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UNUSUAL AGE STRUCTURE OF THE WINTER AGGREGATION OF *NYCTALUS NOCTULA* (MAMMALIA, CHIROPTERA) IN KYIV

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Unusual Age Structure of the Winter Aggregation of *Nyctalus noctula* (Mammalia, Chiroptera) in Kyiv. Godlevska, L. V., Gol’din, P. E. — We analysed the sex and age composition of a large colony of *Nyctalus noctula* (605 specimens), wintering in Kyiv, Ukraine. Age was identified in 113 individuals using the method of counting growth layer groups in dentine. Males contained ca. 70 % both in the colony and in the sample of animals with the estimated ages. Males and females of all ages were in good body condition. There were bats from 0+ to 7+ years old in the sample. In males, 0+ age class was represented by 38 %; 1+ class, by 20 % of individuals. In females, 0+ and 1+ year old individuals were found in similar numbers: 29 % and 32 % correspondingly. The observed sex ratio and proportions of males and females across age classes cannot be explained only by demography. The data are interpreted in terms of migratory behaviour and mating strategy of the species: the unusual female age structure is possibly due to age-specific preferences in wintering habitat selection and search for potential mating partners.

Key words: *Nyctalus noctula*, wintering, sex and age structure, migration, mating strategy.

Необычная возрастная структура зимовочного скопления *Nyctalus noctula* (Mammalia, Chiroptera) в Киеве. Годлевская Л. В., Гольдин П. Е. — Проанализирован половозрастной состав большой колонии рыжих вечерниц (605 особей), зимовавших в Киеве (Украина). Возраст определён у 113 особей с использованием метода подсчёта ростовых слоёв дентина. Самцы, как в колонии, так и в выборке с оцененным возрастом, составляют около 70 %. Самцы и самки были в одинаково хорошем состоянии, независимо от возраста. В выборке присутствовали животные возрастом от 0+ до 7+ лет. Среди самцов 0+ класс представлен 38 %, 1+ класс — 20 % особей. У самок 0+ класс представлен в меньшем количестве, чем 1+ класс — 29 % и 32 % соответственно. Наблюдаемые соотношения полов и распределение самцов и самок по разным возрастным классам не могут быть объяснены только демографией. Данные рассмотрены в контексте миграционного поведения и брачной стратегии вида: необычная возрастная структура скопления самок может быть обусловлена возрастными особенностями выбора места зимовки и поиска потенциальных брачных партнеров.

Ключевые слова: *Nyctalus noctula,* зимовка, половозрастная структура, миграция, брачная стратегия.

Introduction

The common noctule bat *Nyctalus noctula* (Schreber, 1774) is the widely distributed migratory species; its summer range occupies the most part of Europe, whereas the winter range is limited to regions with relatively warm winters (Hutterer et al., 2005; Gebhard, Bogdanowicz, 2011). Kyiv city is situated on the north of the present-day winter range of *N. noctula*. Winter aggregations of *N. noctula* have only been recorded in Kyiv since 2001: this is possibly the result of the recent northward expansion due to winter warming and appearance of new appropriate roosts (Godlevska, 2014). Therefore, non-typical composition of the population may be expected in this recently colonised wintering area, similarly to some terrestrial small mammals under dispersal (Gaines, McClenaghan, 1980).

Here we analyze an age and sex composition of a large wintering aggregation of *N. noctula* in Kyiv and interpret it in terms of migratory behaviour and mating strategy.

Material and methods

We examined 605 specimens of *N. noctula* taken from a winter shelter in a ventilation duct in a building in the central part of Kyiv city during reconstruction operations on February 7, 2007. Of them, 270 died during transportation to the Kyiv Zoo; 5 died during hibernation in captivity; others were successfully released in spring (Tyshchenko, Godlevska, 2008). The sex was identified in all dead specimens. The dead bats were weighted after the transportation, so their weight was the weight at death (fig. 1). Age was identified in 113 individuals. We examined thin cross-sections of decalcified teeth (preferably upper canines; lower canines were used in a few cases) stained by Ehrlich haematoxylin. Upper canines were preferred, since their overall size and pulp cavity were the greatest among all teeth; therefore, the growth layers were better readable and the pulp cavity was open in all studied specimens. We preferred the distal portion of the root for the cross-sections, since the annual growth layer groups were better distinct in this portion of the teeth, and the main (primary or annual) layers were easily distinguished from the secondary layers (see also Klevezal, 1988: fig. 28 and 33 a). Such a technique allowed minimizing errors of age identification which usually originated from confusion in primary and secondary layers (e. g., Phillips et al., 1982 and following discussion in Klevezal, 1988). We counted growth layer groups in dentine and estimated the age as the number of complete growth layer groups, following the recommendations by G. A. Klevezal (1988: 138–142, fig. 33). The last growth layer groups were incomplete due to the winter season of sampling. Thus, all age estimates were codified as the Age+ (age groups of 0+, 1+, 2+, etc.): for example, the group 0+ included the animals born during the previous warm season, with the first incomplete growth layer group. Here we apply the conditional term "adult animals" to the bats at least two years old, the age classes in which all noctules are involved in reproduction.

