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HAREM SIZE AND MALE MATING TACTICS IN *NYCTALUS LEISLERI* (KUHL, 1817) (CHIROPTERA, VESPERTILIONIDAE)

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ABSTRACT - Between 1994 and 2008, we studied the structure of harems in *Nyctalus leisleri* and factors that determine their size by monitoring 90 bat-boxes placed in a beech forest in the natural reserve Pian degli Ontani (Tuscany, northern Italy). The number of females in the harem positively correlated with the number of males defending a harem. The number of males in the mating area did not significantly influence harem size, whilst we found a significant correlation between the variance in harem size and mean harem size. This may be explained by the existence of an uneven aggregation favouring few males. A strong relation was found between males' age (estimated by teeth wear) and mean harem size.

Key words: Bats, *Nyctalus leisleri*, bat-box, mating behaviour, Italy

RIASSUNTO - ***Dimensioni del harem e tattiche riproduttive dei maschi di* Nyctalus leisleri *(Kuhl, 1817) (Chiroptera, Vespertilionidae)*.** Sono presentati i risultati di uno studio sulla struttura del harem in *Nyctalus leisleri* e sui fattori che ne determinano la dimensione. Tra il 1994 e il 2008, sono stati monitorati 90 rifugi artificiali (bat-box) per pipistrelli collocati in una faggeta della Riserva Statale di Pian degli Ontani (Pistoia, Toscana). Il numero di femmine presenti nel harem è risultato positivamente correlato con il numero di maschi presenti nell'area di accoppiamento. Il numero di maschi presenti non influenza la dimensione media del harem mentre una significativa correlazione positiva è stata evidenziata tra il valore della varianza delle dimensioni del harem e la sua dimensione media. Tale relazione suggerisce che le femmine tendono ad aggregarsi, favorendo i maschi più competitivi.
Infine è stato evidenziato un modello generale dove sia i maschi giovani sia quelli ad età più avanzata (stimata in base all'usura dei denti) hanno minor capacità di formare harem con un numero elevato di femmine.

Parole chiave: Chiroptera, *Nyctalus leisl,* bat-box, comportamento di accoppiamento, Italia

INTRODUCTION

Several studies have demonstrated that mating patterns in mammals, particularly bats, depend on the behaviour of females (see Clutton-Brock, 1989; Altringham, 1996; McCracken and Wilkinson, 2000). When females ranges are especially large, i.e. they are particularly mobile, male bats tend to occupy tree roosts and call from there to advertise their presence. In this way,

males try to attract as many females as possible in order to aggregate temporary harems.
Leisler's bat (*Nyctalus leisleri*, Kuhl, 1817) is a medium-sized, western Palaearctic species, with scattered records in the western part of the eastern Palaearctic. It is widely distributed in Europe from Portugal and the British Isles to western Russia (Bogdanowicz and Ruprecht, 2004). This species has a migratory behaviour (Ohlendorf *et al.*, 2000; Hoch *et al.*, 2005; Hutterer *et al.*, 2005) with movements of thousands of kilometres inside the European continent.
Although the species exhibits a mating system characterized by resource defence polygyny (Bogdanowicz and Ruprecht, 2004), its mating behaviour is still poorly known. As with other highly migratory species, e.g. *Pipistrellus nathusii* (Petersons, 1990; Jarzembowski, 2003), the mating behaviour of *N. leisleri* is strongly influenced by female migration, which prevents the formation of stable harems over time. Females generally move from breeding areas to wintering grounds following north-east to south-west migratory routes (Bogdanowicz and Ruprecht, 2004; Hutterer *et al.*, 2005). When crossing mating territories, strong sexual selection results in a high reproductive success for a few males while others fail to mate, supporting the hypothesis of a strong link between polygyny and sexual selection (Wade and Shuster, 2004). Heckel and von Helversen (2002) also suggest that mating tactics in males may vary with their age.
We analysed harem formation in *N. leisleri*, in order to address two main issues: i) to quantify harem size variation, gaining insights in the female per-harem distribution patterns, ii) to assess the success of different males in forming harems over time.

