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Does the barn owl (*Tyto alba*) selectively predate individual great mouse-eared bats (*Myotis myotis*)?

Loví sova pálená (*Tyto alba*) jedince netopýra velkého (*Myotis myotis*) výběrově?

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Abstact. There is good evidence that owls prefer to prey on smaller and younger rodents, but nothing is known about possible selective predation on bats. We studied predation on the mouse-eared bat (*Myotis myotis*) by the barn owl (*Tyto alba*). A set of skulls of *Myotis myotis* from pellets of *Tyto alba* was compared with a control one (samples from museum collection) and it was found out that skulls from owl pellets were smaller. The differences were mainly in lengths of upper and lower toothrow and rostral breadths across upper teeth. Our results indicate that *Tyto alba* most probably prefer to prey on volant inexperienced yearlings which are easier to catch, whilst reaching almost adult size. Volant yearlings lack flying skills, they are conspicuous during the emergence and they often concentrate near the roost during their early practice flights, making them more vulnerable to owl predation then adults.

INTRODUCTION

Bats are usually a minor component of the diet of their avian predators, despite their tendency to form large and potentially vulnerable colonies. Only few tropical and subtropical birds specialize on bats, e.g. *Macheiramphus alcinus* (Accipitridae), *Falco rufigularis* (Falconidae) and *Strix nigrolineata* (Strigidae) (Cade 1987, Gerhart et al. 1994). However in other raptor and owl species particular individuals can specialize to prey on bats, e.g. *Tyto alba* (Bauer 1956, Romano et al. 1999, our unpublished data), *Strix aluco* (Obuch 1992) or *Falco tinnunculus* (Negro et al. 1992, Lee & Kuo 2001). Speakman (1991) estimated that predation by birds account for about 11% of the annual mortality of British bats despite the apparent low representation of bats in the diets of predatory birds. Obuch (1998) showed that owls in Slovakia catch more bats compared with e.g. Germany or Hungary. This could be promoted by more various natural conditions and higher occurrence of rocky and karstic regions in Slovakia, which are attractive for bats. A review of published results of owl pellet analyses in the Czech and Slovak Republics revealed that bats occurred in 39% of samples across all owl species. Most successful in catching bats was *Strix aluco*, bats occurred in 77% of the samples and consisted 4% of the diet (Petrželková & Zukal 1999).

Prey selection of bats by owls with regards to the prey size has not been closely studied yet. Previous studies were focused on bat species preference in owl diet (e.g. Bekker & Mostert 1991, Kowalski & Lesiński 1990, Ruprecht 1979, Obuch 1998) and there are indications that owls prefer bigger species (Bekker & Mostert 1991, Petrželková & Zukal 1999) and species hunting in an open habit (Perez-Barberia 1990).

We compared a set of skulls from pellets of *Tyto alba* with a control set of skulls from museum collection to test whether owls prefer any size/age group within a population of *Myotis myotis*.

MATERIALS AND METHODS

We examined 121 craniums (upper parts of skulls) and 142 mandibles of *Myotis myotis* from the pellets of *Tyto alba* collected at 7 localities in the Czech and Slovak Republic and 120 crania and 120 mandibles of the same species from 30 localities deposited in the collection at the Institute of Vertebrate Biology AS CR in Brno in the Czech Republic. Only at one locality – Ratková, Slovakia – were *Myotis blythii* registered with insignificant dominance (Uhrin et al. 2002). There were samples collected by the last author and he has high experiences with bone determination to be able excluded *Myotis blythii* from sample. We did not include museum specimens collected at hibernacula. We also excluded juvenile prevolant specimens from analyses, because the number of juveniles in the collections did not reflect the situation in the *Myotis myotis* population. Finally, we excluded the specimens with unclear origin to ensure that in the analysis will be not included specimens of *Myotis blythii*. We were aware of a possible bias in our control sample. Once prevolant individuals and possible *Myotis blythii* were excluded from the analyses, no size/age bias between sample of individuals in the collections and individuals in maternity colonies was detected. Thus we believe that our sample presents a valid control.

