "number of individuals" for the remainder of the discussion, and the reader should keep in mind that these terms are equated for convenience.

The investigated period comprised the months May to September. Previous studies have identified and consequently focused on late summer and early fall as the principal swarming period in various bat species (e.g. Davis, 1964 (cited by Fenton 1969; Fenton, 1969; Klawitter, 1980; Lesiński, 1987; Mumford and Whitaker, 1975; Thomas *et al.*, 1979; Whitaker and Rissler, 1992). The current results confirm the period between late July and mid-September as the time of most extensive swarming activity in the pipistrelle bat. This also conforms with the findings of Grimmberger and Bork (1978) who, however, have erroneously associated summer activity of pipistrelles at the investigated hibernaculum with "roosting" because their methods only allowed to determine the presence but not the movements of bats. Moreover, swarming activity occurred during the entire study period. In one year with an unusually warm spring, it even started in the final decade of April, what was also predicted by the regression model. The fact that summer swarming is extended until mid-spring seems surprising at a first glance. However, this finding should be quite plausible if we acknowledge that the components of a bat's annual life cycle – such as summer swarming – are subject to considerable variation as a result of a variable environment, as underlined by the suggested temperature-dependence. I will discuss this topic in detail below. Timing of summer swarming as early as mid-May and June – also recorded by means of automatic registration – was first reported by Degn *et al.* (1995) of *Myotis daubentonii* and *M. nattereri.* A study parallel to the present one demonstrated that the swarming population in August and September is predominantly made up of large numbers of juveniles and, in early August, reproductive females (Chapter 4). Consequently, these groups account for the midsummer peak. Earlier in the summer, the swarming population is almost exclusively formed by adult males (also see Grimmberger and Bork, 1978). Thus, swarming activity of male pipistrelles is less intensive and can occur at almost any time between late April and late July. Here, I will not discuss the functional significance of this behaviour, and refer the reader to Chapter 4.

The present study suggests that the timing of summer swarming is partly determined by ambient temperature. In a previous study, Sendor *et al.* (2000) already described apparent parallelism between changes in swarming activity and ambient temperature, contrasting the findings of Grimmberger (1979). Analogous to Maier (1992) who found longer absence of female pipistrelle bats from their summer roosts at higher temperatures, Sendor *et al.* (2000) concluded that the presumed association between temperature and swarming could be attributed to increased insect availability at higher temperatures: Increased food supply leads to more rapid feeding success and hence to an enlarged time budget for greater numbers of bats who may then participate in summer swarming. However, these conclusions were rather speculative as they were founded on a merely descriptive single-year data set. The present results allow a more rigorous evaluation of the insect availability hypothesis: T_{mean} performed better as a predictor for swarming activity than T_{min} and there was still a lot of unexplained, apparently nonlinear variance even after incorporation of wind speed. If swarming activity was a mere quasi-heterothermic, i.e. physiological, reaction to nightly temperatures we should have expected T_{min} to be the better predictor because of its temporal coincidence with the bats' activity period. However, as flight activity of insects at dusk is more likely to be influenced by daily mean instead of nightly minimum temperatures, the insect availability hypothesis provides a plausible explanation for the observed temperature-swarming relationship. The relationship between ambient temperature and density of flying insects has frequently been suggested (e.g. Bursell, 1974; Tobias and Tobias, 1968). Correlations between insect availability and bat activity – in the context of foraging – have been demonstrated by, e.g., Racey and Swift (1985), Rautenbach *et al.* (1996), Swift (1980), and Swift *et al.* (1985). Insect availability may also explain the large amount of residual variation in the temperature-swarming relationship: Insect abundance, and consequently summer swarming, may show a retarded reaction to abrupt changes in temperature.

In the context of the insect availability hypothesis it seems plausible that summer swarming may occur as early as April: If temperatures, and consequently food supply, are high enough to outweigh an individual's energy requirements, the excess energy and time budgets may be invested in summer swarming. In the paper on the function of summer swarming (Chapter 4), swarming of males has been discussed as a mechanism to detect potentially new hibernacula and to transfer this information to their potential offspring via the intermediate step of the adult females. Thus, as swarming is energetically costly, the decision to or not to swarm after foraging can be regarded as a trade-off between immediate survival (forage and return to the summer roost) and reproductive fitness (gather information on hibernation sites from which potential offspring may benefit). The amount of energy, i.e. food, received on a given night may serve as a criterion for this decision. As males are, unlike females, energetically not constrained by breeding (Burnett and August, 1981; Kurta *et al.*, 1987; Kurta and Kunz, 1988; Wilkinson and Barclay, 1997), they may decide to swarm at virtually any time between spring and the onset of the mating season (mid-August). Clearly, as all bats need to recover energy reserves after the end of hibernation, we may not expect the onset of summer swarming before, say, mid-April.

Wind speed had a negative influence on bat activity in this study. An analogous effect has already been demonstrated in foraging and commuting bats (Verboom and Spoelstra, 1999), supposedly caused by decreased insect density due to wind, as well as by a direct negative effect on bat manoeuvrability. Both effects could also play a role in the wind influence on swarming. Insect availability might be involved in an analogous manner as discussed for temperature-dependence. A direct wind effect on bat activity, e.g. on the commuting flights between summer roosts and the swarming site, would conform with the pseudothreshold function used in the present study. However, as this relationship is relatively weak and a linear wind effect was almost equally supported as the pseudothreshold it is not useful to continue speculations about the exact type of wind impact.

Although two important environmental factors that influence the level of swarming activity have been identified, there is still a considerable amount of unexplained variation. One possible explanation for unexpectedly low activity in midsummer could be precipitation. Clearly, there was a small number of nights during this study when rainfall lead to a drop of activity close to zero. However, I did not include precipitation data in the analysis since nightly rainfall was a rare event and the gain of information would presumably be negligible. Furthermore, the residual analysis shows that the most severe deviations from expectations were positive. Precipitation cannot be expected to provide a useful explanation for this. Thus, in conclusion, the relationships found in this study are useful to describe the most important ecological factors that influence the phenology of summer swarming, but there are probably further nonlinear effects, too complex to grasp analytically.

Clearly, the results of the present study are restricted in the sense that the model coefficients and the observed activity levels are specific to the hibernaculum at Marburg Castle. Nevertheless, as a comparison with Grimmberger and Bork (1978) shows, the processes described by our model can generally be applied to summer swarming in the pipistrelle bat.

5.5 Acknowledgements

The equipment for this study was partially funded by the "Stiftung Hessicher Naturschutz". T.S. was supported by doctoral grant of the "Hessische Graduiertenförderung". I further thank Markus Kaempf and Tilman Holfelder for providing the weather data. Sandra Hüttenbügel and Roland Brandl made constructive comments on the manuscript.

References

Bauerová, Z. and J. Zima (1988): Seasonal changes in visits to a cave by bats. *Folia Zoologica (Brno)* **37**: 97–111.

Buckland, S. T., K. P. Burnham, and N. H. Augustin (1997): Model selection: an integral part of inference. *Biometrics* **53**: 603–618.

Burnett, C. D. and P. V. August (1981): Time and energy budgets for dayroosting in a maternity colony of *Myotis lucifugus*. *Journal of Mammalogy* **62**: 758–766.

Burnham, K. P. and D. R. Anderson (1998): *Model Selection and Inference: A Practical Information-Theoretic Approach.* New York, Berlin, Heidelberg: Springer Verlag.

Bursell, E. (1974): Environmental aspects – temperature. In M. Rockstein (Ed.), *The Physiology of Insecta*, vol. II, 2nd edn., p. 568, New York, London: Academic Press.

Davis, W. H. (1964 (cited by Fenton 1969)): Fall swarming of bats at Kentucky caves. *Bulletin of the National Speleological Society* **26**: 82–83.

Degn, H. J. (1987): Summer activity of bats at a large hibernaculum. In V. Hanák, I. Horáček, and J. Gaisler (Eds.), *European Bat Research*, pp. 523–526, Praha: Charles University Press.

Degn, H. J., B. B. Andersen, and H. Baggoe (1995): Automatic registration of bat activity through the year at Mønsted Limestone Mine, Denmark. *Zeitschrift für Säugetierkunde* **60**: 129–135.

Fenton, M. B. (1969): Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology* **47**: 597–602.

Grimmberger, E. (1979): Untersuchungen über den Einfluß klimatischer Faktoren auf das Verhalten der Zwergfledermaus, *Pipistrellus pipistrellus* (Schreber 1774), im Winterquartier und während der sogenannten Invasionen. *Nyctalus (N.F.)* **1**: 145–157.

Grimmberger, E. and H. Bork (1978): Untersuchungen zur Biologie, Ökologie und Populationsdynamik der Zwergfledermaus, *Pipistrellus p. pipistrellus* (Schreber 1774), in einer großen Population im Norden der DDR, Teil 1. *Nyctalus (N.F.)* **1**: 55–73.

Horáček, I. and J. Zima (1978): Net-revealed cave visitation and cave dwelling in European bats. *Folia Zoologica (Brno)* **27**: 135–148.

Klawitter, J. (1980): Spätsommerliche Einflüge und Überwinterungsbeginn der Wasserfledermaus (*Myotis daubentoni*) in der Spandauer Zitadelle. *Nyctalus (N.F.)* **1**: 227–234.

Kretzschmar, F. and B. Heinz (1995): Social behaviour and hibernation of a large population of *Pipistrellus pipistrellus* (Schreber, 1774) (Chiroptera: Vespertilionidae) and some other bat species in the mining-system of a limestone quarry near Heidelberg (South West Germany). *Myotis* **32-33**: 221–231.

Kugelschafter, K., T. Horvath, W. Kimpel, G. Steffny, and T. Volk (1995): Neue Techniken zur Überwachung von Fledermäusen. In M. Stubbe, A. Stubbe, and D. Heidecke (Eds.), *Methoden feldökologischer Säugetierforschung*, vol. 1, pp. 373–382, Halle/Saale: Martin-Luther-Universität Halle-Wittenberg.

Kurta, A., K. A. Johnson, and T. H. Kunz (1987): Oxygen consumption and body temperature of female little brown bats (*Myotis lucifugus*) under simulated roost conditions. *Physiological Zoology* **60**: 386–397.

Kurta, A. and T. H. Kunz (1988): Roosting metabolic rate and body temperature of male little brown bats (*Myotis lucifugus*) in summer. *Journal of Mammalogy* **69**: 645–651.

Lesiński, G. (1987): Summer and autumn dynamics of *Myotis daubentoni* in underground shelters in central Poland. In V. Hanák, I. Horáček, and J. Gaisler (Eds.), *European Bat Research*, pp. 519–521, Praha: Charles University Press.

Maier, C. (1992): Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in Oxfordshire. *Journal of Zoology (London)* **228**: 69–80.

Mumford, R. E. and J. O. Whitaker (1975): Seasonal activity of bats at an Indiana cave. *Proceedings of the Indiana Academy of Science* **84**: 500–507.

Racey, P. A. and S. M. Swift (1985): Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *Journal of Animal Ecology* **54**: 205–215.

Rautenbach, I. L., M. B. Fenton, and M. J. Whiting (1996): Bats in riverine forests and woodlands: a latitudinal transect in southern Africa. *Canadian Journal of Zoology* **74**: 312–322.

Sendor, T., K. Kugelschafter, and M. Simon (2000): Seasonal variation of activity patterns at a pipistrelle (*Pipistrellus pipistrellus*) hibernaculum. *Myotis* **38**: 91–109.

Swift, S. M. (1980): Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *Journal of Zoology (London)* **190**: 285–295.

Swift, S. M., P. A. Racey, and M. I. Avery (1985): Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. Diet. *Journal of Animal Ecology* **54**: 217–225.

Thomas, D. W., M. B. Fenton, and R. M. R. Barclay (1979): Social behavior of the little brown bat, *Myotis lucifugus*. I. Mating behavior. *Behavioral Ecology and Sociobiology* **6**: 129–136.

Tobias, W. and D. Tobias (1968): Zur Schlüpfperiodik innerhalb der Gattung *Potamophylax* Wallengren (Trichoptera, Limnephilidae). *Oikos* **19**: 396–399.

Verboom, B. and K. Spoelstra (1999): Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. *Canadian Journal of Zoology* **77**: 1393–1401.

Whitaker, J. O. and L. J. Rissler (1992): Seasonal activity of bats at Copperhead Cave. *Proceedings of the Indiana Academy of Science* **101**: 127–134.

Wilkinson, L. C. and R. M. R. Barclay (1997): Differences in the foraging behaviour of male and female big brown bats (*Eptesicus fuscus*) during the reproductive period. *Ecoscience* **4**: 279–285.

Yamamura, K. (1999): Transformation using $(x{+}0.5)$ to stabilize the variance of populations. *Researches on Population Ecology* **41**: 229–234.

6. Ecology of hibernating pipistrelle bats: microclimate, mass loss, and implications for hibernal roost switching and energetics

Manuscript, unpublished

Abstract

This study aimed to investigate an aspect of the hibernal ecology of the pipistrelle bat that has so far received little attention: the significance of hibernal roost switching, as observable at so-called mass hibernacula. Flight activity also occurred below the freezing point: The number of individuals immigrating to the large hibernaculum “Marburg Castle” in early winter was partially explained by frost. In the second half of the winter, immigration continued at low temperatures, while emigration occurred as soon as the weather became mild. Extensive movements to and from the hibernaculum occurred at any time of the winter. Although the inside of the hibernaculum is thermally buffered against the environment, inside temperatures immediately respond to fluctuations of ambient temperatures, which the pipistrelle bats obviously use as a cue to predict a good point of time for emigration. The bats lost body mass at rates between approx. 13 and 20 mg × d^{-1} (depending on the method), irrespective of sex, age, and year. The hibernaculum is characterised by low humidities. Theoretical predictions of evaporative water loss exceeded the measured mass losses by almost the factor 10. Thus, pipistrelle bats are apparently adapted to low humidities. Simple deterministic scenarios of energy expenditure revealed that roost switching, although energetically costly, has a relatively small effect on the hibernal energy budget, while the metabolic rate in deep hibernation largely determines how long a bat can survive without feeding. As the mass losses estimated in the present study were far lower than those previously reported, it is quite possible that the energy demands of hibernating pipistrelle bats have been overestimated. Hibernal roost switching, in contrast, does not collide with the necessity to save energy.

Key Words: Chiroptera, energetics, hibernacula, hibernation, winter activity.