STUDY AREA AND METHODS

The study was carried out between 1994 and 2008 in a 80-100 years old beech forest in the Pian degli Ontani Nature Reserve (Pistoia, Tuscany). In total, 90 bat boxes (74 "2F Universal" and 16 "2FN Special" bat boxes, Schwegler, Germany) were located in six circular areas, each with a radius of about 50 m, including 14-18 boxes arranged in pairs. Each pair was hung to a tree at a height of about 5 m and oriented randomly. The six areas were 200-300 m apart and located at an altitude between 1200 m a.s.l. and 1400 m a.s.l.
Bat boxes were surveyed every two weeks in summer (June - September) and monthly during the rest of the year. Bats found inside the boxes were sexed, aged and weighed; the maximum length of both their testicles and buccal pads was measured (Dondini *et al.*, 2003). Age was estimated by visually assessing teeth wear, rating it on a 0 to 4 scale (0 = perfectly pointed teeth, 4 = dentition extremely worn out). Reproductive status and harem size were also recorded. In particular, harem size was defined as the maximum number of females found with a male during each mating season. From May 1996, all bats were ringed (rings produced by Lambournes Ltd. snf coded WWF Italy C ####; ring size: 4.2 mm). Analyses on harem size were conducted on the whole 1994-2008 dataset, whereas the effect of age on harem forming success was assessed on a 2003-2008 subset of our data.
Kolmogorov-Smirnov's non parametric test was employed to evaluate the frequency distribution of harem size. Variance was used as an index of dispersal of harem size. A linear regression between variance in ha-

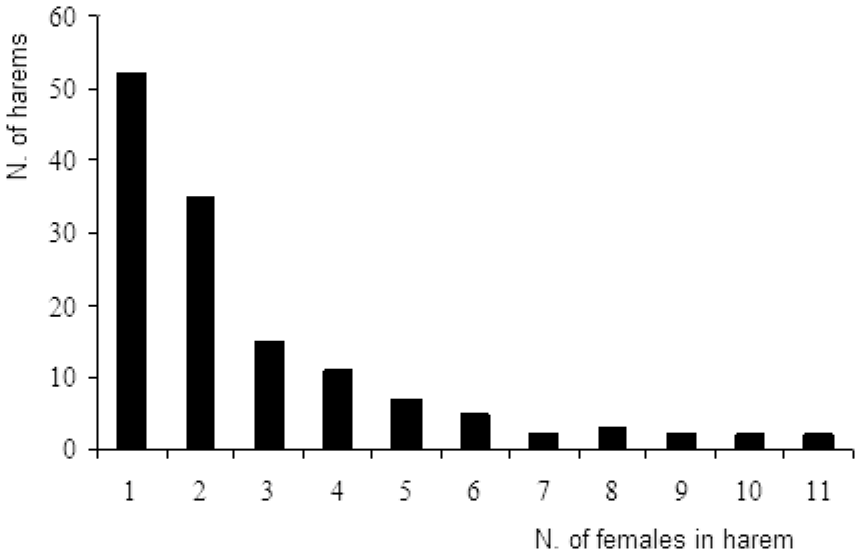

Figure 1 - Harem size in *Nyctalus leisleri* (1994-2008).

rem size (Vh) and mean harem size (H) was used to test whether females tend to aggregate around a few males (Wade and Shuster, 2004).

In particular, we compared two groups of males whose ability to form harem was followed for several years. The influence of bats' age on the average harem size was assessed by means of a polynomial regression between mean harem size and age, as estimated by observing teeth wear.

Statistical analysis was performed with Easystat software (Vannini, 1991) and with PAST, a free data analysis package (Hammer *et al.*, 2009).

RESULTS

The distribution of harem size in the period 1994-2008 (Fig. 1) showed great asymmetry and was log-normal distributed (D = 0.72, P<0.01). Most males (37%) were associated to a single female. Harems with more than 4 females accounted for 25% of all cases. There was a significant positive relation between the variance in harem size and mean harem size (R^2 = 0.42, N = 15, P < 0.01) (Fig. 2).

Mean harem size ranged from 1.38 females in 2005 to 4.4 females in 2002 (Table 1). The number of females dwelling in the mating area increased with that of males defending a harem (R^2 = 0.85, P<0.001, N = 15; Fig. 3).