The following skull measurements were taken from each cranium: greates length of skull (LCr), condylobasal length (LCb), zygomatic breadth (LaZ), breadth of interorbital constriction (LaI), infraorbital breadth (LaInf), breadth of braincase (LaN), lengths of upper tooth-row (IM^3, CM^3, P^4M^3, M^1M^3, CP^4, P^2P^3), rostral breadth across upper canines (CC), upper premolars (P^4P^4) and molars (M^3M^3). Mandibular measurements included: mandible length (LMd), coronoid process height (ACr) and lengths of lower toothrows (IM_3, CM_3, P_4M_3, M_1M_3, CP_4). Dental measurements had to be taken from alveoli on both pellet and collection material, because skulls from pellets often had teeth out. Skulls from owl pellets were often damaged so we could not take all measurements on some of them. Caliper and digital image analyses (MicroImage 3.0) were used for measuring.

Comparisons between 'owl' and 'control' groups were carried out separately for craniums and mandibles. Firstly we compared single measurements by univariate statistical methods. Kolgomorov-Smirnov tests were used to test if the distributions did not differ significantly, while Mann-Whitney U-tests were used to compare medians of the groups. Further, we performed two principal component analyses. Thereafter we compared factor scores between 'owl' and 'control' group.

RESULTS

Using univariate tests we found significant differences between 'owl' and 'control' groups mainly in lengths of upper and lower toothrow and rostral breadths across upper teeth (CC, P^4P^4, M^3M^3, IM^3, CM^3, P^4M^3, M^1M^3, CP^4, P^2P^3, LCb, IM^3, CM^3, P^4M^3, M_1M_3, CP_4 – Tab. 1). Skulls from collections were larger in all these measurements then the skulls from owl pellets (Fig. 1).

First component (PC1-u) of the PCA carried out on all cranial measurements was driven mainly by lengths of toothrow (IM^3, CM^3, P^4M^3, M^1M^3, CP^4) and rostral breadths across teeth (CC, P^4P^4, M^3M^3) but also by LCb. Second principal component (PC2-u) mostly correlated