6.1 Introduction

In adaptation to the energetic challenge caused by low temperatures and reduced food availability during winter, most bats of temperate latitudes hibernate (e.g. Davis, 1970). The fact that pipistrelle bats can regularly be observed flying outside their hibernacula during winter (e.g. Avery, 1985, and references therein) has raised questions about the ecological function and energetic consequences of this behaviour. While Avery (1985) stated that pipistrelle bats need to feed to compensate the fat loss resulting from hibernation, Speakman and Racey (1989) convincingly demonstrated that the more likely function of winter emergence flights is to drink.

Nevertheless, there are still conflicting results about the energy demands of bats in hibernation. After Speakman and Racey (1989), pipistrelle bats still would starve if they do not feed within the hibernation period. Specifically, the published estimates of the energy requirements in deep hibernation (Speakman and Racey, 1989; Speakman *et al.*, 1991) exceed corresponding estimates for other species, like *Myotis lucifugus*, by almost the factor 10 (cf. Hock, 1951; Thomas *et al.*, 1990b). Particularly with respect to their small size, and consequently their restricted fat reserves (body mass approx. 5–6 g), the question arises how pipistrelle bats manage to survive the winter if their energy demands are actually so large. Also the water balance, particularly evaporative water loss (EWL) is an important aspect of hibernation (Davis, 1970; Speakman and Racey, 1989; Thomas and Cloutier, 1992). This applies particularly to the pipistrelle bat, whose hibernacula seem to be unusually dry (Haagen and Arnold, 1955; Racey, 1974b). While Speakman and Racey (1989) have demonstrated the fundamental importance of access to water under laboratory conditions, the water balance of pipistrelle bats in natural hibernacula is largely unexplored.

Like all hibernators, bats periodically arouse from hibernation (Brack and Twente, 1985; Davis, 1964; Lyman *et al.*, 1982; Menaker, 1964; Thomas *et al.*, 1990b). Arousals are energetically costly: they account for more than 75% of the total energy expenditure of hibernation (Thomas *et al.*, 1990b). Arousals are apparently associated with hibernal flight activity, predominantly reported as “internal migration” within hibernacula (Dorgelo and Punt, 1969; Hardin and Hassel, 1970; Kuipers and Daan, 1970). Beyond that, pipistrelle bats appear to perform extensive hibernal roost switching (Sendor *et al.*, 2000), but these findings are preliminary and still require confirmation on a broader data basis. Also flight activity is energetically costly (Thomas and Suthers, 1972). Thus, one should expect that extensive hibernal roost switching faces pipistrelle bats with severe problems in achieving energy balance. Solutions to this apparent dilemma would either lead to a higher rating of the significance of winter feeding – in agreement with Avery (1985) – or require a reevaluation of the energy demands in deep hibernation.

Pipistrelle bats are known to occasionally form so-called mass hibernacula, comprising up to several thousand individuals (Dumitresco and Orghidan, 1963; Grimmberger and Bork, 1978; von Helversen *et al.*, 1987; Lustrat and Julien, 1997). The number of hibernating bats underlines the biological significance of these sites. Furthermore, they provide an excellent opportunity to investigate the processes involved in hibernation.

The aims of this study were to assess the importance of hibernal roost switching at a hibernaculum used by more than 5,000 pipistrelle bats (Sendor *et al.*, 2000), specifically to describe its microclimate and the dynamics of the hibernal population in relation to relevant environmental variables, to estimate mass loss rates during hibernation, to evaluate the significance of evaporative water loss under the given microclimate, and to evaluate their consequences for energy balance and for surviving the winter.

6.2 Material and methods

6.2.1 Study site

This study was conducted at a large bat hibernaculum, Marburg Castle (Hesse, Germany). The castle is situated on top of a hill at about 290 m a.s.l., in the centre of the city of Marburg, on the western side of the Lahn valley. The site is almost exclusively used by pipistrelle bats of the 45-kHz phonic type. The pipistrelle hibernaculum is located in a vaulted cellar of this building, partially situated at ground level, measuring about 32.5 × 12.5 × 6 m ($l \times w \times h$). During winter, the bats roost in narrow crevices in the walls (3.5 to 4.5 m thick) and the ceiling, built of coarse sandstone pieces. The only relevant possibility for the bats to enter and leave the cellar is an embrasure of approx. 1.2 m height and 0.25 m width.

6.2.2 Microclimate and weather data

Temperature and relative humidity were continuously monitored using a custom-made data logger (G. Steffny, Gießen, Germany). Both parameters of microclimate were simultaneously measured in the open air space of the cellar as well as in a typical crevice used by the bats for hibernation. By the placement of the sensors the complete range of microclimatic conditions the bats may encounter is covered. The humidity sensors were temperature compensated. Due to equipment failure, the microclimate data are not continuous. However, as data were recorded under all relevant winter weather conditions, they describe the microclimate of the hibernaculum sufficiently well.

Temperature data were obtained from a weather station located within the municipal area of Marburg, about 4.5 km south-east from the study site, that is operated by the Technical University of Darmstadt. Barometric pressure was read from the weather station “Hünstein”, 17 km west of Marburg.

All weather and microclimate data are presented as daily mean values.

6.2.3 Analysis of hibernal population dynamics

Due to the fact that no other flight paths that the bats could use to enter and leave the hibernaculum exist, the corresponding bat movements could be reliably monitored using a light barrier placed in the embrasure. The double-beam light barrier is capable of distinguishing the direction (in/out) of passing objects. All detected movements were directly logged to an IBM-compatible computer using the software FM (Kugelschafter *et al.*, 1995), which was also used for basic data analysis. Kugelschafter *et al.* (1995) also provide a more detailed description of the technical equipment. The day-to-day dynamics of the hibernal population was monitored by substracting the daily counts of bat exits from the entries. Light barrier and weather data from the winters 1995/96 to 1999/2000 were used for this analysis. The potential influence of various weather variables was analyzed by correlation and regression analysis. The following working hypotheses regarding the dynamics of the hibernal population – and combinations of the corresponding factors – were assessed:

1. The number of immigrating bats (a) varies with ambient temperature vs. (b) follows a purely circannual pattern.

2. As the inside of the hibernaculum is more or less buffered against variations of ambient temperature, there are three possible mechanisms that could aid the pipistrelle bats to determine the optimal schedule to leave hibernation and to emigrate:

   (a) emigration follows a completely circannual pattern (unlikely, as a coincidence of waves of emigration and ambient temperature has already been demonstrated by a preliminary study (Sendor *et al.*, 2000));

   (b) the small variations of temperature in the crevices suffice as a cue in the decision to or not to emigrate;

   (c) pipistrelle bats use fluctuations of barometric pressure to predict good conditions for emergence from the hibernaculum.

Accordingly, the light barrier balances were related to the day-to-day changes of crevice temperatures, and barometric pressure as explanatory variables. Time was considered as a linear and a quadratic effect. The latter corresponds to the hypothesis that there is a period of maximum emigration. The origin of the time axis in the analysis of both, the immigration and the emigration process, was set to the 31st October, so that the hibernation period began on 1st November (day no. 1).

6.2.4 Body mass dynamics

In the winters 1996/97 to 1999/2000 pipistrelle bats were caught during the entire hibernation period using mist nets. The bats were caught close to the embrasure when they attempted either to enter or to leave the hibernaculum. The capture sessions took place soon after dusk, around the pipistrelles' activity peak (Sendor *et al.*, 2000) and lasted two hours. As only actively flying bats were handled, disturbance was kept at a minimum. The pipistrelles were sexed, aged, and weighed to the nearest 0.1 g. They were individually marked with numbered alloy bands of sizes H and M (2.4–2.9 mm diameter) attached to the forearm and released immediately after the end of the respective capture session. Age determination was unambiguous in individuals that had already been marked as juveniles in the previous summer. Sometimes even unmarked individuals could be aged, when unfused phalangeal epiphyses were still visible (Anthony, 1988). Likewise, males with a pigmented *tunica vaginalis* (Racey, 1974a) were classified as juveniles, while this was impossible in the females.

Capture, handling and marking of the bats was done under license of the Regierungspräsidium Giessen (Upper Nature Conservation Authority). Bat bands were obtained from the Museum Alexander Koenig, Bonn.

Body mass dynamics on the basis of all captured bats was analyzed using analysis of covariance (ANCOVA) with sex, age, and year as fixed factors, time (no. of days since 1st Nov) as a continuous covariate and body mass as the response variable. This design corresponded to the working hypotheses that starting weights (intercepts with the y-axis) and mass loss rates (slopes) differed among sexes, age classes and years or were common to various combinations of factors and covariates. Parallelism between regression lines was tested by considering a model with all interactions.

Likewise, mass loss of individuals that were caught at least twice in a given winter was estimated by dividing their mass difference by the number days between the two captures. The resulting individual mass loss rate was used as the response variable in an ANCOVA in order to test if it was influenced by year, age, sex (fixed factors), date of first capture, and mass at first capture (continuous covariates).

Furthermore, I used and reanalyzed a data set produced by S. Schweizer (Schweizer, Sendor and Simon, in prep.) that describes the mass loss of known individuals in continuous hibernation on a day to day basis: In the 1998/99 capture period a number of pipistrelle bats were placed in small wooden boxes. Those individuals who accepted the boxes as a roost and fell into hibernation were regularly weighed to the nearest 0.01 g using a laboratory balance until they left their box. Consequently, these data describe the mass loss of pipistrelle bats in continuous hibernation, ensuring that no mass gain either from drinking or feeding occurred. I used these data, among other, to develop scenarios in order to predict energy demands and evaporative water loss (see below) under the climatic conditions provided by the study site.

6.2.5 Evaporative water loss

Thomas and Cloutier (1992) found that evaporative water loss (EWL) in little brown bats (*Myotis lucifugus*) was independent of temperature and body mass, but directly related to the difference in water vapour pressure (ΔWVP) between tissue surfaces and atmosphere. The estimated relationship for EWL ($\mathrm{mg\ H_2O} \times \mathrm{bat}^{-1} \times \mathrm{d}^{-1}$) was

$$\mathrm{EWL} = 376.3 \times \Delta\mathrm{WVP\ (kPa)} \tag{6.1}$$

I used this equation to test if *P. pipistrellus* behaves like *M. lucifugus* with respect to EWL. If the hypothesis of equal EWL rates is true, this equation should reliably predict EWL also in the pipistrelle bats as the two species are of comparable body size (Thomas *et al.*, 1990b). I calculated the WVP conditions for bats roosting in open air space and crevices, respectively, using the microclimate data (temperature and relative humidity) and the WVP table in Lide (1999). Temperature values were rounded to the nearest integer °C to conform with the WVP table. With the resulting ΔWVP values EWL was predicted using equation 6.1.

6.2.6 Scenarios of energy expenditure

In the present study, I did not aim at obtaining direct estimates of energy expenditure. Instead, by calculating simple deterministic scenarios I assessed the effects of varying frequencies of winter activity and levels of energy expenditure in hibernation on the energy budget and on the chance to survive the winter. Energy demands for various combinations of arousal frequencies, body mass, and energy expenditure in deep hibernation were estimated using data from the literature and the weight loss rates of the pipistrelles in continuous hibernation (boxes) in their natural habitat. The complete hibernal metabolism was assumed to be exclusively based on fat. Energy demands are reported as the amount of fat required for the complete hibernal period under the respective scenario. Fat amounts were calculated from energy expenditure assuming that 1 g of fat releases 39.3 J energy (Schmidt-Nielsen, 1997). If the original data have been reported as oxygen consumption, they were transformed into energy sums under the assumption that 1 ml O_2 releases 20.1 J.

The heating phase of each arousal cycle was assumed to last 45 min and to require 86.6 $\mathrm{J} \times \mathrm{g}^{-1}$ (Thomas *et al.*, 1990b). This conforms with observed durations of the heating phase of pipistrelle bats at Marburg Castle (S. Schweizer, unpublished thesis). Each arousal cycle in the scenarios comprised flight activity of $\frac{1}{2}$ h. This seems a reasonable value required for roost switching and drinking, as alternative hibernacula and open water are available within a distance of a few hundred metres (Smit-Viergutz and Simon, 2000). Flight requires a power of 1.43 W in pipistrelle bats, independent of body mass (Speakman and Racey, 1991). Costs of re-entry into hibernation have been estimated as 67.2% of heating (Thomas *et al.*, 1990b), corresponding to a cooling time of 30 min. The observation that captured pipistrelle bats regularly became torpid within half an hour (personal observation) conforms with this assumption. No periods of homoeothermy at rest were included in the arousal cycles. Again, this conforms with the observations of quick re-entry into torpor and that pipistrelle bats flew off immediately at the end of the heating phase. Accordingly, an arousal cycle was assembled of 45 min heating phase, 30 min flight and 30 min cooling.

In the calculations of energy demands for the hibernation bouts temperature was ignored because hibernal metabolism in the pipistrelle bat seems, in contrast to other species, to be independent of temperature in the range of 4–10°C (Speakman *et al.*, 1991). I calculated three types of scenarios by varying the assumed metabolic rate in continuous hibernation. The scenarios are named after the locations where the respective studies were conducted:

1. **Aberdeen**. Direct estimates of energy expenditure of pipistrelle bats in hibernation range between approx. 0.16 and 0.23 ml $\times$ g^{-1} $\times$ h^{-1} (Speakman and Racey, 1989; Speakman *et al.*, 1991). In this scenario, the more optimistic value of 0.16 was used.

2. **Quebec**. This scenario assumed a rate of oxygen consumption of 0.02 ml $\times$ g^{-1} $\times$ h^{-1}, as reported for *M. lucifugus* by Thomas *et al.* (1990b).

3. **Marburg**. Energy expenditure in natural hibernation was estimated from the weight loss rates of the pipistrelle bats in the boxes, taking into consideration evaporative water loss (see results section), and used as the basis for this scenario.

6.2.7 Model selection

For model selection among a set of several candidate models, corresponding to multiple working hypotheses (Anderson *et al.*, 2000), I used Akaike's information criterion (AIC, Burnham and Anderson, 1998). The most parsimonious model was selected by minimising AICc, a small-sample corrected version of AIC (Anderson *et al.*, 2000; Burnham and Anderson, 1998). Furthermore, ΔAICc, the simple difference to the best model, and the relative Akaike weight w_i are reported. These allow the models to be ranked and their relative support among the set of the candidate models to be assessed (Buckland *et al.*, 1997).

