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Effects of age and season on body mass and reproductive condition in male Daubenton's bats (*Myotis daubentonii*)

Jorge A. Encarnação*, Uwe Kierdorf, and Volkmar Wolters

Justus Liebig University, Department of Animal Ecology, Giessen, Germany

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ABSTRACT

We analyzed the effects of age and season on body mass and reproductive condition in male Daubenton's bats (*Myotis daubentonii*) from a study area in central Germany, which were captured during April to October of the years 1998-2003. On first capture, animals (n=336) were banded and classified as either young of the year or adults (i.e. males ≥ 1 year of age). On recapture, animals first caught as young of the year could be assigned an exact age in years. Epididymal distension in young of the year indicated that some males had reached sexual maturity (defined as onset of spermatogenesis) already in their year of birth, while others did so in their second summer. Body mass and epididymal distension showed pronounced variation related to age and season, with highest values reached in late summer/early autumn. Generally, older males (>2 years of age) tended to be heavier and in better reproductive condition than younger ones. Our data suggest that the physical condition of male Daubenton's bats, and their reproductive condition, both increase after the initial onset of fertility (start of spermatogenesis) until three years of age. This relatively late physical maturation is in line with other life-history traits characterizing long-lived bats as K-strategists among small mammals.

Key words: body mass, epididymal distension, life history, maturation, *Myotis daubentonii*, reproduction

Introduction

The typical life history of small mammals is characterized by early physical maturation, start of breeding at young age, high number of offspring per litter and short life-span (MILLAR, 1977; MILLAR and HICKLING, 1991; PROMISLOW and HARVEY, 1990). Bats are an exception to this rule. They exhibit unusual life histories for small-sized mammals in that they are long-lived, develop more slowly and produce few offspring

* Contact address:

Dr. Jorge A. Encarnação, Justus Liebig University of Giessen, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany, Phone: +49 641 99 35714; Fax: +49 641 99 35709; E-mail: Jorge.A.Encarnacao@allzool.bio.uni-giessen.de

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per litter (GAISLER, 1989; PROMISLOW and HARVEY, 1990; AUSTAD and FISCHER, 1991; PARTRIDGE and BARTON, 1993; HOLMES and AUSTAD, 1994; WILKINSON and SOUTH, 2002).

All bat species of the temperate climate zones are insectivorous and subject to seasonal fluctuations in the availability of their prey. Food intake, energy expenditure, and reproductive activity of bats from temperate zones are thus tightly constrained by both ambient temperature and food availability (WILSON, 1979). Hibernation is an adaptation to overcome the food shortage in winter, and hibernating species exhibit pronounced seasonal variation in body mass (RANSOME, 1990). To cover their energy demands during hibernation, the animals build up body-fat reserves after the breeding season (EWING et al., 1970; KUNZ et al., 1998; SPEAKMAN and ROWLAND, 1999). During hibernation, these fat reserves gradually decline. In consequence, bats are lightest when they leave their hibernation roosts. Mating activity starts in late summer when the animals have again increased their body mass and are in best physical condition.

While the seasonal variation in body mass and in reproductive condition of adult male Daubenton's bats and male young of the year were analyzed in previous studies (ENCARNAÇÃO et al., 2004a,b), the question of differences between male age classes with respect to these factors has not been studied in this species so far. Such studies require information on the age of the bats, which can only be obtained by individual marking of animals in a given area and subsequent recapturing over a period of several years. The present study reports data on body mass and epididymal distension in free-living, male Daubenton's bats from a German study area in which such marking and recapturing was performed over 6 years. We analyzed whether differences of these parameters existed depending on animal age and season of the year. Main interests were to study at what age males reach sexual maturity, and whether physical condition and reproductive condition of male Daubenton's bats tend to improve beyond their first year of life.

Materials and methods

The study was conducted in the years 1998 to 2003 near Staufenberg (Hesse, Central Germany) in the summer habitat of a male dominated *M. daubentonii* population. Males use tree roosts singly or in groups of up to 51 individuals in a mixed forest (highest elevation 274 m a.s.l.) that is situated at the border of a valley and is dominated by deciduous trees. In the valley, a brook with accompanying vegetation is used as a flight-path to a fishpond (170 m a.s.l.) situated a few hundred meters away. The pond and the brook are the most important foraging areas of the population. (ENCARNAÇÃO et al., 2002).