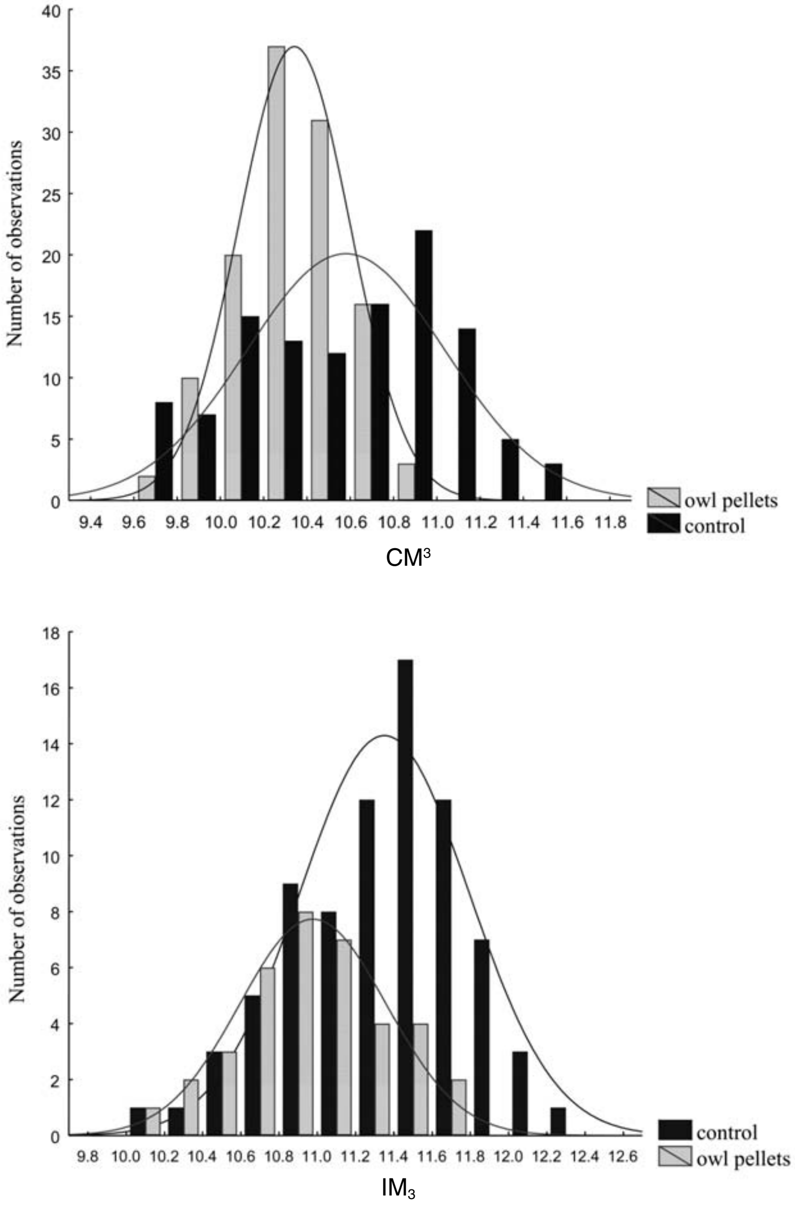

Fig. 1. Length-frequency distribution of CM^3 (above) and IM_3 (below) from control group and from owl pellets with a significant difference.
Obr. 1. Histogram hodnot rozměrů CM^3 (nahoře) a IM_3 (dole) u kontrolní skupiny lebek a u skupiny lebek z vývržků. Vysvětlivky: number of observations – počet pozorování, control – kontrolní soubor, owl pellets – soví vývržky.

Tab. 1. Medians and results of Mann-Whithey tests and Kolgomorov-Smirnov tests on (a) cranial and (b) mandibular measurements. C – control, O – owl pellets, MW – Mann-Whitney test, KS – Kolgomorov-Smirnov test
Tab. 1. Mediány a výsledky Mann-Whitney a Kolgomorov-Smirnov testů vypočtených na rozměrech (a) horní, (b) dolní čelisti. C – kontrolní soubor, O – soví vývržky, MW – Mann-Whitney test, KS – Kolgomorov-Smirnov test, p-level – hladina významnosti

	median C	median O	Z	MW p-level	KS p-level
LaInf	6.42	6.47	–1.91	0.056	> .10
LaI	5.24	5.23	–1.54	0.125	> .10
LaZ	15.02	15.11	–0.86	0.389	> .10
LaN	10.86	10.91	–1.58	0.114	> .10
CC	6.21	6.11	4.41	**<.001**	**< .001**
P^4P^4	7.71	7.76	1.73	0.083	**< .05**
M^3M^3	10.12	10.03	2.99	**0.003**	**< .005**
IM^3	11.40	10.98	5.68	**<.001**	**< .001**
CM^3	9.97	9.68	5.40	**<.001**	**< .001**
$P4M^3$	7.39	7.27	3.97	**<.001**	**< .001**
$M1M^3$	5.75	5.78	1.13	0.258	> .10
CP^4	4.37	4.17	5.72	**<.001**	**< .001**
P^2P^3	1.47	1.40	5.83	**<.001**	**< .001**
LCr	23.55	23.63	1.33	0.184	> .10
LCb	22.47	22.43	2.08	**0.037**	> .10
LMd	17.92	17.87	–0.26	0.798	> .10
ACr	6.03	6.07	1.07	0.282	> .10
IM_3	11.96	11.65	–3.78	**<.001**	**< .001**
CM_3	10.65	10.34	–4.55	**<.001**	**< .001**
P_4M_3	7.81	7.66	–3.51	**<.001**	**< .001**
M_1M_3	6.31	6.17	–4.26	**<.001**	**< .001**
CP_4	4.37	4.14	–8.37	**<.001**	**< .001**

mainly with LaZ and LaN, also with LCb and LCr (Tab. 2a). First component accounts for 45.3% of the variation and the second for 14.3%. The graph of PC1-u and PC2-u indicated that owl selected a group within a bat population (Tab. 2a). Significant differences between PC1-u factor scores of 'owl' and 'control' groups (Mann-Whitney test, $Z= -2.3$, $p=0.02$) proved that skulls from owl pellets were smaller, but differences between PC2-u showed opposite trend (Mann-Whitney test, $Z= -2.28$, $p=0.02$) (see also Tab. 2a). However PC2-u explained less of variability in comparison with PC2-u and LaZ, LaN, LCb and LCr also contribute to the PC1-u considerably (Tab. 2a).