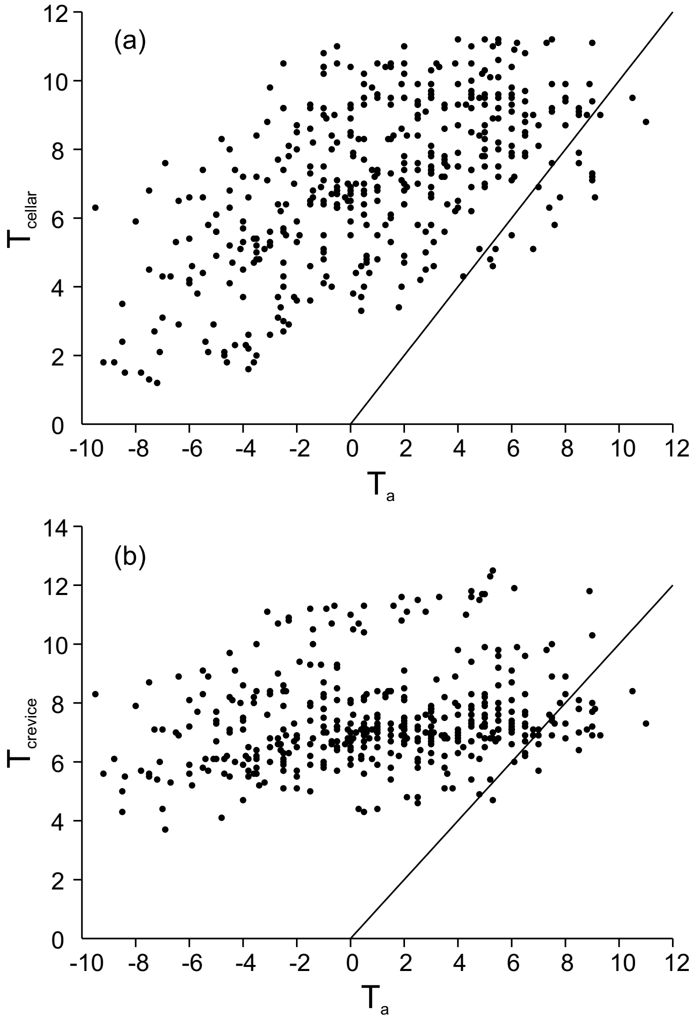


Fig. 6.1: Relationship of temperatures in the open air space of the hibernaculum (a; $r = 0.590$; $p < 0.01$; $n = 430$) and in a typical roost crevice (b; $r = 0.217; p < 0.01; n = 444$) to ambient temperatures, respectively. The line of temperature equivalence ($T_a = T_{inside}$) is shown in both subfigures.

6.3 Results

6.3.1 Microclimate

The temperatures inside the hibernaculum varied between approx. 1°C and 11°C with a median of 7.3°C (open air space, Fig. 6.1a) and 3.5°C and 13°C (roost crevice, median = 7.1°C, Fig. 6.1b), respectively. Both were related to ambient temperature. The inside of the hibernaculum is thermally buffered against the environment (the crevices more than the open air space), which is reflected by the finding that the slopes were less steep than the line of temperature equivalence. The thermal buffering also resulted in a retarded response in fluctuations of inside to ambient temperatures, which precipitated in the large variation, particularly of T_{cellar} (Fig. 6.1).

Relative humidity in the open air space of the cellar varied between 36 and 90% (median = 60.0%) and was closely related to ambient temperature (Fig. 6.2a). The crevice was generally more humid (median = 93.8%), but humidity values also fell close to 50% at low T_a (Fig. 6.2b). However, there was no strong correlation to ambient temperature due to the temporal delay, similar to the buffering effect in the case of temperature. Consequently, short-term drops of T_a even to very low values had only a negligible effect on humidity. This effect is also the reason for the obvious clusters of data points, as different courses of T_a in various winters lead to different responses of humidity.

The variation of temperatures and humidities presented here represents the range of environmental conditions pipistrelle bats may encounter during hibernation at Marburg Castle. Most bats hibernate deep in the crevices, thus under quite stable conditions. However, a few hundred individuals can be seen roosting close to the surface of the walls, who are consequently exposed to more variable, in mid-winter colder and drier conditions.

6.3.2 Immigration and emigration dynamics of the hibernal population

Immigration regularly began around 15th November and the hibernal population approached maximum values around the turn of the year. The exact onset of immigration depended on the occurrence of frost. Likewise, low temperatures were associated with high immigration rates and vice versa. This correlation was significant but weak (correlation of $\log_e$ of positive light barrier balances to ambient temperature: $r = -0.203$; $p < 0.01$; Fig. 6.3). It was not possible to determine a more accurate mathematical description of the immigration process. Obviously, there are too complex nonlinear processes involved. For instance, immigration sometimes was also high at positive temperatures (e.g. in late November 1997). Moreover, extremely deep temperatures, like in December 1996, suppressed further immigration. While the latter finding is biologically plausible, because deep temperatures limit bat activity beyond a certain threshold, there is no obvious explanation for the nonlinearities at positive temperatures. A more depictive presentation, allowing immigration, emigration, and temperature to be tracked over time is given in the appendix.

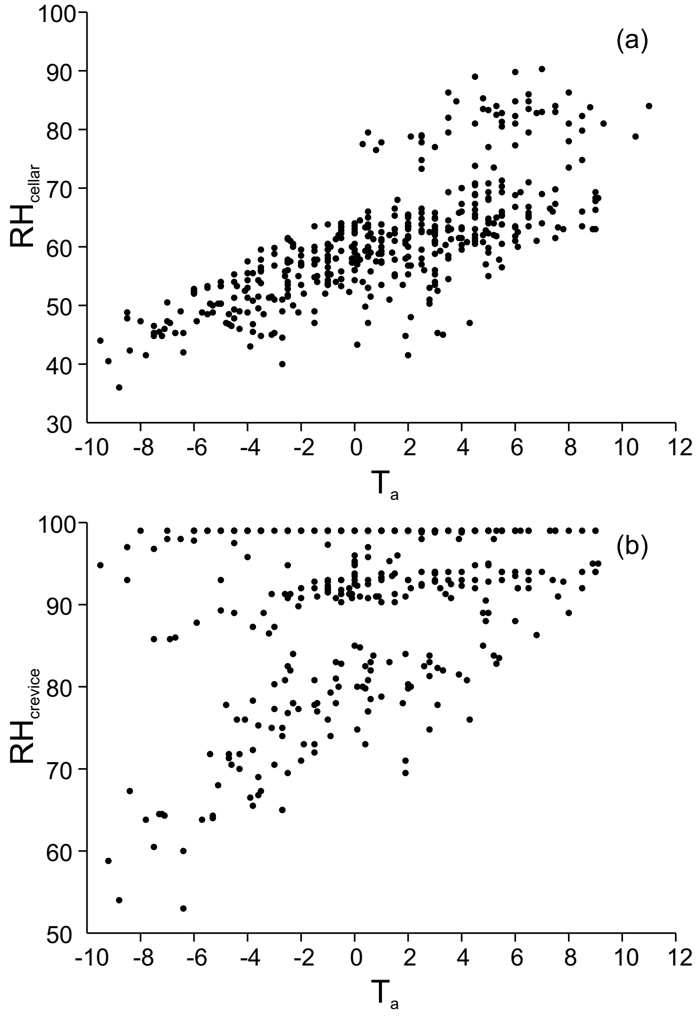


Fig. 6.2: Relationship between ambient temperature and relative humidity in the open air space of the hibernaculum (a; $r = 0.728$; $p < 0.01$; $n = 444$) and in a typical roost crevice (b; $r = 0.385$; $p < 0.01$; $n = 393$).

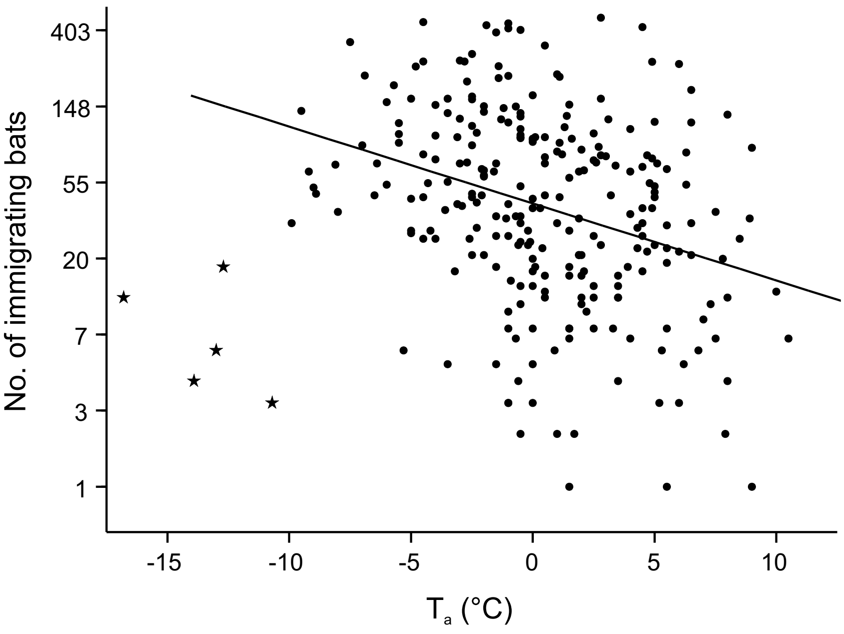


Fig. 6.3: Relationship between ambient temperature and the number of immigrating bats ($\log_e$-scaled) ($r = -0.319$; $p < 0.001$; $n = 300$); the asterisks mark data points that have been excluded from the correlation analysis because they lie below the obvious threshold beyond which transfer flights of bats are suppressed.

Around the turn of the year, emigration from the hibernaculum started if ambient temperatures were mild (see appendix). The temporal course of emigration showed a peak around late February, which is accounted for by the quadratic time function (Table 6.1). Emigration waves were best explained by variation of crevice temperature, but were not influenced by changes of barometric pressure (Table 6.1). There was still some support for the models combining $T_{crevice}$ and p, but as the additional parameters did not result in a gain of information, the hypothesis of influence of pressure is discarded.

6.3.3 Body mass dynamics

There was an approximately linear decrease of body masses over time in the captured pipistrelle bats (Fig. 6.4). These data were best described by the model $\mathrm{t} + \mathrm{S} \times \mathrm{A} \times \mathrm{Y}$, which was clearly favoured over all competing models (Table 6.2). Accordingly, the regression lines differed among sexes, ages and years, but were parallel, i.e. they shared a common slope: ($\hat{\beta}_1 = -13.4$ mg × d^{-1}; 95%CI $= -13.0 - (-13.8)$). This means that all

Tab. 6.1: Results of model selection in order to determine the best model of the spring emigration process related to time (t), crevice temperature ($T_{crevice}$), and barometric pressure (p).

No.	Model	r^2	AICc	ΔAICc	w_i	K
1	$t^2 + T_{crevice}$	0.198	75.40	0.00	0.457	5
2	$t^2 + T_{crevice} \times p$	0.209	76.30	0.90	0.291	7
3	$t^2 + T_{crevice} + p$	0.201	76.60	1.20	0.251	6
4	$t + T_{crevice}$	0.123	95.04	19.65	0.000	4
5	$t + T_{crevice} + p$	0.124	96.88	21.48	0.000	5
6	t^2	0.115	97.38	21.98	0.000	4
7	$t + T_{crevice} \times p$	0.126	98.39	22.99	0.000	6
8	$t^2 + p$	0.115	99.45	24.05	0.000	5
9	t	0.041	114.72	39.32	0.000	3
10	$t + p$	0.042	116.55	41.16	0.000	4
11	NULL	0.000	122.88	47.49	0.000	2

sexes and age classes had different starting weights across all years but that the weight loss rate of $13.4\,\mathrm{mg} \times \mathrm{d}^{-1}$ was common to all sexes, age classes and years. The intercepts with the y-axis (Table 6.3) can be interpreted as the extrapolated mean starting values of body mass on 1^{st} November, provided that the linearity assumption holds between this date and the earliest capture session.

There were 192 recaptures of bats within a given winter, whose individual mass losses could be analyzed. Similar as in the entire population, the model selection results indicated that mass loss was independent of age, sex and year (Table 6.4). Likewise, there was no influence of the date of first capture. However, mass loss was dependent on body mass at first capture (initial mass, IM). Nevertheless, the influence of initial mass was weak, as indicated by the resulting regression equation $\Delta\mathrm{m} = -0.00336 \times$ initial mass (no intercept included because the estimate of the intercept would be very close to zero; not shown). Hence, a 6.0 g bat would lose body mass at an average rate of $20\,\mathrm{mg} \times \mathrm{d}^{-1}$.

The bats placed in the wooden boxes for continuous monitoring of mass loss were all adults (n = 6 males, 12 females). There was no evidence that the rates of mass loss differed between the sexes (ANOVA, $F_{1,16} = 2.922$, $p = 0.107$). The pooled estimate of mass loss rate was $18.4\,\mathrm{mg} \times \mathrm{d}^{-1}$; 95%CI = 15.9 − 20.9.

Tab. 6.2: Model selection results of models in order to estimate time-dependent (t) mass loss of pipistrelle bats hibernating in Marburg Castle, adjusted for sex (S), age (A), and year (Y); AICc = Akaike's information criterion, small sample corrected; ΔAICc = difference of AICc to the best-fitting model; w_i = normalised Akaike weight; K = number of estimated parameters; $n = 4164$.

No.	Model	r^2	AICc	ΔAICc	w_i	K
1	$t + \mathrm{S} \times \mathrm{A} \times \mathrm{Y}$	0.639	−6860.8	0.0	0.977	18
2	$t + \mathrm{Y} + \mathrm{S} \times \mathrm{A}$	0.637	−6852.9	7.9	0.019	9
3	$t \times \mathrm{S} \times \mathrm{A} \times \mathrm{Y}$	0.641	−6849.7	11.1	0.004	33
4	$t + \mathrm{S} + \mathrm{A} \times \mathrm{Y}$	0.637	−6843.7	17.1	0.000	11
5	$t + \mathrm{A} + \mathrm{S} \times \mathrm{Y}$	0.637	−6841.9	18.9	0.000	11
6	$t + \mathrm{S} + \mathrm{A} + \mathrm{Y}$	0.636	−6840.2	20.6	0.000	8
7	$t + \mathrm{S} + \mathrm{Y}$	0.602	−6475.3	385.5	0.000	7
8	$t + \mathrm{A} + \mathrm{Y}$	0.551	−5971.8	889.0	0.000	7
9	$t + \mathrm{Y}$	0.495	−5482.1	1378.7	0.000	6
10	$t + \mathrm{S} + \mathrm{A}$	0.145	−3294.2	3566.6	0.000	5
11	$t + \mathrm{S}$	0.119	−3169.2	3691.6	0.000	4
12	$t + \mathrm{A}$	0.056	−2882.5	3978.3	0.000	4

Tab. 6.3: Sex-, age- and year-specific intercepts ($\hat{\beta}_0 \pm \widehat{\mathrm{SE}}$) on 1st Nov of the body masses of pipistrelle bats related to time, conditional on model $\mathrm{t} + \mathrm{S} \times \mathrm{A} \times \mathrm{Y}$.