We found no significant relation between either mean harem size and the number of males present in the area (R^2 = 0.20, N = 14, P = N.S.) or harem variance and the number of males (R^2 = 0.21, N = 14, P = N.S.). The percentage of males which never associated with any female ranged between 0% in 1995 and 80% in 1998, with a per cent mean value calculated over the 14 years of study of 43% (Table 1).

We identified two mating groups. A first group (group 1) of males increased harem size after a phase of low success in attracting females (Fig. 4), while a second group (group 2) of males showed

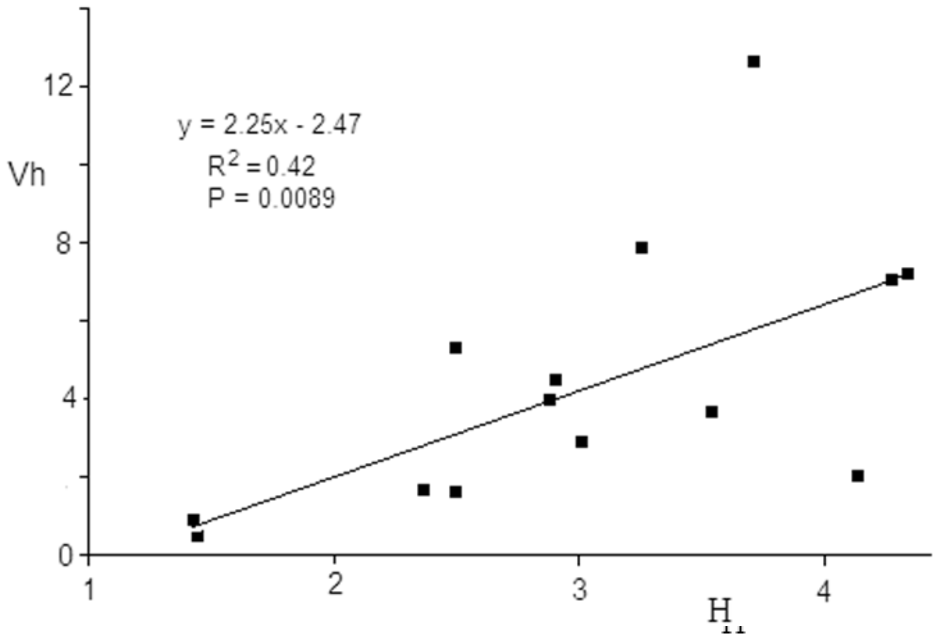

Figure 2 - Linear regression between variance in harem size (Vh) and mean harem size (H).

Table 1 - Parameters of the harem of *N. leisleri*. H = mean harem size; Vh = variance in harem size; N. h.m. = number of males with harem; N. m. = number of males; N. f. = number of females; 1-(N. h.m./N. m.) = proportion of males which did not form a harem.

Year	H	Vh	N. h.m.	N. m.	N. f.	1-(N. h.m./N. m.)
1994	2.36	1.65	11	13	26	0.15
1995	2.91	3.90	22	22	64	0
1996	2.85	4.64	14	24	41	0.42
1997	2.36	1.91	13	21	27	0.38
1998	1.40	0.30	5	25	7	0.80
1999	3.00	3.11	12	24	36	0.50
2001	2.50	1.50	6	19	15	0.68
2002	4.40	7.20	16	30	70	0.47
2003	4.29	7.10	17	34	73	0.50
2004	4.38	7.21	26	36	114	0.28
2005	1.38	0.55	8	30	11	0.73
2006	3.55	3.68	32	38	103	0.16
2007	2.52	5.15	20	35	50	0.43
2008	3.72	12.8	11	31	41	0.65
Mean	2.99	4.58	15.47	27.13	49.33	0.43