First principal component (PC1-l) of the PCA performed on all mandibular measurements reflected variability in lengths of lower toothrow (IM_3, CM_3, P_4M_3, M_1M_3, CP_4). Second factor (PC2-l) correlated mainly with LMd and ACr (Tab. 2b). First axis explains 66.3% of the variation and the second 20.7%. The graph of PC1-l and PC2-l again showed that owl selected a particular group within a population of *Myotis myotis* (Tab. 2b). Mann Whitney U-tests on the factor scores for PC1-l demonstrated that skulls from pellets were smaller ($Z= -4.6$, $p< 0.01$) while differences between 'owl' and 'control' group in factor scores of PC2-l showed an opposite trend

(Mann-Whitney, Z= 2.73, p< 0.01). However PC2-l did not extract a lot of variability and LMd and ACr which mainly affected PC2-l correlated also with PC1-l considerably (Tab. 2b).

DISCUSSION

It is widely accepted that vertebrate predators typically capture substandard individuals (e.g. the young, weak, sick, aged, and inexperienced) from prey population in higher than expected proportions (Begon et al. 1990). Ideally, individuals captured by a predator should be characterized in terms of a variety of traits that could influence their vulnerability to predation (Temple 1987). Predators forage optimally and they prefer prey which gives them the highest rate of energy return (Krebs & Davis 1987). Numerous studies have shown that owls preferred younger (and lighter) rodents than those typically found in population (Beacham 1979, Marti & Hougue 1979, Longland & Jenkins 1987, Dickman et al. 1991), but data on potential differential predation of size/age classes of bats by owls are missing. However Hartley & Hustler (1993) demonstrated that a pair of bat hawk *Machaeramphus alcinus* took advantage of easily-caught

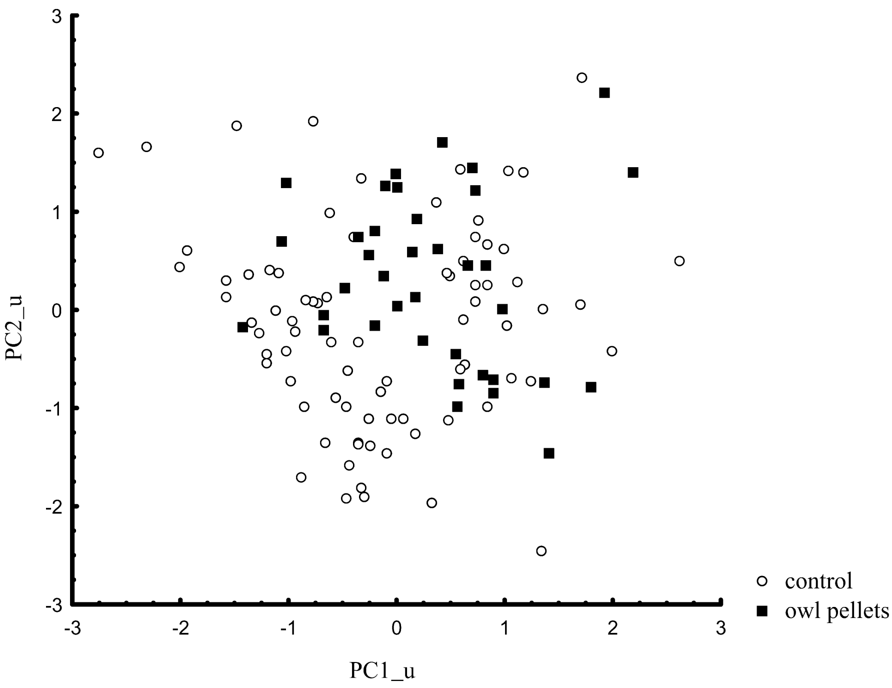

Fig. 2. Results of the PCA on cranial measurements.
Obr. 2. Výsledky analýzy hlavních komponent (PCA) provedené na rozměrech horní čelisti. Vysvětlivky viz obr. 1.