	1996/97	1997/98	1998/99	1999/2000
juv. males	5.773 ± 0.044	5.824 ± 0.043	5.853 ± 0.042	5.822 ± 0.040
juv. females	6.011 ± 0.069	6.132 ± 0.053	6.160 ± 0.047	6.216 ± 0.049
ad. males	6.102 ± 0.033	6.139 ± 0.030	5.995 ± 0.031	6.150 ± 0.033
ad. females	6.480 ± 0.029	6.604 ± 0.029	6.527 ± 0.030	6.592 ± 0.024

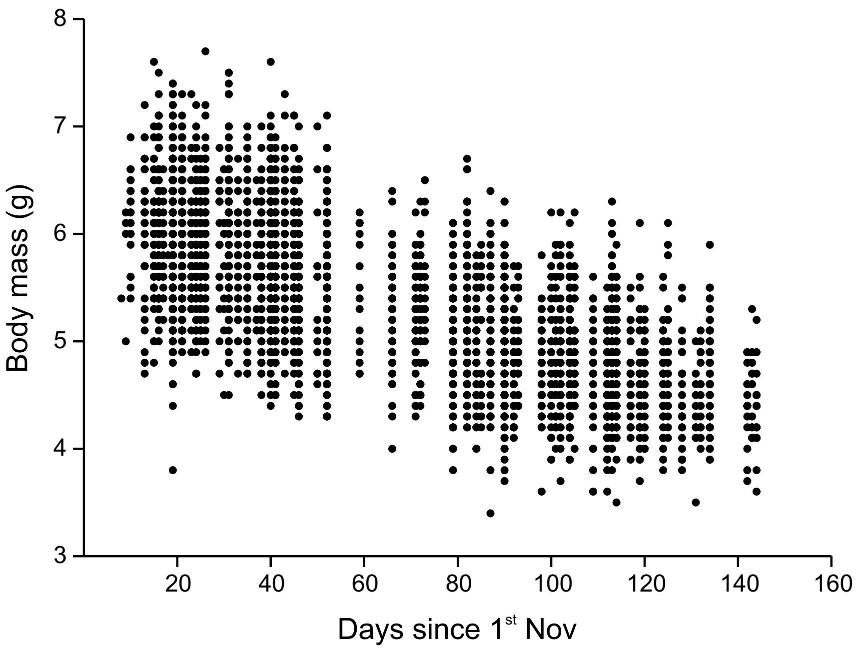


Fig. 6.4: Body masses of the pipistrelle bats caught at the hibernaculum "Marburg Castle" during the winters 1996/97–1999/2000 (all sexes, age classes and years pooled; $n = 4164$).

6.3.4 Predicted evaporative water loss

The EWL rates predicted by equation 6.1 are shown in Figure 6.5. The boxes for continuous mass monitoring were exposed to the climatic conditions of the open air space of the hibernaculum. Therefore, EWL rates derived for these conditions were expected for the boxed bats. A direct comparison to the mass loss rates of the boxed individuals shows that the predicted EWL based on microclimate data from the experimental period (Fig. 6.5a) exceeds the estimated mass loss of $18.4\,\mathrm{mg} \times \mathrm{d}^{-1}$ by almost the factor 10. If we regard the predictions for the crevices the median of the predicted EWL rate ($3.8\,\mathrm{mg} \times \mathrm{d}^{-1}$) would be only a fraction of the mass loss estimates. If we regard the predictions based on data from all over the winter there is no great difference to the predictions for the open air space, while even for the crevice EWL would be mainly higher than expected from mass loss rates (Fig. 6.5b).

Tab. 6.4: Results of model selection in order to determine the best model for estimating average daily weight loss rate from data of recaptured pipistrelle bats ($n = 192$), depending on age (A), sex (S), year (Y), date of first capture (FC), and initial body mass (IM). The notation specific for model selection is the same like in Table 6.2.

No.	Model	r^2	AICc	ΔAICc	w_i	K
1	IM[‡]	0.602	−1592.47	0.00	0.696	2
2	NULL	0.000	−1588.15	4.32	0.080	2
3	Y	0.030	−1587.78	4.69	0.067	5
4	A	0.008	−1587.69	4.78	0.064	3
5	FC	0.001	−1586.21	6.26	0.030	3
6	S	0.000	−1586.17	6.30	0.030	3
7	S × Y	0.057	−1584.54	7.93	0.013	9
8	S × A	0.010	−1583.86	8.61	0.009	5
9	A × Y	0.049	−1582.94	9.53	0.006	9
10	FC + A × S	0.011	−1581.81	10.66	0.003	6
11	S × A × W	0.114	−1577.85	14.62	0.000	17
12	FC + A × S × Y	0.116	−1575.87	16.60	0.000	18

[‡]: intercept fixed at 0

6.3.5 *Energy budget scenarios*

The energy budget scenarios were calculated under a set of assumptions derived from the results obtained so far in this study:

1. We have seen above that emigration from the hibernaculum starts around the turn of the year as soon as ambient temperatures get mild. This does not mean the end of hibernation for the respective individuals; they merely switch their roost to continue hibernation somewhere else. However, we may consider the core period when the hibernaculum is occupied (15th Nov – 15th March) as the hibernation period. Before and after this period, the weather is usually so mild that I restrict the definition of hibernation to this period. Thus, I assume a hibernation period of 120 d (= 2880 h) that the pipistrelle bats have to survive without feeding.

2. According to the light barrier data, there is considerable flight activity virtually every day (see appendix). Thus, it is reasonable to assume that pipistrelle bats fly during each arousal cycle. Schweizer *et al.*(in

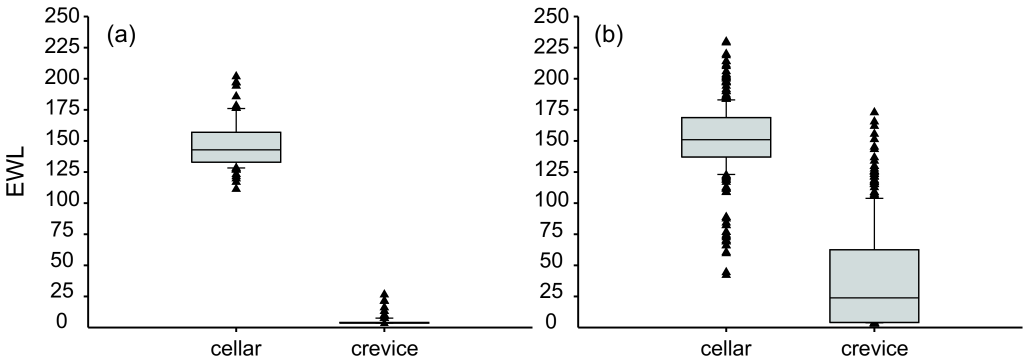


Fig. 6.5: Box plots for the predicted evaporative water loss (EWL, mg × d^{-1}) of the pipistrelle bats hibernating at Marburg Castle: (a) for the time period when continuous body mass monitoring took place ($n = 87$), (b) for all data points available (cellar: $n = 354$, crevice: $n = 333$) .

prep.) have observed a mean length of hibernation bouts of 13.2 d (range: 1–42 d); this is somewhat shorter than – but generally conforming with – the bouts observed by Brack and Twente (1985) in *Pipistrellus subflavus*. The observed length of hibernation bouts is also assumed to occur in other, unknown hibernacula. During a 120 d hibernal period, an average pipistrelle bat would hence arouse nine times. This arousal frequency is probably overestimated as the observed bats were not completely undisturbed. Assuming that a pipistrelle bat switches roosts (not necessarily to and from Marburg Castle) at each arousal, I chose a set of integer numbers (10, 8, and 6) to account for movements between various hibernacula and to incorporate a range of fairly realistic roost switching frequencies into the scenarios.

3. The mass loss rates of the boxed individuals comprise an unknown proportion of evaporative water loss (EWL). As demonstrated above, EWL cannot be reliably estimated from the microclimate data using the relationship found by Thomas *et al.* (1990b). Therefore, energy expenditure cannot be directly derived from the mass loss data. Hence, I assume for convenience that EWL accounts for 69% of mass loss (Speakman and Racey, 1989). This is quite hypothetical in the situation at hand but seems reasonable because the boxed pipistrelle bats certainly were affected by EWL, at humidities similar to those reported by Speakman and Racey (1989).

Tab. 6.5: Energy budgets in terms of fat requirements (g) for hibernating pipistrelle bats of different body mass at the begin of winter under various scenarios of metabolic rate in deep hibernation and for various frequencies of hibernal roost switching.

		body mass at start		
Scenario	No. of roost switches	5.5 g	6.0 g	6.5 g
Aberdeen	10	2.15	2.28	2.42
	8	1.98	2.11	2.24
	6	1.81	1.94	2.06
Quebec	10	1.02	1.05	1.09
	8	0.85	0.88	0.91
	6	0.68	0.70	0.73
Marburg	10	1.49	1.57	1.65
	8	1.32	1.41	1.47
	6	1.15	1.22	1.29

4. The energy demands for arousal cycles are the same in all scenarios. The scenarios differ by the underlying mass-dependent metabolic rate in deep hibernation. The analysis of body masses of captured pipistrelle bats (Table 6.2) has revealed average masses varying between 5.7 and 6.6 g at the beginning of the 120 d hibernation period (Table 6.4). Hence, the scenarios were calculated for bats of 5.5, 6.0, and 6.5 g, respectively.

Each arousal cycle of a 6 g pipistrelle bat requires 519.6 J for 45 min of heating plus 2,574 J for 30 min in flight ($1.43\,\mathrm{W} \times 1800\,\mathrm{s}$) plus 349.2 J for the cooling phase (30 min), summing up to 3,442.8 J in 1.75 h. This bat, arousing and switching the roost 10 times would thus expend 34428 J for its activities not spent in hibernation. In the remaining time of 2,862.5 h in deep hibernation it would, under the Aberdeen scenario, expend $3.216\,\mathrm{J} \times \mathrm{g}^{-1} \times \mathrm{h}^{-1}$ ($\equiv 0.16\,\mathrm{ml\,O_2} \times \mathrm{g}^{-1} \times \mathrm{h}^{-1}$), which gives 55,234.8 J. Arousal cycles and hibernation bouts sum up to 89,662.8 J, which corresponds to 2.282 g fat. The results of all scenarios, calculated in the same way, are presented in Table 6.5.

The critical mass below which an individual would quickly die without feeding has been estimated at 4.03 g (Speakman and Racey, 1989). Thus, under the Aberdeen scenario bats of 5.5 or 6.0 g body mass at the beginning of the hibernation season are likely not to survive until mid-March irrespective of the roost switching frequency. Even a 6.5 g pipistrelle would approach close to the critical value if it aroused 10 times. Under the Quebec scenario the fat reserves even of a 5.5 g bat would by far suffice to survive the winter. And even under the Marburg scenario the fat reserves would not be depleted, perhaps apart from a 5.5 g pipistrelle that switching its roost 10 times (Table 6.5).

6.4 Discussion

This study illustrated the dynamics of a hibernal pipistrelle bat population of a large hibernaculum and the relationships of the immigration process to ambient temperature and of the emigration process to crevice temperature. The bats lost body mass at average rates between 13 and 20 mg $\times$ d^{-1}. Evaporative water loss in reality was considerably lower than predicted from theory. Scenarios of hibernal energy budgets gave some insight in the significance of winter activity.

6.4.1 Microclimate

The microclimate of the hibernaculum at Marburg Castle is quite typical with respect to humidity. Also other pipistrelle bat hibernacula are unexpectedly dry (Haagen and Arnold, 1955; Racey, 1974b). However, the site investigated in the present study is warmer and thermally more stable, i.e. more buffered against fluctuations of ambient temperature than the hibernacula described by Racey (1974b) or Speakman and Racey (1989). This is important in the discussions of hibernal population dynamics and energetics (see below).

6.4.2 Hibernal population dynamics

The dynamics of the population hibernating in the cellar at Marburg Castle was characterised by permanently high fluctuations of individuals. The immigration phase lasted from approx. mid-November to late December / early January. Low temperatures favoured immigration of large numbers of individuals. Afterwards, even from early January onwards, the prevalence of immigration and emigration coincided with low and mild ambient temperatures, respectively. Consequently, pipistrelle bats perform extensive hibernal roost switching. These results corroborate the more preliminary findings of Sendor *et al.* (2000), now more rigorously derived from a much broader data basis. The permanent activity at the hibernaculum and the resulting roost switching of *P. pipistrellus* is a strategy that sharply contrasts that found in various *Myotis* species (Degn *et al.*, 1995), who perform almost no activity between immigration in October/November and emigration in March/April.

However, ambient temperature is no adequate explanative variable for the observed midwinter emigration waves as the hibernating bats have no means to directly measure the respective changes. Which factor could thus explain such an immediate response to rises in temperature? I hypothesised that barometric pressure might be a cue that pipistrelle bats use to predict favourable conditions for emergence because the hibernaculum seemed climatically too strongly buffered that temperature could explain such an immediate response. Paige (1995) could demonstrate that *Pipistrellus subflavus* roosting in temperate caves during the summer use barometric pressure to assess good conditions for feeding. The analogous hypothesis for hibernating *P. pipistrellus* was clearly rejected. Hence, barometric pressure does obviously not play a role in the hibernal roost switching process. In contrast, the temperature fluctuations in the roost crevices provide a good explanation for the emigration waves (Table 6.1). With these observational data it is difficult to assess if temperature fluctuations in the magnitude of a fraction of a °C suffice to induce arousal and subsequent emergence. Nevertheless, metabolic responses to transient – but relatively large – temperature increases have been demonstrated experimentally (Speakman *et al.*, 1991).