Mist-netting was conducted from April to October during fly-off time at different

locations along the flight-path to the fishpond. In addition to mist-netting, animals were caught with a funnel-shaped basket trap at known roosts.

On first capture, adult males and young of the year were distinguished based on the presence of unfused and translucent phalangeal epiphyses (ANTHONY, 1988; RACEY, 1988) and the presence of a black, well-defined „chin-spot" (RICHARDSON, 1994) in the latter. Most of the young are born between mid-June and early-July. In total, 336 males were captured and marked by forearm-banding (Fig. 1). Individuals that were marked as young of the year could be assigned an exact age (in years) on first capture and recapture, respectively. Individuals that were already adult when caught the first time, could on recapture be assigned only a minimum age.

Fig. 1. Male Daubenton's bat marked by forearm-banding at fly-off from the roost (photo: Marko König).

Body mass was measured with a digital balance (Kern, EM 150-1, Ballingen-Frommern, Germany) to the nearest 0.1 g. Degree of distension of the cauda epididymidis was visually estimated and recorded as 0, 25, 50, 75 or 100% (Fig. 2). Values were recorded for each epididymis separately, and the mean of the two recordings per animal was used for evaluation.

General Linear Model analysis (GLM) was performed to study the effects of age and day of the year (season) on body mass and epididymal distension. All animals were assigned to one of the following five age classes: young of the year (0), 1, 2, and 3 year

olds, and males ≥ 4 years of age (4+). Age class 4+ comprised animals that were either known to be 4 years of age, because they were first captured and marked as young of the year, or older animals that were first captured and marked as adults and whose exact age was not known. Forward stepwise selection was applied in order to exclude non-significant independent variables from the model.

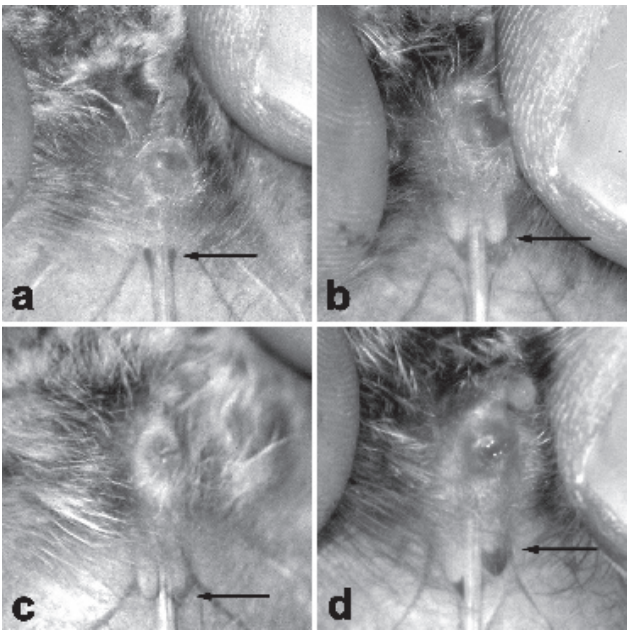

Fig. 2. Ventral view of genital region of male Daubenton's bats showing different degrees of epididymal distension (arrows). (a) un-distended caudae epididymides (0%), (b) epididymal distension 50%, (c) epididymal distension 100%, (d) epididymal distension: left 75%, right 25% (from ENCARNAÇÃO et al., 2004b)

In addition, we performed a comparison of body mass and degree of epididymal distension among three age groups (young of the year (0), 1-2 yr old animals, >2 year old animals) in each of the following three periods: late spring (15 April – 14 June), mid-summer (15 June – 14 August) and late summer/early autumn (15 August – 14 October). Moreover, we compared the differences in body mass and epididymal distension between the periods for each of the three age groups. Date were compared by non-parametric ANOVA (Kruskal-Wallis), followed by multiple pairwise comparisons with the Mann-Whitney-U-Test. To correct for error accumulation due to replicate testing, we applied

Bonferroni α-adjustment in the case of the pairwise comparisons.