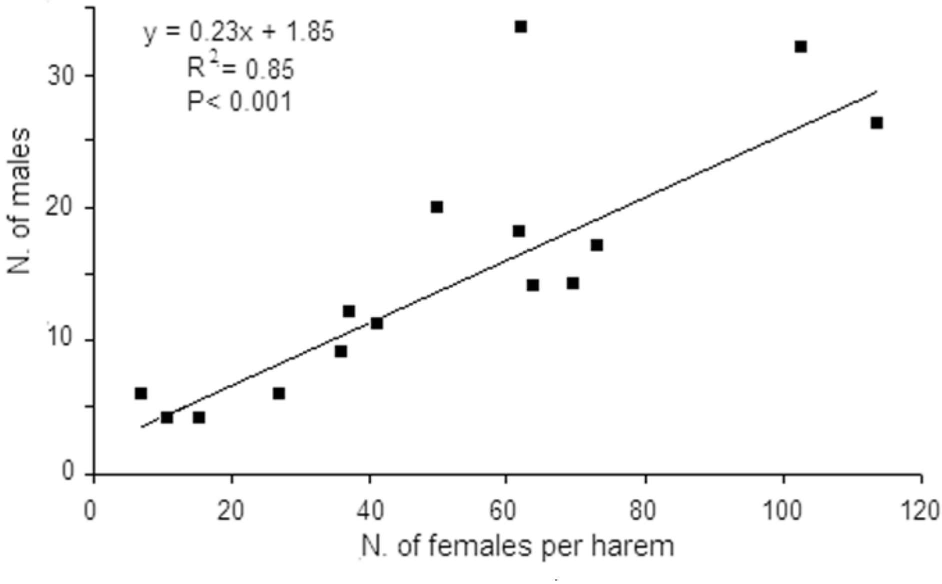

Figure 3 - Linear regression between the number of males and females per harem.

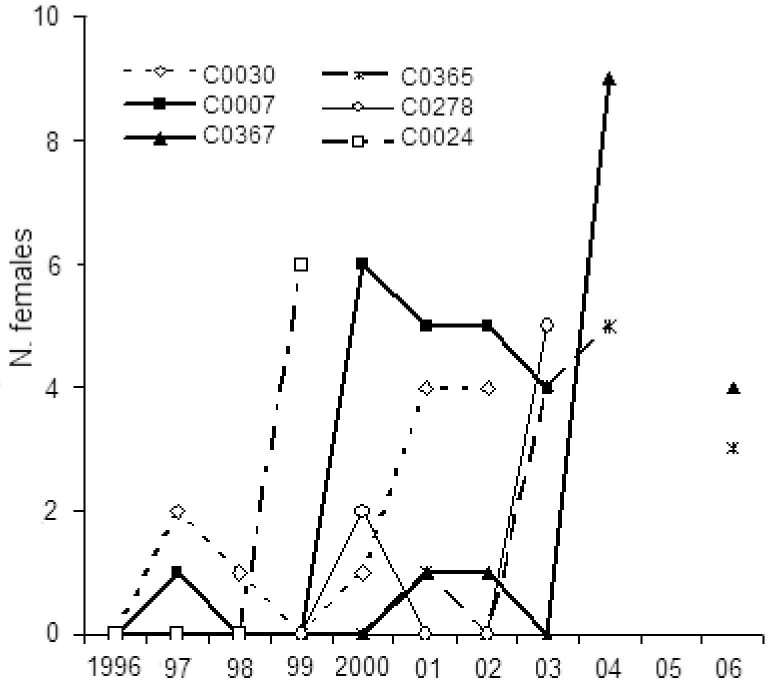

Figure 4 - Group of males showing a significant increase in harem size over time. In 2005 C0367 and C0365 were not found in the study area.

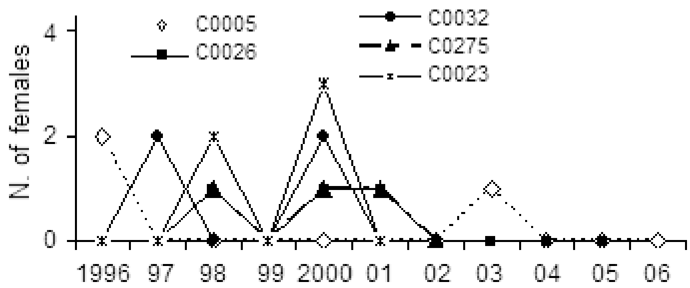

Figure 5 - Group of males constantly associated to small harems.