Winter activity in pipistrelle bats as well as in some other species, e.g. the brown long-eared bat, (*Plecotus auritus*), the noctule (*Nyctalus noctula*), and the greater horseshoe bat (*Rhinolophus ferrumequinum*), is a commonly known phenomenon (Avery, 1985, 1986; Hays *et al.*, 1992; Park *et al.*, 1999, 2000). However, flight activity of bats has been associated with mild winter evenings in the past. The functional explanation for winter emergence flights has been to feed and to drink (Avery, 1985, 1986; Brigham, 1987; Park *et al.*, 1999, 2000; Speakman and Racey, 1989). When pipistrelle bats hibernating in Marburg Castle need to drink, they are clearly forced to emerge from the hibernaculum due to its microclimate and the absence of water. The present study shows that transfer flights between roosts occurred at temperatures of both, below and above the freezing point. These results suggest that the primary function of winter activity in the pipistrelle bat is probably rather an adaption to changing environmental conditions via roost site selection. Such an adaptive evasion from adverse environmental conditions has also been demonstrated in hibernating *Tadarida teniotis* (Arlettaz *et al.*, 2000). The transfer flights may additionally be used for drinking and even feeding if adequate conditions (weather and prey abundance) are fulfilled. Moreover, it is likely that in the milder climate of the British Isles, where most studies on hibernal ecology were conducted (Avery, 1985; Hays *et al.*, 1992; Park *et al.*, 1999, 2000; Speakman and Racey, 1989), the function of winter activity is more shifted towards feeding than in continental Europe. Hibernal roost switching has some important energetic implications which will be discussed in more detail below.

6.4.3 Body mass dynamics, water balance and energetics

The estimates of mass loss from either data source (all captures, recaptures, daily monitoring) were quite close to each other, ranging from 13 to 20 mg × d^{-1}. There was good evidence that mass loss rates were constant irrespective of sex, age, and year (Table 6.2). The estimate from all captures lay at the lower end. As the captured individuals had just been through a transfer flight with presumed opportunities to drink, this difference represents some evidence for drinking during hibernal roost switching.

The difference to the mass loss rate of 78 mg × d^{-1} estimated by Speakman and Racey (1989) is quite remarkable. This may be due to the fact that Speakman and Racey (1989) used captive bats kept in an artificial hibernaculum. Although their experimental site may be climatically similar to many natural hibernacula, as stated by the authors, captivity may have negative energetic consequences due to the missing possibility of free roost site selection. The cellar at Marburg Castle is thermally more stable because stronger buffered against fluctuating ambient temperatures than the artificial hibernaculum studied by Speakman and Racey (1989). However, as the hibernal metabolism of the pipistrelle bat seems to be largely independent of temperature in the usual range of hibernal conditions (Speakman *et al.*, 1991), the respective microclimatic differences should have little energetic consequences.

Evaporative water loss (EWL) is an important source of mass loss in all species of hibernating bats and even is probably involved in regulating the length of hibernation bouts (Thomas and Cloutier, 1992; Thomas and Geiser, 1997). Hence, EWL accounts for a considerable fraction of the mass loss rates estimated from recaptured as well as the boxed pipistrelle bats. However, this study failed to estimate the specific amount of EWL. An important result, though, was that the equation of Thomas and Cloutier (1992) predicted far too high EWL rates on the basis of the microclimate data. The relationship found by Thomas and Cloutier (1992) should have been applicable because *P. pipistrellus* and *M. lucifugus* are of comparable body size. The overestimation of EWL represents preliminary evidence that *P. pipistrellus* is physiologically adapted to low humidities, in contrast to e.g. *M. lucifugus.* Differences in pulmonary water loss can probably not be accounted for this because pipistrelle bats, in contrast to *M. lucifugus*, apparently leave the glottis open during apneic intervals in hibernation (cf. Hays *et al.*, 1991;

Thomas *et al.*, 1990a). Accordingly, as an open glottis would allow diffusion of water vapour and thus promote EWL, water loss would be expected to be greater in the pipistrelle bat if pulmonary evaporation played a significant role. Hence, one might suspect that morphological adaptations of the skin could be involved in the restriction of cutaneous evapotranspiration.

As we lack of a reliable estimate of EWL in the pipistrelle bats hibernating at Marburg Castle, inferences with respect to energetics on the basis of the estimated mass loss rates should be made with caution. Clearly, metabolising fat accounts only for a fraction of the observed mass loss rates. It seems convenient to assume the 69% EWL proportion estimated by Speakman and Racey (1989), which is furthermore justified by the fact that the relative humidities were comparable to those measured in the present study. However, EWL could as well account for only approx. 30% of mass loss, resulting in the double metabolic rate than assumed in the Marburg energy budget scenario.

Further shortcomings of the energy budget scenarios are made up of some of the assumptions for parts of the arousal cycles, chosen on account of (at best) anecdotal data: The assumed 30 min period of flight activity was purely chosen on the reasoning that a bat would tend to minimise the time required for roost switching, possibly combined with visits to a body of water for drinking (see above). Other authors have measured euthermic intervals of 1 h to 3 h length (French, 1985; Thomas, 1995; Thomas *et al.*, 1990b), but without including flight activity. If the distances between hibernacula are short (which is likely, cf. Smit-Viergutz and Simon 2000) the time spent in flight would even be overestimated by using these values. Furthermore, own observations during this study suggest that pipistrelle bats may enter torpor within $\frac{1}{2}$ h after stopping flight activity. Thus, the assumed 30 min of flight activity as well as the cooling phase of equal length may be fairly realistic estimates. The 45 min of time required for heating, in contrast, are well documented in the literature and therefore reliable (e.g. Thomas *et al.*, 1990b). Stones and Wiebers (1967) report even shorter heating times. In conclusion, even if the assumptions for the arousal cycles still contain some uncertainties, the time of 1.75 h as well as the resulting energy demands seem to be a useful approximation to reality.

Notwithstanding these objections and the simplistic nature of the scenarios, we may learn two things from the mass loss estimates and the energy budget scenarios:

1. Energy expenditure of hibernating pipistrelle bats has apparently been overestimated by indirect calorimetry (cf. Speakman and Racey, 1989; Speakman *et al.*, 1991). This does not mean that the corresponding measurements were flawed. Rather, the artificial laboratory conditions

may lead to increased metabolic rates in pipistrelle bats. Recently, this issue has been pointed out by Geiser *et al.* (2000).

2. If, and only if, the ancillary conditions and parameters of the Marburg scenario approximately reflect reality, an average pipistrelle bat would not be forced to forage in order to survive hibernation until mid-March even if roosts are frequently (i.e. 10 times per winter) switched. Although flight activity is costly, it seems to have less impact on total energy expenditure if it occurs with the presumed frequency, than metabolic rates in hibernation varying by, say, the factor two (the difference between the Aberdeen and the Marburg scenario).

Consequently, the current results support the conclusion of Speakman and Racey (1989) that the function of winter emergence flights is rather to drink than to feed (cf. Avery, 1985). Furthermore, the involvement of hibernal roost switching is probably energetically beneficial or at least not detrimental. Immigration to stable hibernacula like Marburg Castle clearly appears as an immediate evasion from roost temperatures below which thermoregulation would be necessary (Geiser *et al.*, 1990; Hock, 1951). Sticking to these roosts would therefore be more costly than switching, or even lethal if they freeze.

With the midwinter emergences at mild temperatures, things are more complicated. Following Speakman *et al.* (1991), I have assumed approximate independence of hibernal metabolism from temperatures. Consequently, it is not clear if switching to an alternative roost is per se energetically advantageous. However, the regulation of arousal frequency through EWL (Thomas and Geiser, 1997) could explain this phenomenon. Fluctuations of roost crevice temperature might then serve as cue to determine a favourable point of time for emergence.

6.5 Conclusions

After all, the hibernal ecology of the pipistrelle bat still still remains somewhat puzzling. I could not perform own metabolic measurements in this study and information in the literature is inconsistent. Although rates of oxygen consumption down to 0.024 mg $\times$ g^{-1} $\times$ h^{-1} have been reported (Kayser, 1964), which corresponds to those determined in other bat species (Hock, 1951; Thomas *et al.*, 1990b), these are only minima among a large set of much higher values (Kayser, 1940). Thus, it is currently not possible to reliably assess the costs and benefits of the hibernal roost switching strategy of the pipistrelle bat. Furthermore, the significance of winter feeding cannot be conclusively assessed. More research in this field needs to be done, focusing on the estimation of the actual roost switching frequency, of EWL and metabolic rates under *natural* conditions of hibernation.

6.6 Acknowledgements

T.S. was supported by a doctoral grant of the “Hessische Graduiertenförderung”. Parts of the equipment were funded by the “Stiftung Hessicher Naturschutz”. Data of ambient temperature were provided by Markus Kaempf and Tilman Holfelder. Andreas Knoll made available the data of barometric pressure. Special thanks go to the many people who assisted in catching bats, too numerous to be named.

References

Anderson, D. R., K. P. Burnham, and W. L. Thompson (2000): Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* **64**: 912–923.

Anthony, E. L. P. (1988): Age determination in bats. In T. H. Kunz (Ed.), *Ecological and Behavioural Methods for the Study of Bats*, pp. 47–58, Washington D.C. & London: Smithsonian Institution Press.

Arlettaz, R., C. Ruchet, J. Aeschimann, E. Brun, M. Genoud, and P. Vogel (2000): Physiological traits affecting the distribution and wintering strategy of the bat *Tadarida teniotis*. *Ecology* **81**: 1004–1014.

Avery, M. I. (1985): Winter activity of pipistrelle bats. *Journal of Animal Ecology* **54**: 721–738.

Avery, M. I. (1986): The winter activity of noctule bats. *Journal of Zoology (London)* **209**: 296–299.

Brack, V. j. and J. W. Twente (1985): The duration of the period of hibernation of three species of vespertilionid bats. I. Field studies. *Canadian Journal of Zoology* **63**: 2952–2954.

Brigham, R. M. (1987): The significance of winter activity by the big brown bat (*Eptesicus fuscus*): the influence of energy reserves. *Canadian Journal of Zoology* **65**: 1240–1242.

Buckland, S. T., K. P. Burnham, and N. H. Augustin (1997): Model selection: an integral part of inference. *Biometrics* **53**: 603–618.

Burnham, K. P. and D. R. Anderson (1998): *Model Selection and Inference: A Practical Information-Theoretic Approach.* New York, Berlin, Heidelberg: Springer Verlag.

Davis, W. H. (1964): Winter awakening patterns in the bats *Myotis lucifugus* and *Pipistrellus subflavus*. *Journal of Mammalogy* **45**: 645–647.

Davis, W. H. (1970): Hibernation: Ecology and physiological ecology. In W. A. Wimsatt (Ed.), *Biology of Bats*, vol. I, pp. 266–300, New York, London: Academic Press.

Degn, H. J., B. B. Andersen, and H. Baggoe (1995): Automatic registration of bat activity through the year at Mønsted Limestone Mine, Denmark. *Zeitschrift für Säugetierkunde* **60**: 129–135.

Dorgelo, J. and A. Punt (1969): Abundance and "internal migration" of hibernating bats in an artificial limestone cave ("Sibbergroeve"). *Lynx N.S.* **10**: 101–125.

Dumitresco, M. and T. Orghidan (1963): Contribution à la connaissance de la biologie de *Pipistrellus pipistrellus* Schreber. *Annales de Spéléologie* **18**: 511–517.

French, A. R. (1985): Allometries of the durations of torpid and euthermic intervals during mammalian hibernation: A test of the theory of metabolic control of the timing of changes in body temperature. *Journal of Comparative Physiology B* **156**: 13–19.

Geiser, F., S. Hiebert, and G. J. Kenagy (1990): Torpor bout duration during the hibernation season of two sciurid rodents: interrelations with temperature and metabolism. *Physiological Zoology* **63**: 489–503.

Geiser, F., J. C. Holloway, G. Körtner, T. A. Maddocks, C. Turbill, and R. M. Brigham (2000): Do patterns of torpor differ between free-ranging and captive mammals and birds? In G. Heldmaier and M. Klingenspor (Eds.), *Life in the Cold*, pp. 95–102, Berlin, Heidelberg: Springer Verlag.

Grimmberger, E. and H. Bork (1978): Untersuchungen zur Biologie, Ökologie und Populationsdynamik der Zwergfledermaus, *Pipistrellus p. pipistrellus* (Schreber 1774), in einer großen Population im Norden der DDR, Teil 1. *Nyctalus (N.F.)* **1**: 55–73.

Haagen, G. and J. Arnold (1955): Zur Überwinterung von *Pipistrellus pipistrellus* (Schreber, 1774). *Säugetierkundliche Mitteilungen* **3**: 122.

Hardin, J. W. and M. D. Hassel (1970): Observation on waking periods and movements of *Myotis sodalis* during hibernation. *Journal of Mammalogy* **51**: 829–831.

Hays, G. C., J. R. Speakman, and P. I. Webb (1992): Why do brown long-eared bats (*Plecotus auritus*) fly in winter? *Physiological Zoology* **65**: 554–567.

Hays, G. C., P. I. Webb, and J. R. Speakman (1991): Arrhythmic breathing in torpid pipistrelle bats, *Pipistrellus pipistrellus. Respiration Physiology* **85**: 185–192.

von Helversen, O., M. Esche, F. Kretzschmar, and M. Boschert (1987): Die Fledermäuse Südbadens. *Mitteilungen des Badischen Landesvereins für Naturkunde und Naturschutz, N.F.* **14**: 409–475.

Hock, R. J. (1951): The metabolic rate and body temperature of bats. *The Biological Bulletin* **101**: 289–299.

Kayser, C. (1940): Echanges respiratoires des hibernants à l'état de sommeil hibernal. *Annales de Physiologie et de Physiochimie Biologique* **16**: 127–221.

Kayser, C. (1964): La dépense d'énergie des mammiferes en hibernation. *Archives des Sciences Pysiologiques* **18**: 137–150.

Kugelschafter, K., T. Horvath, W. Kimpel, G. Steffny, and T. Volk (1995): Neue Techniken zur Überwachung von Fledermäusen. In M. Stubbe, A. Stubbe, and D. Heidecke (Eds.), *Methoden feldökologischer Säugetierforschung*, vol. 1, pp. 373–382, Halle/Saale: Martin-Luther-Universität Halle-Wittenberg.

Kuipers, B. and S. Daan (1970): "Internal migration" of hibernating bats: response to seasonal variation in cave microclimate. *Bijdragen tot de Dierkunde* **40**: 51–55.

Lide, D. R. (Ed.) (1999): *CRC Handbook of Chemistry and Physics*. 80th edn., Boca Raton, London, New York, Washington D.C.: CRC Press.