The study was performed in compliance with the current animal care and nature conservation laws of Germany and approved by the nature conservation authority of the administrative district of Giessen, federal state of Hesse.

Results

Both body mass and epididymal distension showed pronounced seasonal variation in all age classes (Figs 3 and 4). A particularly steep increase in body mass and epididymal distension was recorded for older males (age classes 3 and 4+) during late summer.

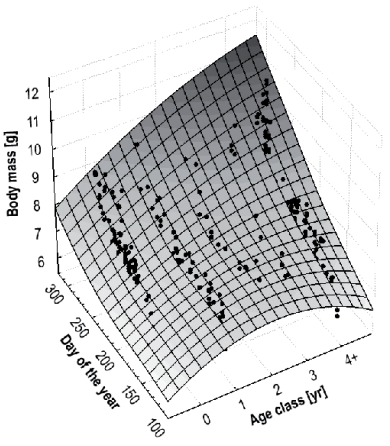

Fig. 3. 3D-plot showing the seasonal variation of body mass for the different age classes of male Daubenton's bats; 0 = Young of the year, 4+ animals ≥ 4 years of age.

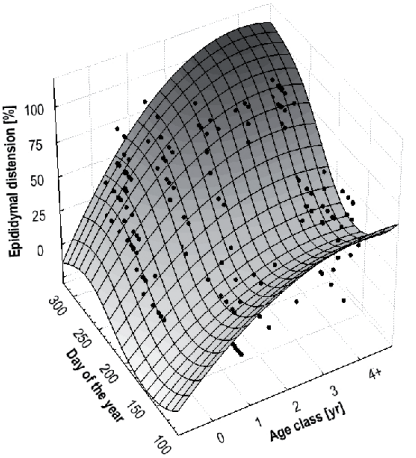

Fig. 4. 3D-plot showing the seasonal variation of epididymal distension for the different age classes of male Daubenton's bats; 0 = Young of the year, 4+ animals ≥ 4 years of age.

Between mid-August and October, all captured adult males showed at least some degree of epididymal distension, indicating that they had undergone spermatogenesis. Epididymal distension could also be observed in some young of the year, indicating previous spermatogenetic activity. A visible distension of the caudae epididymides in animals from this age class was first recorded in August and values peaked in September. However, contrary to the situation in adult males, young of the year with un-distended caudae epididymides were recorded in all months from birth until the end of the seasonal

observation period. These findings indicate that not all young of the year had reached sexual maturity already in their year of birth.

GLM analysis revealed a significant main effect of the variables "Day of the year" (season) and "Age class" on body mass. In addition, the interaction of the two variables was significant (Table 1). For epididymal distension, the effect of the variable "Day of the year" and the interaction effect "Age class × Day of the year" were significant (Table 1). This indicates that an age influence on epididymal distension (reproductive condition) was only given during a certain period of the year, i.e. during the reproduction period.

Table 1. Results of the GLM analysis for body mass and epididymal distension of male Daubenton's bats.

	Body mass		Epididymal distension	
	SS	p-Value	SS	p-Value
Intercept	215.1	< 0.000001	21797.2	< 0.000001
Day of the year	33.7	< 0.000001	85726.8	< 0.000001
Age class	14.8	0.000182	pooled	n.s.
Age class x Day of the year	16.5	0.000059	100902.6	< 0.000001
Error	208.1		253577.9	

In late spring, no significant differences in body mass existed between 1-2 yr old males and older ones. Young of the year were not yet present at that time of the year. In mid-summer, young of the year were significantly lighter than both groups of older males. In late summer/early autumn, younger males were always significantly lighter than older ones (Fig 5, Table 2). A significant increase in body mass from earlier to later periods was observed in >2 yr old males (Fig 5)

In late spring, epididymal distension in >2 yr old males was significantly higher compared with 1-2 yr old males, while in mid-summer epididymal distension in >2 yr old males was significantly higher than in young of the year. In late summer/early autumn, both 1-2 yr old males and >2 year old males had significantly more distended caudae epididymides than young of the year (Fig 6, Table 2).

Epididymal distension in >2 yr old males significantly declined from late spring to mid-summer, and afterwards significantly increased from mid-summer to late summer/early autumn. In this age-group, values for late summer/early autumn were significantly higher than for late spring. In 1-2 yr old males a significant increase from late spring to late summer/early autumn was recorded, whereas in young of the year a significant increase occurred from mid-summer to late summer/early autumn (Fig 6).