Tab. 2. Results of the PCA on cranial (a), and mandibular measurements (b). Factor coordinates based on correlations

Tab. 2. Výsledky analýzy hlavních komponent (PCA) provedené na rozměrech horní (a) a dolní čelisti (b). Korelace proměnných s hlavními komponentami

(a)	PC1-u	PC2-u	(b)	PC1-l	PC2-l
LaInf	–0.31	0.45	LMd	–0.55	**-0.73**
LaI	–0.11	0.40	ACr	–0.37	**-0.83**
LaZ	–0.44	**0.64**	IM_3	**–0.96**	0.07
LaN	–0.24	**0.60**	CM_3	**–0.98**	0.14
LCr	–0.57	0.57	P_4M_3	**–0.92**	0.28
LCb	**–0.60**	0.52	M_1M_3	**–0.88**	0.33
CC	**–0.83**	0.03	CP_4	**–0.83**	-0.04
P^4P^4	**–0.77**	<–0.01			
M^3M^3	**–0.86**	–0.09			
IM^3	**–0.89**	–0.24			
CM^3	**–0.91**	–0.29			
P^4M^3	**–0.87**	–0.30			
M^1M^3	**–0.75**	–0.29			
CP^4	**–0.74**	–0.17			
P^2P^3	–0.49	–0.22			

pregnant female bats in order to attain breeding condition, whereas their fledglings took advantage of recently independent but naive juvenile bats.

We found out that analyzed skulls from owl pellets were smaller, mainly in lengths of upper and lower toothrow and rostral breadths across teeth. *Myotis myotis* shows age variability in most of the cranial measurements, but the differences are most apparent in rostral breadths across teeth (Benda 1993). The growth of skull is probably finished at the age of 2 or 3 years, although the greatest changes had occurred in the first year (Benda 1993, 1994). According to Benda (1993), geographical variability in cranial measurements of *Myotis myotis* within Czech and Slovak Republic could be neglected. Idem sexual dimorphism is not important from the point of population or species variability. Therefore we conclude that our results could indicate that *Tyto alba* preferred to prey on inexperienced yearlings which were easier to catch whilst were almost as big as adults.

Bats are captured by owls probably mainly during the periods of emergence or return from roosts (Barclay et al. 1982, Roberts et al. 1997, Gerhardt et al. 1994, Hoetker & Gobalet 1999, Romano et al. 1999), but owls are in general not adapted for catching bats (Cramp 1989). The relative benefits of capturing substandard individuals are greatest just when a predator is attacking a species of prey which is typically difficult to capture and kill (Temple 1987).

Both prevolant and newly volant bats are especially susceptible to predation. Flightless young, if not protected by physical barriers, may be taken directly by a variety of predators that range from cockroaches (Wilson 1971) and snakes (Rice 1957) to birds and mammals (Allen 1939, Gillette & Kimbrough 1970). Although *Tyto alba* often shares the roost with a bat colony, this owl hunts for bats in flight and picking hanging bats inside the roost is probably very exceptional (Bauer 1956, König 1961, Ruprecht 1979). Newly volant young are unskilled flyers and often concentrate near the roost during early practice flights (Kunz 1974b, Bradburry

1977, BUCHLER 1980). At such times these slow-flying bats with poor maneuverable abilities are especially vulnerable. KUNZ (1974a) discussed that more then half of all *Eptesicus fuscus* caught by an individual of *Tyto alba* were young of the year. Also *Antrozous pallidus* seems to be most vulnerable to predation when bats are beginning to fly. These young bats are extremely clumsy and frequent collisions with walls, other bats and the observer were noted. Skulls of young *Antrozous pallidus* were found in the pellets of *Bubo virginianus* (O'SHEA & VAUGHAN 1977). Roost selection is an important factor in determining the survival of juvenile bats. The young of species that roost in relatively exposed places are especially vulnerable to predation during emergence (HUMPHREY 1975).