Lustrat, P. and J.-F. Julien (1997): Monitoring of an important hibernaculum in Paris (France). *Myotis* **35**: 109–110.

Lyman, C. P., J. S. Willis, A. Malan, and L. C. H. Wang (1982): *Hibernation and Torpor in Mammals and Birds*. New York: Academic Press.

Menaker, M. (1964): Frequency of spontaneous arousal from hibernation in bats. *Nature* **203**: 540–541.

Paige, K. N. (1995): Bats and barometric pressure: conserving limited energy and tracking insects from the roost. *Functional Ecology* **9**: 463–467.

Park, K. J., G. Jones, and R. D. Ransome (1999): Winter activity of a population of greater horseshoe bats (*Rhinolophus ferrumequinum*). *Journal of Zoology (London)* **248**: 419–427.

Park, K. J., G. Jones, and R. D. Ransome (2000): Torpor, arousal and activity of hibernating Greater Horseshoe Bats (*Rhinolophus ferrumequinum*). *Functional Ecology* **14**: 580–588.

Racey, P. A. (1974a): Ageing and assessment of reproductive status of pipistrelle bats, *Pipistrellus pipistrellus. Journal of Zoology (London)* **173**: 264–271.

Racey, P. A. (1974b): The temperature of a pipistrelle hibernaculum. *Journal of Zoology (London)* **173**: 260–262.

Schmidt-Nielsen, K. (1997): *Animal Physiology: Adaptation and Environment.* 5th edn., Cambridge: Cambridge University Press.

Sendor, T., K. Kugelschafter, and M. Simon (2000): Seasonal variation of activity patterns at a pipistrelle (*Pipistrellus pipistrellus*) hibernaculum. *Myotis* **38**: 91–109.

Smit-Viergutz, J. and M. Simon (2000): Eine vergleichende Analyse des sommerlichen Schwärmverhaltens der Zwergfledermaus (45 kHz Ruftyp, *Pipistrellus pipistrellus* Schreber, 1774) an den Invasionsorten und am Winterquartier. *Myotis* **38**: 69–89.

Speakman, J. R. and P. A. Racey (1989): Hibernal ecology of the pipistrelle bat: energy expenditure, water requirements and mass loss, implications for survival and the function of winter emergence flights. *Journal of Animal Ecology* **58**: 797–813.

Speakman, J. R. and P. A. Racey (1991): No cost of echolocation for bats in flight. *Nature* **350**: 421–423.

Speakman, J. R., P. I. Webb, and P. A. Racey (1991): Effects of disturbance on the energy expenditure of hibernating bats. *Journal of Applied Ecology* **28**: 1087–1104.

Stones, R. C. and J. E. Wiebers (1967): Temperature regulation in the little brown bat, *Myotis lucifugus.* In K. C. Fisher (Ed.), *Mammalian hibernation*, pp. 97–109, Edinburgh: Oliver and Boyd.

Thomas, D. W. (1995): The physiological ecology of hibernation in vespertilionid bats. *Symposia of the Zoological Society of London* **67**: 233–244.

Thomas, D. W. and D. Cloutier (1992): Evaporative water loss by hibernating little brown bats, *Myotis lucifugus. Physiological Zoology* **65**: 443–456.

Thomas, D. W., D. Cloutier, and D. Gagné (1990a): Arrythmic breathing, apnea and non-steady-state oxygen uptake in hibernating little brown bats (*Myotis lucifugus*). *Journal of Experimental Biology* **149**: 395–406.

Thomas, D. W., M. Dorais, and J.-M. Bergeron (1990b): Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus. Journal of Mammalogy* **71**: 475–479.

Thomas, D. W. and F. Geiser (1997): Periodic arousals in hibernating mammals: is evaporative water loss involved? *Functional Ecology* **11**: 585–591.

Thomas, S. P. and R. A. Suthers (1972): The physiology and energetics of bat flight. *The Journal of Experimental Biology* **57**: 317–335.

7. Zusammenfassung

Fledermäuse der gemäßigten Breiten überwintern aus energetischen Gründen in kühlen, klimatisch stabilen Winterquartieren. Darüber hinaus können sie auch im Sommer in großen Zahlen in Winterquartieren angetroffen werden, wobei es sich um nächtliche Flugaktivität handelt (sommerliches Schwärmen). Fledermäuse sind demnach über weite Strecken des Jahres in Winterquartieren zu beobachten. Winterquartiere sind aufgrund der genannten nahezu ganzjährigen Zugriffsmöglichkeit in besonderem Maße zur Untersuchung der Ökologie von Fledermäusen geeignet. Einerseits sind die mit Winterquartieren an sich verbundenen Prozesse und ihre Funktion (Überwinterung, sommerliches Schwärmen) von Interesse. Andererseits lassen sich neuartige, allgemeinere populationsökologische Fragestellungen hier besonders gut untersuchen, da aufgrund der nahezu ganzjährigen Präsenz der Tiere jahreszeitlich variierende Prozesse beobachtet werden können. Ein solches Winterquartier, das nahezu ausschließlich von Zwergfledermäusen genutzt wird, ist der Rittersaalkeller des Marburger Landgrafenschlosses.

Die Ziele der vorliegenden Arbeit waren, die ökologische Bedeutung der ganzjährigen Nutzung eines Massenwinterquartiers für den Lebenszyklus ("life history") der Zwergfledermaus, bzw. die Funktion einzelner saisonaler Phänomene, darzustellen. Die Ergebnisse liegen als Serie separater Manuskripte vor und werden nachfolgend kurz zusammengefaßt:

1. Die Art "Zwergfledermaus" *Pipistrellus pipistrellus* wurde vor kurzem in zwei Arten aufgespalten, die bei unterschiedlichen Frequenzen echoorten, nach äußeren Merkmalen jedoch kaum unterscheidbar waren. Daher war es notwendig festzustellen, ob das Quartier von beiden oder nur von einer der beiden Zwergfledermaus-Arten genutzt wird, und ggf. von welcher. Nach der Analyse der Echoortungslaute nutzt das Quartier ausschließlich der 45-kHz-Ruftyp (wird den Namen *Pipistrellus pipistrellus* behalten). Zugleich wurde ein kürzlich publiziertes angebliches Merkmal zur morphologischen Unterscheidung der Arten, das Längenverhältnis zweier endständiger Fingerglieder, widerlegt. Stattdessen wird nach gegenwärtiger Datenlage empfohlen, zur morphologischen Unterscheidung u.a. eine Struktur auf der Nase der Tiere heranzuziehen.

2. Ziel des zweiten Teils der Arbeit war, die saisonale Variation der Überlebenswahrscheinlichkeiten der Zwergfledermäuse in Abhängigkeit von den Einflußfaktoren Geschlecht, Altersklasse und winterliches Wetter mit Fang-Wiederfang-Methoden zu analysieren. Das kombinierte Auftreten von "transience" und "trap-dependence" (Verletzungen der Annahmen des Cormack-Jolly-Seber Modells) erschwerte die Analyse. Die

Wiederfangraten zeigten ein saisonales Muster und waren gruppenspezifisch (juv. ♂♂, ad. ♂♂, juv. ♀♀, ad. ♀♀). Der lediglich saisonal aufgetretene “transience”-Effekt konnte wegen zu geringer Stichprobengröße nicht modelliert werden, was zu einer Unterschätzung der sommerlichen/herbstlichen Überlebensraten um einen unbekannten Betrag führte. Die Überlebenswahrscheinlichkeiten von Männchen und Weibchen unterschieden sich – im Gegensatz zur Arbeitshypothese – nicht. Jungtiere wiesen im ersten Jahr eine gegenüber adulten konstant um ca. 25–30% verminderte Überlebensrate auf. Die winterliche Überlebenswahrscheinlichkeit adulter Tiere war überraschend hoch, im Mittel $0,892$ ($\widehat{\text{SE}} = 0,028$), und war nicht durch die Schwere des Winters beeinflußt. Es gab keine Hinweise auf verringertes winterliches Überleben, wiederum im Gegensatz zur Arbeitshypothese. Demnach stellt der Winter keinen Überlebensengpaß im Jahreszyklus dar. Auch die Schätzung der jährlichen Überlebensrate mit $0,799$ ($\widehat{\text{SE}} = 0,051$) weist darauf hin, daß die Langlebigkeit der Zwergfledermaus bisher vermutlich unterschätzt wurde.

3. Ziel des dritten Teils war es, eine plausible Erklärung für die (verhaltens-) ökologische Funktion des sommerlichen Schwärmens zu finden. Es existieren mehrere Erklärungsmöglichkeiten für die Funktion des sommerlichen Schwärmens, deren wichtigste die Paarungshypothese sowie die Hypothese des mütterlich angeleiteten Winterquartier-Erkundens sind. Die Phänologie war durch eine jährlich wiederkehrende Abfolge der Gruppen adulte ♂♂ (Mitte Mai–Mitte Juli), reproduktive ♀♀ (Mitte Juli–Mitte August), Jungtiere beiderlei Geschlechts (Anfang August–September) gekennzeichnet. Paarungsbereite Männchen waren kaum vertreten. Die Populationsgrößenschätzungen für adulte Weibchen und Jungtiere waren in etwa gleich. Jungtiere und adulte Weibchen schwärmten pro Nacht länger als adulte Männchen und nichtreproduktive Weibchen. Verhalten, welches auf Paarungsgeschehen hinweist, wurde nicht beobachtet. Diese Ergebnisse unterstützen die Hypothese, sommerliches Schwärmen sei primär ein mütterlich angeleitetes Erkunden von Winterquartieren durch Jungtiere. Die Hypothese, Schwärmen sei Paarungsverhalten wurde für die Zwergfledermaus widerlegt. Dennoch kann, je nach artspezifischem Lebenszyklus, das sommerliche Schwärmen eine Funktion bei der Fortpflanzung haben, was aus verhaltens- und evolutionsökologischer Sicht diskutiert wird.

4. Die Phänologie der Schwärmaktivität im Verlauf des Sommers und ihre Abhängigkeit von Umweltfaktoren war Gegenstand des vierten Teils dieser Arbeit. Die durch eine Lichtschranke gemessene Schwärmaktivität trat zwischen Anfang Mai und Ende September auf. Bis Mitte Juli schwankte das Aktivitätsniveau um relativ niedrige Werte (bis max. 1000 Einflüge pro Nacht) und stieg danach auf bis zu ca. 5000 Einflüge pro Nacht gegen Mitte August. Der zeitliche Verlauf konnte durch polynomiale Regression vierten Grades modelliert werden. Auf dieser Basis wurde nachgewiesen, daß die Schwärmaktivität bei hohen Tagesmitteltemperaturen steigt und umgekehrt. Hohe Windgeschwindigkeiten führten zu einer Verminderung des Schwärmens. Sommerliches Schwärmen kann bei hohen Tagesmitteltemperaturen bereits im Frühjahr, gegen Ende April auftreten, wie z.B. im Jahr 2000. Die Entscheidung eines Individuums zu Schwärmen wird wahrscheinlich aufgrund energetischer Kriterien getroffen. Zeitig im Jahr auftretendes Schwärmen wird durch diesbezügliche große Flexibilität der Männchen erklärt. Allgemein wird sommerliches Schwärmen als Ergebnis einer Entscheidung zwischen unmittelbarem Überleben und reproduktivem Erfolg (s.a. Kapitel 4) diskutiert.

5. Im Mittelpunkt des fünften Teils stand die Frage, wieviel Energie Zwergfledermäuse unter natürlichen Überwinterungsbedingungen verbrauchen, unter welchen Bedingungen winterliche Flugaktivität stattfindet, ob sich diese mit der Notwendigkeit zum Energiesparen verträgt und ob die bestehende Datenlage den winterlichen Energiebedarf korrekt einschätzt. Der Marburger Schloßkeller ist thermisch relativ stabil, die Luftfeuchte ziemlich niedrig. Winterliche Flugaktivität trat bei nahezu allen Umgebungstemperaturen in Form winterlichen Quartierwechsels auf. Zuwanderung in das klimatisch stabile Winterquartier im Marburger Schloß korrelierte mit Frost; bei Milderung setzte Abwanderung ein. Abwanderungsphasen konnten durch Temperaturänderungen in Quartierspalten erklärt werden. Der Verlust an Körpermasse lag – je nach Methode – zwischen 13 und 20 $\text{mg} \times \text{d}^{-1}$. Theoretisch wäre im vorliegenden Mikroklima bereits der ca. zehnfache Masseverlust allein durch Evapotranspiration zu erwarten. Dies weist auf Anpasungen zur Minimierung des Wasserverlusts bei Zwergfledermäusen hin. Einfache deterministische Szenarien zum Energieverbrauch ergaben, daß winterliche Quartierwechsel – trotz des energieaufwendigen Fluges – nur geringe Auswirkungen auf den Energiehaushalt haben, während die Stoffwechselrate im Winterschlaf in weitaus größerem Maße bestimmt, wie lange eine Zwergfledermaus ohne Nahrungsaufnah-

me überleben kann. Die festgestellten Masseverlustraten legen nahe, daß der Energieverbrauch winterschlafender Zwergfledermäuse bisher überschätzt wurde. Winterliche Quartierwechsel stehen zum Energiesparzwang nicht im Widerspruch, sondern sind anscheinend integraler Bestandteil einer Energiesparstrategie.

Appendix

A. Additional details on capture-recapture data

A.1 CJS data summary

Capture-recapture data for the CJS-model are conveniently summarised as reduced m-arrays (Burnham *et al.*, 1987), where the captures are broken down into the number of recaptured individuals from each release cohort at each recapture occasion. The pipistrelle bat data used in this thesis (Chapter 3) are listed in Tables A.1 and A.2.

A.2 Goodness-of-fit test for the CJS-model

The goodness-of-fit of capture-recapture data to the assumptions of the Cormack-Jolly-Seber model is assessed via a series of contingency tables using χ^2 statistics. For the details how the tests are constructed, see Burnham *et al.* (1987) and Pollock *et al.* (1990). By comparing how the differences between observed and expected values are distributed among the cells of the tables, it is possible to assess what type of violation of model assumptions, e.g. trap-shyness or trap-happiness, has been effective in the data. The following example shows the contingency table of TEST 3.SR3 (i.e. 3.SR for the 3$^{\text{rd}}$ occasion) for the adult males to illustrate the meaning of the summary tables (the marginal numbers are the sums of rows and columns, respectively):

	bats seen at occ. 3		
	seen before	not seen before	
vs.	seen again	not seen again	
O	24	59	83
E	17.1	65.9	
O	73	316	389
E	79.9	309.1	
	97	375	472

In this example the expected numbers of individuals in the left upper and right lower cell are below the observed numbers of individuals, while the inverted deviation occurs in the left lower and the right upper cell. This pattern is symbolised in the following test summaries by the symbol $\searrow$, the reverse one by ↗. In the case of TEST 3.SR the pattern given in the example is an indication for transience; the analogous with TEST 2.Ct indicates a negative trap-effect. If no consistent pattern was recognisable, this is symbolised by a tilde (∼). The GOF results are summarised in Tables A.3–A.6.