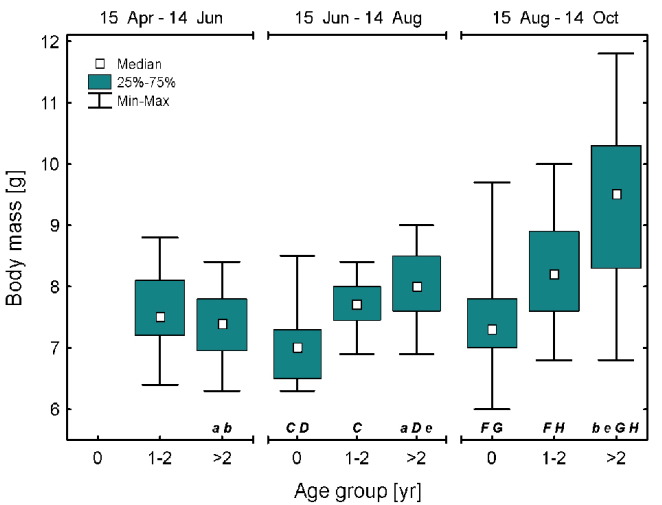

Fig. 5. Variation of body mass of male Daubenton's bats between age groups and seasons. Upper case letters indicate significant differences between age groups within the same period, lower case letters significant differences between periods for a given age group (Mann-Whiney-U-tests with Bonferroni α-adjustment: P<0.05).

Table 2. Body mass and epididymal distension in different age groups of male Daubenton's bats during late spring (15 April – 14 June), mid-summer (15 June – 14 August) and late summer/early autumn (15 August – 14 October).

Period [Date]		15 April – 14 June			15 June – 14 August			15 August – 14 October		
Day of the year		106 – 166			167 – 227			228 – 288		
Age group [yr]		0	1-2	>2	0	1-2	>2	0	1-2	>2
Individuals [n]		0	31	40	22	28	51	76	23	52
Body mass [g]	Mean (SD)	-	7.6 (0.6)	7.4 (0.6)	7.0 (0.6)	7.7 (0.4)	8.0 (0.5)	7.5 (0.8)	8.2 (0.9)	9.3 (1.3)
	Median	-	7.5	7.4	7.0	7.7	8.0	7.3	8.2	9.5
	Min-Max	-	6.4-8.8	6.3-8.4	6.3-8.5	6.9-8.4	6.9-9.0	6.0-9.7	6.8-10.0	6.8-11.8
Epididymal distension [%]	Mean (SD)	-	12.9 (17.2)	39.4 (22.6)	6.3 (16.7)	17.0 (24.6)	23.5 (22.3)	33.1 (32.6)	74.5 (21.2)	83.2 (16.0)
	Median	-	0	43.8	0	0	25	25	75	87.5
	Min-Max	-	0-50	0-75	0-75	0-100	0-100	0-100	25-100	37.5-100

Discussion

The study demonstrated age- and season-related variation in both physical (expressed as body mass) and reproductive condition (expressed as epididymal distension) of male Daubenton's bats. Differences in body mass and epididymal distension between age groups were most pronounced in late summer/early autumn.

Generally, older males (>2 years) were heavier and in better reproductive condition than younger ones, with body mass and epididymal distension showing a tendency to increase with animal age at least until the third year of life. This suggests that the development of physical and reproductive condition in male Daubenton's bats was not completed within one year; rather physical and reproductive condition increased further during later life. It can, therefore, be concluded that the process of physical and related reproductive maturation in male Daubenton's bats extends long beyond the initial onset of fertility, which can occur already in the year of birth. Corresponding findings have been reported for males of other long-lived mammal species (e.g. LINCOLN, 1998).

Our data on the degree of epididymal distension in young of the year indicate that male Daubenton's bats can undergo spermatogenesis for the first time already at about two to three months of age. This is in principal agreement with the findings of KOKUREWICZ and BARTMAŃSKA (1992) who, based on field observations and histological studies on reproductive organs, stated that male Daubenton's bats can reach sexual maturity, i.e. start to produce viable spermatozoa (RACEY, 1974), already in their year of birth. Male young of the year are thus in principle capable to participate in reproduction already prior to their first hibernation period. The findings of the present study further suggest that males that do not achieve sexual maturity in their year of birth do so in their second summer.