However owls are supposed to be able to catch bats also during their foraging (MORRISON 1978, VERBOOM 1998, LAW & LEAN 1999, VARGAS et al. 2002) and we cannot exclude this for *Tyto alba*. In general, *Tyto alba* has two foraging periods a night split by a resting pause around midnight (ERKERT 1969). Thus, foraging activity of bats and owls may partly overlap (CRAMP 1989, AUDET 1990). Some individuals of *Tyto alba* can hunt before sunset or after sunrise (CRAMP 1989) which enable them to prey upon emerging/returning bats. Both *Myotis myotis* and *Tyto alba* prefer to forage on open habitats including meadows, and fields (CRAMP 1989,

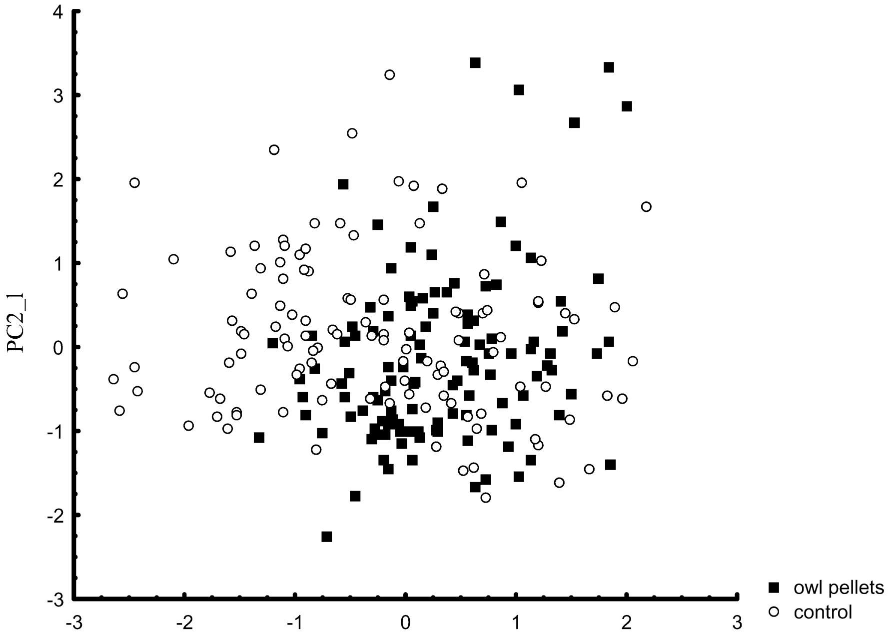

Fig. 3. Results of the PCA on mandibular measurements.
Obr. 3. Výsledky analýzy hlavních komponent (PCA) provedené na rozměrech dolní čelisti. Vysvětlivky viz obr. 1.

Schober & Grimmberger 1993, Arlettaz 1996). *Tyto alba* hunts by dropping to ground (Cramp 1989) so we can speculate that the owl may catch *Myotis myotis* while gleaning a prey on the soil surface (Arlettaz 1996). But bats could be also aerial-pursuit like birds (Cramp 1989). Fledging is a critical period for the survival of young bats and in *Myotis myotis* mothers are not overtly involved in acquisition of foraging skills by its young (Audet 1990). At this time young bats can be easier prey because of their undeveloped foraging skills and lack of experience.

We also speculate that some individuals of *Tyto alba* may prey on bat colonies only or more intensively in postlactation period to exploit a source of easily capture young inexperienced bats. Therefore a bigger proportion of newly volant bats in owl diet could be pronounced by the departure of adult females in the end of summer (Stebbings 1968, Kunz 1974a, Swift 1980). Next research on this problem is required to compare the proportion of particular age classes of bats in different reproductive periods.

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SOUHRN

Sovy selektivně loví menší a mladší hlodavce, ovšem neexistují důkazy o selektivní predaci sov na netopýrech. V této práci jsme se zabývali predací netopýra velkého (*Myotis myotis*) sovou pálenou (*Tyto alba*). Soubor lebek *Myotis myotis* z vývržků *Tyto alba* byl srovnán s kontrolním souborem lebek z muzejních sbírek a bylo zjištěno, že lebky pocházející ze sovích vývržků jsou menší. Rozdíly byly nejvíce zřetelné u délek zubních řad v dolní a horní čelisti a v šířkách rostra mezi zuby v horní čelisti. Naše výsledky naznačují, že sovy preferují tohoroční vzletná mláďata netopýrů, která jsou téměř stejně velká jako dospělci, ale nemají dostatek zkušeností a jsou tedy pro sovy snadnější kořistí. Tato mláďata jsou méně obratná v letu, jsou tudíž nápadná během výletu z kolonie a navíc se po výletu často soustřeďují v blízkosti úkrytu a jsou tedy snáze ulovitelná.

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