Tab. A.1: Summary of the capture-recapture data of male *Pipistrellus pipistrellus* as reduced m-arrays; R_i = number of individuals marked and released at occasion i; m_{ij} = number of individuals recaptured at occasion j last released at occasion i; r_i = number of individuals ever recaptured from the release at occasion i.

			m_{ij}								
i	R_i	$j =$	2	3	4	5	6	7	8	9	r_i
juvenile males											
1	576		35	71	8	3	4	1	3	1	126
2	120			24	3	4	1	1	1	0	34
3	916				59	79	9	9	5	3	164
4	149					28	13	6	2	2	51
5	587						31	93	7	12	143
6	177							33	6	2	41
7	609								42	93	135
8	177									56	56
adult males											
1	868		36	60	30	7	30	9	11	6	189
2	295			28	19	3	17	2	5	1	75
3	472				32	28	17	7	8	5	97
4	368					18	42	3	20	5	88
5	315						27	33	8	5	73
6	309							16	31	6	53
7	406								21	31	52
8	230									21	21

Tab. A.2: Summary of the capture-recapture data of the female *Pipistrellus pipistrellus* as reduced m-arrays; R_i = number of individuals marked and released at occasion i; m_{ij} = number of individuals recaptured at occasion j last released at occasion i; r_i = number of individuals ever recaptured from the release at occasion i.

			m_{ij}								
i	R_i	$j =$	2	3	4	5	6	7	8	9	r_i
juvenile females											
1	906		39	92	19	28	9	16	4	5	212
2	41			5	0	2	2	1	0	0	10
3	1348				68	82	33	34	9	17	243
4	106					19	5	4	1	5	34
5	921						39	75	17	50	181
6	169							30	9	15	54
7	776								38	87	125
8	141									24	24
adult females											
1	1483		71	99	63	45	42	36	26	18	400
2	449			30	24	19	13	3	11	6	106
3	722				38	46	34	25	18	14	175
4	473					37	28	20	19	14	118
5	494						28	38	24	36	126
6	364							29	25	16	70
7	540								25	71	96
8	332									31	31

Tab. A.3: Results of the RELEASE goodness-of-fit tests for the CJS-model in the juvenile males. For the meaning of the symbols see text.

Component	χ^2	df	p	Direction of deviation
3.SR2	3,3121	1	0,0688	↘
3.SR3	3,9054	1	0,0481	↘
3.SR4	1,9537	1	0,1622	↘
3.SR5	0,5279	1	0,4675	↘
3.SR6	1,8312	1	0,1760	↘
3.SR7	1,8256	1	0,1767	↗
3.SR8	5,2897	1	0,0215	↗
3.SR total	18,6456	7	0,0094	
3.Sm2	0,0081	1	0,9283	∼
3.Sm3	8,7078	2	0,0129	↗
3.Sm4	0,6080	2	0,7379	∼
3.Sm5	9,0773	2	0,0107	↘
3.Sm6	4,6058	1	0,0319	↘
3.Sm7	0,0113	1	0,9153	∼
3.Sm total	23,0183	9	0,0062	
TEST 3	41,6640	16	0,0004	
2.Ct2	0,7499	1	0,3865	∼
2.Ct3	0,0053	1	0,9422	∼
2.Ct4	3,3243	1	0,0683	↘
2.Ct5	10,7181	1	0,0011	↘
2.Ct6	0,4710	1	0,4925	∼
2.Ct7	7,8293	1	0,0051	↘
2.Ct total	23,0978	6	0,0008	
2.Cm2	2,3425	2	0,3100	∼
2.Cm3	11,4519	2	0,0033	↗
2.Cm4	3,1295	3	0,3721	∼
2.Cm5	19,2095	2	0,0001	↗
2.Cm6	1,6500	1	0,1990	∼
2.Cm total	37,7835	10	$< 0,0001$	
TEST 2.C	60,8813	16	$< 0,0001$	
TEST 2 + TEST 3	102,5453	32	$< 0,0001$	

Tab. A.4: Results of the RELEASE goodness-of-fit tests for the CJS-model in the adult males. For the meaning of the symbols see text.

Component	χ^2	df	p	Direction of deviation
3.SR2	1,6449	1	0,1997	$\searrow$
3.SR3	4,3158	1	0,0378	$\searrow$
3.SR4	0,2313	1	0,6306	$\searrow$
3.SR5	0,6052	1	0,4366	$\searrow$
3.SR6	9,6416	1	0,0019	$\searrow$
3.SR7	1,3594	1	0,2437	$\nearrow$
3.SR8	4,2756	1	0,0387	$\nearrow$
3.SR total	22,0738	7	0,0025	
3.Sm2	5,3504	2	0,0689	$\nearrow$
3.Sm3	6,5605	2	0,0376	$\searrow$
3.Sm4	6,4242	2	0,0403	$\nearrow$
3.Sm5	0,8038	2	0,6691	$\sim$
3.Sm6	0,3113	2	0,8558	$\sim$
3.Sm7	0,2605	1	0,6098	$\sim$
3.Sm total	19,7108	11	0,0495	
TEST 3	41,7845	18	0,0012	
2.Ct2	0,0752	1	0,7838	$\sim$
2.Ct3	0,1029	1	0,7483	$\sim$
2.Ct4	0,4850	1	0,4862	$\sim$
2.Ct5	7,9162	1	0,0049	$\searrow$
2.Ct6	2,2752	1	0,1315	$\searrow$
2.Ct7	18,1341	1	$< 0,0001$	$\searrow$
2.Ct total	28,9887	6	$< 0,0001$	
2.Cm2	3,1689	5	0,6740	$\sim$
2.Cm3	22,7771	4	0,0001	$\nearrow$
2.Cm4	6,7083	3	0,0818	$\searrow$
2.Cm5	26,0726	2	$< 0,0001$	$\nearrow$
2.Cm6	2,3881	1	0,1223	$\nearrow$
2.Cm total	61,1150	15	$< 0,0001$	
TEST 2.C	90,1037	21	$< 0,0001$	
TEST 2 + TEST 3	131,8882	39	$< 0,0001$	

Tab. A.5: Results of the RELEASE goodness-of-fit tests for the CJS-model in the juvenile females. For the meaning of the symbols see text.

Component	χ^2	df	p	Direction of deviation
3.SR2	0,7478	1	0,3872	
3.SR3	34,3069	1	$< 0,0001$	↘
3.SR4	0,0026	1	0,9592	∼
3.SR5	28,1007	1	$< 0,0001$	↘
3.SR6	0,1572	1	0,6917	∼
3.SR7	3,6783	1	0,0551	↘
3.SR8	1,5068	1	0,2196	∼
3.SR total	70,3572	7	$< 0,0001$	
3.Sm2	1,1111	1	0,2918	
3.Sm3	1,5787	2	0,4541	
3.Sm4	0,0118	1	0,9135	
3.Sm5	6,5019	4	0,1647	
3.Sm6	7,9360	4	0,0940	
3.Sm7	2,3856	2	0,3034	
3.Sm total	19,5252	14	0,1458	
TEST 3	88,0255	21	$< 0,0001$	
2.Ct2	0,0384	1	0,8447	
2.Ct3	1,1331	1	0,2871	
2.Ct4	1,1021	1	0,2938	
2.Ct5	6,1264	1	0,0133	↘
2.Ct6	0,0155	1	0,9009	
2.Ct7	0,0003	1	0,9856	
2.Ct total	8,4157	6	0,2092	
2.Cm2	0,6242	1	0,4295	
2.Cm3	1,3482	4	0,8531	
2.Cm4	1,3740	2	0,5031	
2.Cm5	1,3989	2	0,4969	
2.Cm6	0,7194	1	0,3963	
2.Cm total	5,4647	10	0,8581	
TEST 2.C	13,8804	16	0,6076	
TEST 2 + TEST 3	101,9059	37	$< 0,0001$	

Tab. A.6: Results of the RELEASE goodness-of-fit tests for the CJS-model in the adult females. For the meaning of the symbols see text.

Component	χ^2	df	p	Direction of deviation
3.SR2	7,9172	1	0,0049	↘
3.SR3	10,8759	1	0,0010	↘
3.SR4	0,0814	1	0,7754	∼
3.SR5	5,6562	1	0,0174	↘
3.SR6	0,0918	1	0,7619	∼
3.SR7	0,0480	1	0,8265	∼
3.SR8	2,1007	1	0,1472	↗
3.SR total	26,7714	7	0,0004	
3.Sm2	8,1410	4	0,0865	↗
3.Sm3	2,7395	2	0,2542	↗
3.Sm4	14,3501	6	0,0260	↘
3.Sm5	0,8021	6	0,9920	∼
3.Sm6	1,1523	4	0,8859	∼
3.Sm7	0,7834	2	0,6759	∼
3.Sm total	27,9684	24	0,2614	
TEST 3	54,7397	31	0,0053	
2.Ct2	0,1230	1	0,7258	∼
2.Ct3	2,6116	1	0,1061	↘
2.Ct4	0,0087	1	0,9259	∼
2.Ct5	7,6818	1	0,0056	↘
2.Ct6	0,0786	1	0,7792	∼
2.Ct7	21,5254	1	$< 0,0001$	↘
2.Ct total	32,0291	6	$< 0,0001$	
2.Cm2	7,8169	5	0,1666	∼
2.Cm3	1,3418	4	0,8542	∼
2.Cm4	0,2476	3	0,9696	∼
2.Cm5	5,8037	2	0,0549	↗
2.Cm6	0,9294	1	0,3350	↘
2.Cm total	16,1395	15	0,3728	
TEST 2.C	48,1686	21	0,0007	
TEST 2 + TEST 3	102,9083	52	$< 0,0001$	

A.3 Goodness-of-fit tests for model ϕ_{a2*t}, p_{m*t}

The GOF test for a model combining transience and trap-dependence is based on capture histories that are split in two subsets: The first subset consists of the capture histories including first release and first recapture (treated as losses on capture) of each individual; the second subset contains the rest of the capture history, starting with the first recapture from the original data which is consequently treated as the first release of a newly marked individual.

The complete test for model ϕ_{a2*t}, p_{m*t} is assembled of three components: C1 is the RELEASE TEST 2.Cm applied to the first data subset; C2 consists of the complete RELEASE test (2 and 3) for the second subset only; C3 corresponds to the test of the null hypothesis that the recapture and survival

Tab. A.7: Results of the goodness-of-fit tests of model ϕ_{a2*t}, p_{m*t}.

Component	χ^2	df	p
juv. males			
C1	28.22	5	< 0.0001
C2	31.35	28	0.1337
C3	29.72	13	0.0052
Total	89.29	46	< 0.0001
ad. males			
C1	27.18	5	< 0.0001
C2	31.32	20	0.1337
C3	21.06	13	0.0052
Total	79.56	38	< 0.0001
juv. females			
C1	2.01	5	0.8472
C2	30.57	23	0.1337
C3	31.10	13	0.0033
Total	63.69	41	0.0131
ad. females			
C1	2.04	5	0.8432
C2	48.55	24	0.0022
C3	26.15	13	0.0162
Total	76.74	42	0.0008

parameters do not differ between the two subgroups specified by the split capture histories, which can be obtained as likelihood ratio test using e.g. MARK. Further technicalities are provided by Viallefont *et al.* (1995). The test statistics for the pipistrelle bats are summarised in Table A.7.

A.4 Summary statistics for closed models

The following table (A.8, next page) provides the essential summary statistics needed to estimate (re-)capture probabilities and population sizes using the closed models of program CAPTURE.

Tab. A.8: Summary statistics for closed models of the capture-recapture data of the pipistrelle bats caught at the hibernaculum Marburg Castle during summer swarming and autumnal immigration 1996. Capture occasions are pooled according to the procedure described in the methods section. $\mathrm{n_j}$ = number of animals caught at occasion j; $\mathrm{M_j}$ = number of marked individuals in the population at the time of sample j; $\mathrm{u_j}$ = number of unmarked individuals caught on occasion j; $\mathrm{f_j}$ = frequency of capture, i.e. the number of individuals that have been captured j times.

Occasion j	1	2	3	4	5	6	7	8	9	10	11	12
ad. males												
$\mathrm{n_j}$	83	62	89	101	71	161	109	105	53	51	177	—
$\mathrm{M_j}$	0	83	144	232	325	385	527	620	702	744	779	—
$\mathrm{u_j}$	83	61	88	93	60	142	93	82	42	35	153	—
$\mathrm{f_j}$	816	104	10	2	0	0	0	0	0	0	0	—
ad. females												
$\mathrm{n_j}$	36	28	126	197	219	214	251	141	159	106	106	180
$\mathrm{M_j}$	0	36	63	186	382	595	801	1033	1164	1306	1397	1489
$\mathrm{u_j}$	36	27	123	196	213	206	232	131	142	91	92	134
$\mathrm{f_j}$	1497	115	9	1	1	0	0	0	0	0	0	0
juveniles												
$\mathrm{n_j}$	46	191	133	147	109	68	316	416	225	56	177	—
$\mathrm{M_j}$	0	46	233	363	502	600	659	952	1314	1508	1553	—
$\mathrm{u_j}$	46	187	130	139	98	59	293	362	194	45	130	—
$\mathrm{f_j}$	1504	159	18	2	0	0	0	0	0	0	0	—

References

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock (1987): *Design and analysis methods for fish survival experiments based on release-recapture*, vol. 5 of *American Fisheries Society Monographs*. Bethesda, Maryland: American Fisheries Society.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines (1990): Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**: 1–97.

Viallefont, A., F. Cooke, and J.-D. Lebreton (1995): Age-specific costs of first time breeding. *The Auk* **112**: 67–76.