In a study on brown long-eared bats (Plecotus auritus) from Scotland, ENTWISTLE et al. (1998) found that, while most males reached sexual maturity at about 15 months of age, 29% showed a degree of testicular and epididymal development at three months of age indicating that they had reached sexual maturity already in their first autumn. Because individual reaching sexual maturity already in their first autumn were relatively heavy, ENTWISTLE et al. (1998) concluded that attainment of sexual maturity by male bats in their year of birth was probably dependent on their physical condition.

Based on the findings of the present study it can be hypothesized that mating success of male Daubenton's bats might vary with age and body mass because prime-aged, heavy males might be able to out-compete lighter (younger) males regarding the access to females. It is further supposed that particularly young of the year are out-competed, which are lighter than adult males (≥ 1 yr of age). In a previous study (ENCARNAÇÃO et al., 2004a), we showed that first in October, young of the year are no longer significantly

lighter than adult males. If the above reasoning is correct, it would mean that, although they are potentially capable of reproducing, young of the year may be prevented from doing so by competition with older males and may therefore not form part of the effective breeding population. So far no data is available on the differential reproductive success of male Daubenton's bats of different age and/or body mass that would allow the above hypothesis to be tested. However, recent observations provide some circumstantial evidence to support this hypothesis, in showing that during late summer heavy adult males tend to spent longer periods of the night in day roosts (potential mating roosts) than lighter males (ENCARNAÇÃO et al., 2006)

In conclusion, the results of the present study indicate that male Daubenton's bats can reach sexual maturity already at about three months of age. Our data further suggest that physical and reproductive condition of male Daubenton's bats increases until three years of age. This late maturation is in principal agreement with findings on other life-history traits, such as the low number of offspring per litter (GAISLER, 1989), which characterize long-lived bats as K-strategists. This is in marked contrast to other mammals of similar size, such as shrews, which exhibit early physical and reproductive maturation and can be classified as r-strategists (BARCLAY and HARDER, 2003).

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ENCARNAÇÃO, J. A., U. KIERDORF, V. WOLTERS: Utjecaj starosti i godišnjeg doba na tjelesnu masu i rasplodnu kondiciju mužjaka Daubentonovog šišmiša (*Myotis daubentonii*). Vet. arhiv 76, S239-S249, 2006.

SAŽETAK

U radu su pretraženi utjecaj starosti i godišnjeg doba na tjelesnu masu i rasplodnu sposobnost mužjaka Daubentonovog šišmiša (*Myotis daubentonii*) s područja središnje Njemačke, uhvaćenih u razdoblju od travnja do listopada, od 1998. do 2003. godine. Tijekom prvog hvatanja životinje (n=336) su označene i svrstane prema starosti u dvije kategorije, mlade (1 godina) i odrasle (starije od 1 godine). Tijekom ponovnog hvatanja, mlade životinje iz prošlog ulova bilo je moguće svrstati prema točnoj dobi. Povećanje epididimisa u ponekih mladih mužjaka ukazalo je na činjenicu da spolna zrelost (početak tvorbe spermija) može započeti već u prvoj godini života. Ostali mužjaci su spolno sazreli sljedećega ljeta. Tjelesna masa i povećanje epididimisa značajno su kolebali ovisno o starosti i godišnjem dobu, uz najveće vrijednosti u kasno ljeto i ranu jesen. Općenito, stariji mužjaci (>2 godine) teži su i u boljoj rasplodnoj kondiciji od mlađih. Naši rezultati ukazuju da fizička i rasplodna kondicija mužjaka Daubentonovog šišmiša rastu po početku tvorbe spermija sve do 3. godine starosti. Ovakvo, relativno kasno tjelesno sazrijevanje u skladu je s ostalim životnim osobitostima dugoživućih šišmiša.

Ključne riječi: tjelesna masa, povećanje epididimisa, *Myotis daubentonii*, sazrijevanje, rasplođivanje