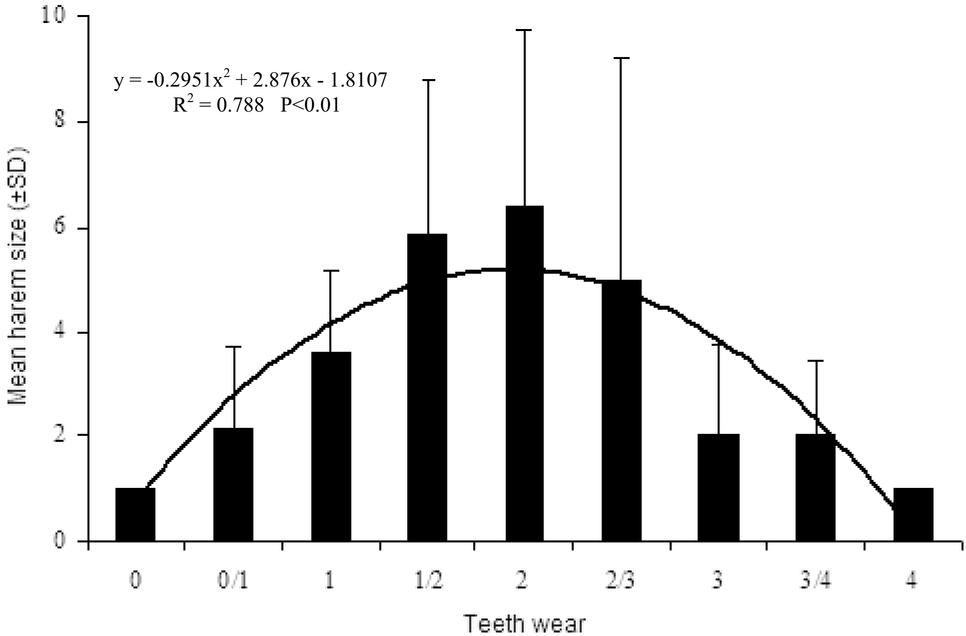

Figure 6 - Relationship between mean harem size and males' teeth wear.

a low success over several years (Fig. 5). Finally, both young and old males showed a lower mean harem size than those belonging to intermediate age classes, as estimated on the basis of teeth wear (R^2= 0.788; P<0.01; Fig. 6).

DISCUSSION

The social and ecological characteristics of females are usually the factors that determine mating strategy in males (Clutton-Brock, 1989). We found that relatively few males can form a harem with ≥ 3 females. This pattern suggests that the short mating period of *N. leisleri* and the low stability of female groups may result in strong competition among males (see also Ohlendorf and

Ohlendorf, 1998 and Wade and Shuster, 2004).

The positive correlation between the variance (Vh) and mean size of harems confirms that females tend to aggregate around most competitive males.

Accordingly, the number of males in the mating area does not significantly influence mean harem size. A few males are highly successful while many others do not mate or only attract a single female, as documented for other species (see Ciechanowski and Jarzembowski, 2004).

Sexual selection is basically composed of two mechanisms: male competition and female choice. The competition between males is closely linked to their capacity to attract the females and mate. As for *Saccopteryx bilineata* (Heckel and von Helversen, 2002), we found that male age is an important factor: bats either too young or too old have a smaller harem than intermediate age classes. But within this model we also found that in some males, the success in forming harems drastically increases in time after a temporary phase of little or no success. This may suggest that age alone is not sufficient to fully explain the observed pattern. Conversely other males maintained for many years a low ability to attract females and always behaved as satellites, regardless of their age. Unfortunately the data at our disposal are insufficient to ascertain whether this may be a proper reproductive strategy or whether such specimens may simply be inadequate as harem-makers. One of the specimens with the highest recorded longevity ranks in the group of males which, over the study period, were never found associated to more than two females (C0005, see Fig. 5).