B. Winter immigration and emigration dynamics

The dynamics of hibernal immigration to and emigration from the hibernaculum at Marburg Castle is a complex process that could not be presented in the original manuscript (Chapter 6) in a simple manner using a single graph when several years are considered. The following series of figures illustrates immigration and emigration processes over time and their coincidence with fluctuations of ambient temperatures in a depictive manner separately for each winter.

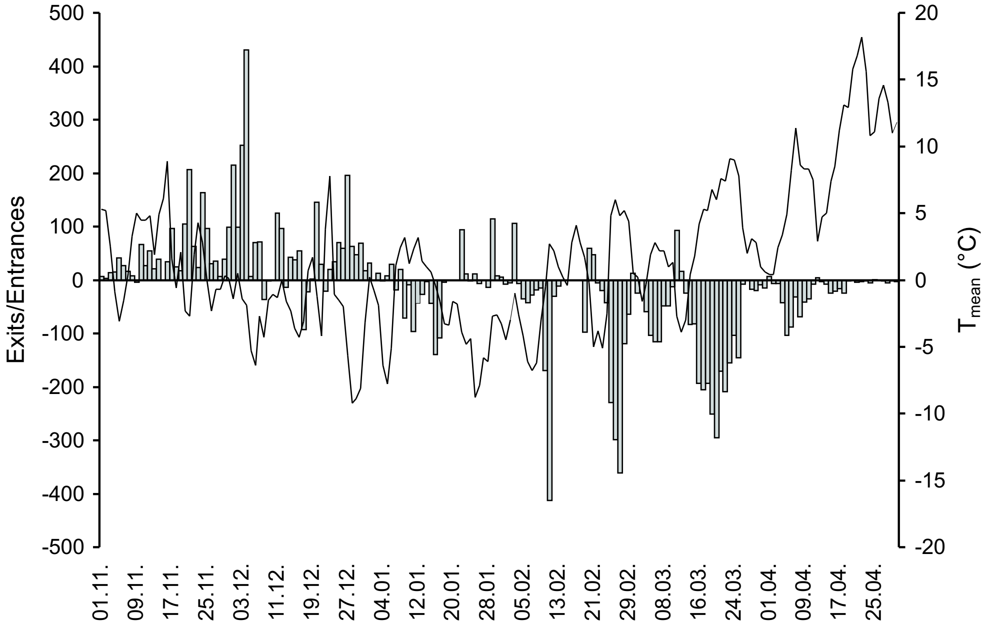


Fig. B.1: Daily numbers of immigrating and emigrating bats as light barrier balances (columns) and ambient temperature (line) in the winter 1995/96.

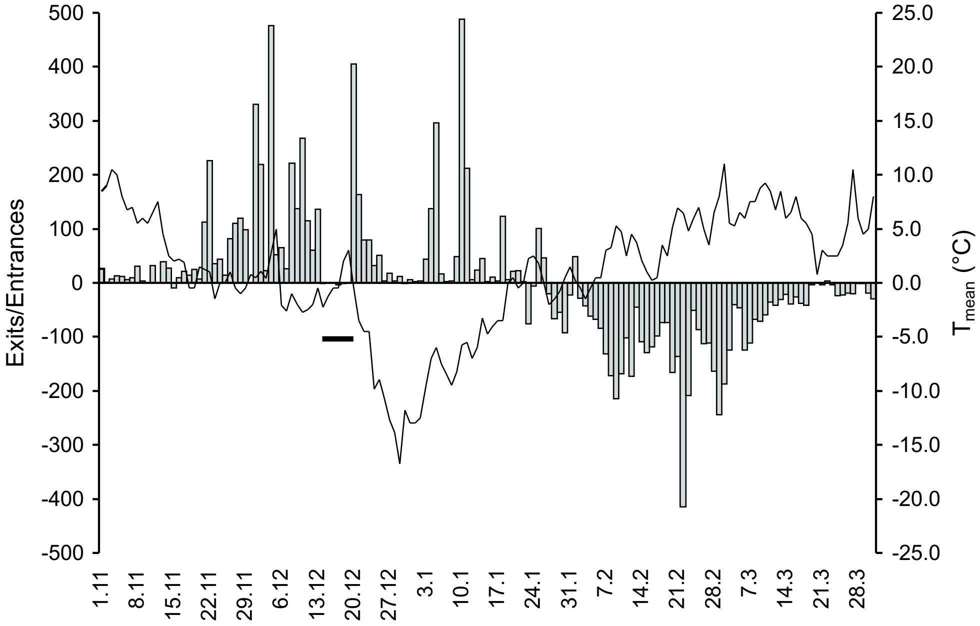


Fig. B.2: Daily numbers of immigrating and emigrating bats as light barrier balances (columns) and ambient temperature (line) in the winter 1996/97. The black bar indicates periods of data loss due to equipment failure.

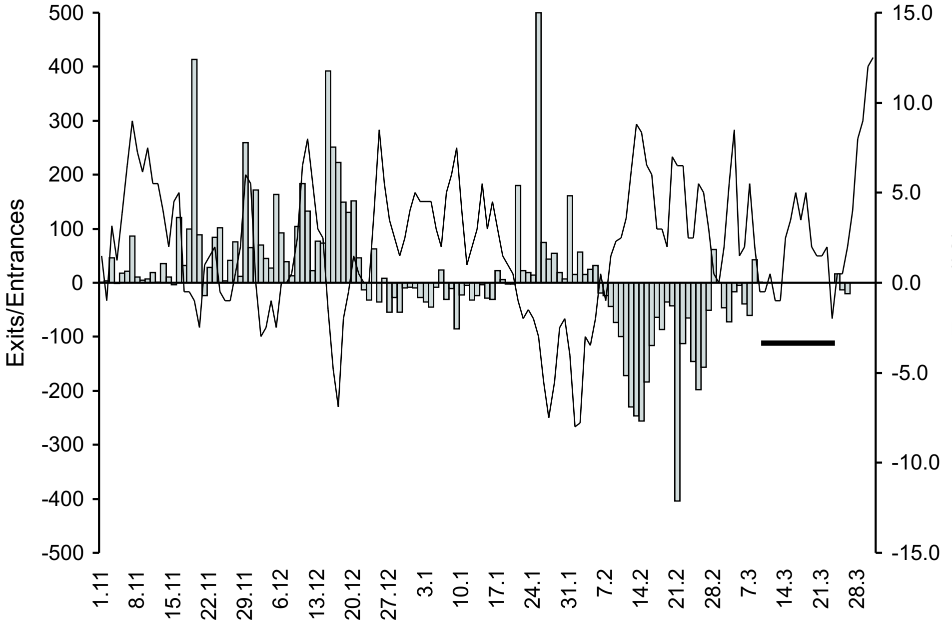


Fig. B.3: Daily numbers of immigrating and emigrating bats as light barrier balances (columns) and ambient temperature (line) in the winter 1997/98. The black bar indicates periods of data loss due to equipment failure.

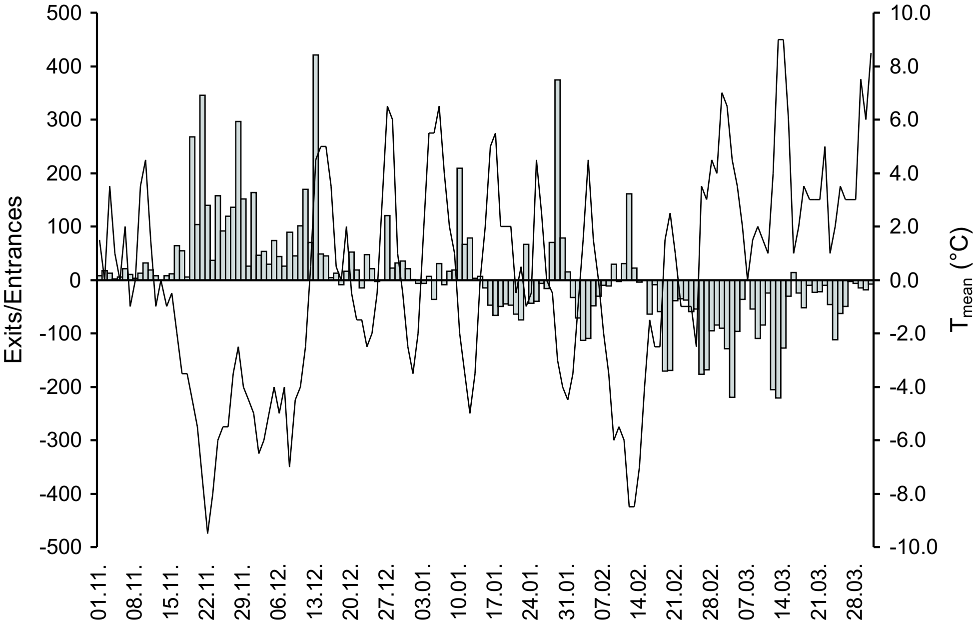


Fig. B.4: Daily numbers of immigrating and emigrating bats as light barrier balances (columns) and ambient temperature (line) in the winter 1998/99.

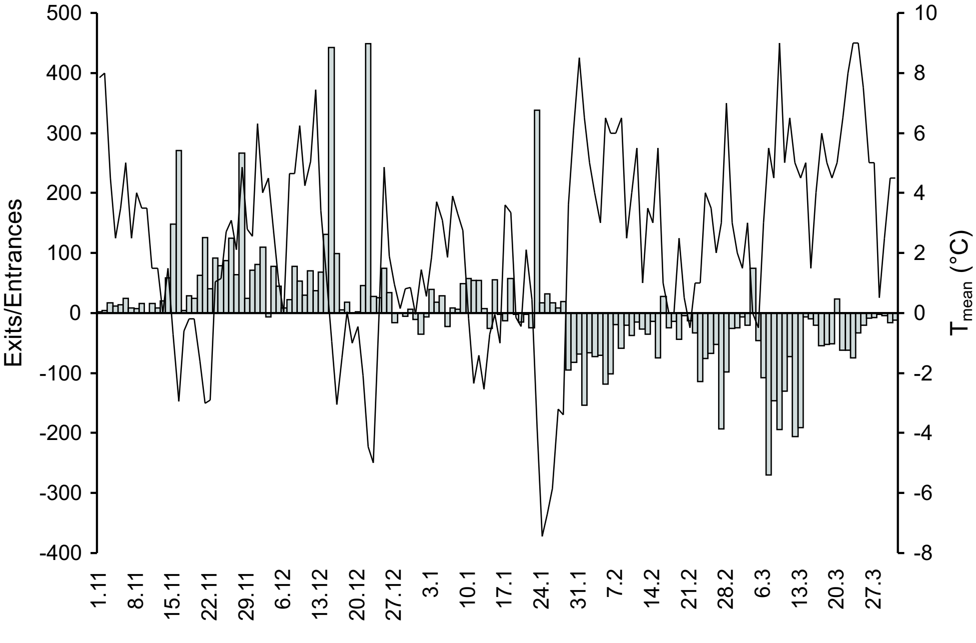


Fig. B.5: Daily numbers of immigrating and emigrating bats as light barrier balances (columns) and ambient temperature (line) in the winter 1999/2000.

C. Acknowledgements

At this point I wish to acknowledge – in some more detail than this was possible in the individual manuscripts – the assistance of all the people who contributed to the success of this thesis.

This work was done under supervision of Professors Dr. Hans-Wilhelm Bohle and Dr. Roland Brandl. Thanks for their time and advice.

This work would not have been feasible without existence of the "E&E-Project" "Schaffung eines Quartierverbundes für gebäudebewohnende Fledermausarten durch Sicherung und Ergänzung des bestehenden Quartierangebotes an und in Gebäuden" by the German Federal Agency for Nature Conservation (thanks to Dr. Peter Boye from the Federal Agency). The colleagues in the project, namely Sandra Hüttenbügel, Janna Smit-Viergutz, and Matthias Simon, were heavily engaged in my work at all stages, as well as I hope that the entire bat project benefitted from our mutual help.

Furthermore, there were many people without whose valuable assistance the extensive field work (catching bats) would not have been possible, as there are – in alphabetical order: Dorothea Adelberg, Edith Albertz, Christina Belle, Daniela Bergmann, Roman Biek, Antje Burgard, Eva Daubert, Martin Dresler, Christian Engel, Miro Ferreri, Frank Feyerabend, Natascha Friedrich, Fabian Frohn, Oliver Geuß, Svenja Hampl, Frank Heilert, Martina Huxol, Kathrin Jeß, Dr. Andreas Kaiser, Claudia Kaißling, Heidrun Kern, Andreas Kiefer, Jens-Peter Kiel, Kristina König, Heiko Köstermeyer, Karl Kugelschafter, André Kuklik, Solveig Lubeley, Claudia Maerker, Daniel Manwire, Katharina Markmann, Andreas Marten, Christine Meyer-Cords, Matthias Piontek, Mirco Plath, Dörte Poszig, Maren Prigge, Richard Rehn, Nadine Reisinger, Silvia Rhiel, Inga Roedenbeck, Almut Schemm, Jürgen Schicker, Sandra Schweizer, Niels Spilker, Matina Treutlein, Ilka Westermann. Apologies to any folks I may have forgotten.

Thanks to the "weathermen" Markus Kaempf, Tilman Holfelder, and Andreas Knoll; Sonja Klein and Andreas Marten helped to prepare the wind speed data.

I am grateful to my family, namely my mother and my sister, for their support whenever needed.

Finally, I want to express my gratitude to Claudia for her infinite patience, warmth and love.

Schulischer und akademischer Werdegang

Persönliche Daten

Name	Thomas Sendor
Geburtsdatum	15.03.1967
Geburtsort	Starnberg
Staatsangehörigkeit	deutsch

Schulbildung

1973–1977	Grundschule Schäftlarn
1977–1986	Gymnasium Icking Abschluß: Allgemeine Hochschulreife

Studium

1988–1991	Studium der Chemie an der Universität München
1991–1992	Grundstudium der Biologie an der Universität Mainz
1992–1997	Hauptstudium der Biologie an der Universität Marburg
06/96–06/97	Diplomarbeit in Zoologie bei Herrn Prof. Dr. H.-W. Bohle Thema: Populationsökologische Untersuchungen zu Quartiernutzungsstrategien der Zwergfledermaus mit Schwerpunkt auf einem ganzjährig genutzten "Winterquartier"; Gesamtnote: "sehr gut"

Promotion

1998–2002	Doktorand in der Arbeitsgruppe Tierökologie an der Universität Marburg; Promotionsthema: "Population ecology of the pipistrelle bat (*Pipistrellus pipistrellus* Schreber, 1774): the significance of the year-round use of hibernacula in the context of life histories"