In conclusion, the dynamics governing harem size in *N. leisleri*, as in *Pipistrellus nathusii* (Rachwald, 1992; Gerell-Lundberg and Gerell, 1994; Ciechanowski and Jarzembowski, 2004), seem to depend both on the number of females present in the mating area and on male age. Unfortunately, the factors causing strong fluctuations in the number of females arriving annually in the mating areas, and even their geographical areas of origin are unknown (Hutterer *et al*., 2005). Moreover, the factors causing a male to remain for several years an "unsuccessful" harem gatherer, or determining the increase in harem size after some years are still unknown.

More information on such issues would probably greatly help in fully unravelling the process of harem formation in *N. leisleri*.

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REFERENCES

Altringham J.D. 1996. Bats, biology and behaviour. Oxford University Press, 262 pp.

Bogdanowicz W. and Ruprecht A.L. 2004. *Nyctalus leisleri*. In: Krapp F. (ed.), Handbuch der Säugetiere Europas, Vol. 4/II, 93-108, Fledertiere II. *Aula-Verlag*, Wiebelsheim.

Ciechanowski M. and Jarzembowski T. 2004. The size and number of harems in the polygynous bat *Pipistrellus nathusii* (Keyserling and Blasius, 1839) (Chiroptera: Vespertilionidae). *Mamm. Biol*., 4: 277-280.

Clutton-Brock T.H. 1989. Mammalian mating systems. *Proc. R. Soc. Lond*., B236: 339-372.

Dondini G., Lanza B. and Vergari S. 2003. The buccal pad of bats and its seasonal cycle in *Nyctalus leisleri* (Kuhl, 1817) (Mammalia, Chiroptera, Vespertilionidae). *Boll. Mus. Reg. Sci. nat. Torino*, 20: 105-118.

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

Hammer Ø, Harper D.A.T. and Ryan P.D. 2009. PAST - Paleontological Statistics, ver. 1.90. Available from: http://folk.uio.no/ohammer/past/.

Heckel G. and von Helversen O. 2002. Male tactics and reproductive success in the harem polygynous bat *Saccopteryx bilineata*. *Behav. Ecol*., 13: 750–756

Hoch S., Zambelli N., Moretti M. and Roseli M. 2005. Zwei weitere Fernfunde von im Kanton Tessin (CH) und in Fürstentum Liechtenstein markierten Kleinabendseglern (*Nyctalus leisleri*). *Nyctalus*, 10: 288-294.

Hutterer R., Ivanova T., Meyer-Cords C. and Rodrigues L. 2005. Bat migrations in Europe: a review of banding data and literature. *Naturschutz und Biologische Vielfalt*, 28, 162 pp.

Jarzembowski T. 2003. Migration of the Nathusius' pipistrelle *Pipistrellus nathusii* (Vespertilionidae) along Vidstula Split. *Acta Theriol*., 48: 301-308.

McCracken G.F. and Wilkinson G.S. 2005. Bats and balls: sexual selection and sperm competition in the Chiroptera. In: Kunz T.H. and Fenton M.B. (eds), Pp., Bat Ecology, University of Chicago Press, 128-155.

Ohlendorf B. and Ohlendorf L. 1998. Zur Wahl der Paarungsquartiere und zur Struktur der Haremsgesellschaften des Kleinabendseglers (*Nyctalus leisleri*) in Sachsen-Anhalt. *Nyctalus*, (N.F.), 6: 476-491.

Ohlendorf B., Hecht B., Stassburg D. and Agirre-Mendi P.T. 2000. Fernfund eines Kleinabendseglers (*Nyctalus leisleri*) in Spainien. *Nyctalus*, 7: 239-242.

Petersons G. 1990. Die Rauhhautfledermaus, *Pipistrellus nathusii* (Keyserling u. Blasius, 1839), in Lettland: Vorkommen, Phänologie und Migration. *Nyctalus*, 3: 81-98.

Rachwald A. 1992. Social organisation, recovery frequency and body weight of the bat *Pipistrellus nathusii* from northern Poland. *Myotis*, 30: 109-119.

Vannini M. 1991. Easy-stat. Lezioni di statistica elementare. Dipartimento Biologia Animale e Genetica, Università di Firenze, 216 pp.

Wade M.J. and Shuster S.M. 2004. Sexual selection: harem size and the variance in male reproductive success. *American Naturalist*, 164: E83-E89.