The normality of weight distribution was estimated by Shapiro-Wilk test. The Mann-Whitney U test was used to compare the between-group differences in weight. Differences in proportions of males and females across age classes, as well as proportions of specific age classes, were estimated by chi-square test (observed vs. expected). The expected values and ratios in the specific age classes were calculated from the values predicted by the model of logarithmic regression on the total sample with the estimated ages (fig. 2).

Results

Sex structure of the colony. The colony consisted of 428 males and 172 females (the sex of 5 animals was not identified). Among the dead animals, there were 191 males and 84 females. Therefore, the sex ratio in the dead animals was the same as in the total sample: males contained 70 % (71 % in total, 69 % among the dead animals); no sex bias in mortality was observed.

Body weight structure. The body weight was normally distributed and amounted 20–32.4 g. All dead animals were in normal body condition as compared to those who has survived. No difference in weight between females and males was observed, $p < 0.05$ (fig. 1, *A*–*C*). Thus, there was no selectivity in male or female body weight in the examined sample. Males and females of all ages were in normal body condition. Body weights were similar across almost across all age categories. 0+ year old animals were slightly lighter than older animals (mean weights were 25.7 vs. 26.8 g) but all the differences between age classes were not statistically significant except for 0+ and 5+ age classes (mean weights 25.7 and 28.0 g; U test, $p < 0.05$).The weight of individuals of 0+ and 1+ age classes, both in females and males, was also normally distributed. No difference between sexes in these classes was observed; as well, there was no difference in comparison to the total samples of weighted animals and those with the estimated age (fig. 1, *D*–*F*).

Age structure. There were bats from 0+ to 7+ years old in the sample (fig. 2, *A*). The age structure in females and males was substantially different (fig. 2, *B*, *C*).

The age distribution of males showed a large portion of bats born during the previous summer (0+ age class): they contained 38 % of the male sample, and the ratio of 0+ and 1+ age classes was 1.9. The other age classes were distributed within a sigmoid curve. In total, combined 0+ and 1+ age classes contained 57.1 %.

In females, combined 0+ and 1+ age classes contained 61.3 % of the sample. However, 1+ year old specimens were found even in a slightly greater number than 0+: the ratio of 0+ and 1+ age classes was 0.90 (which significantly differs from the expected ratio of 1.52, $p < 0.05$), and 1+ year old bats contained 32 % of the female sample (contrary to 20 % within males). The other age classes were represented by minor numbers.

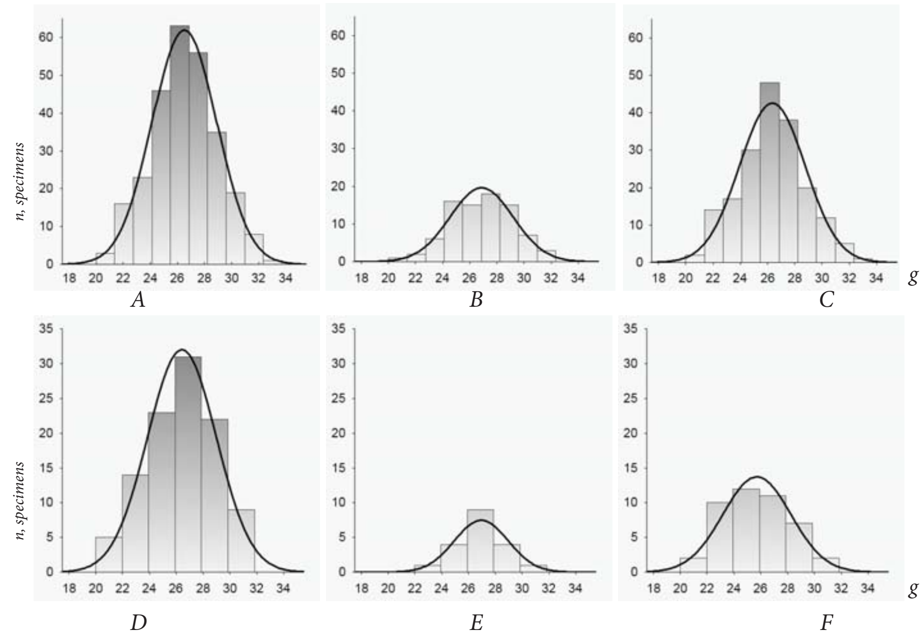

Fig. 1. Distribution of body weight in the wintering colony of *N. noctula* in Kyiv: *A* — total sample (n = 270; 20.0–32.4 g); *B* — females (n = 83; 21.2–31.8 g); *C* — males (n = 187; n = 20.0–32.4 g); *D* — total sample of individuals with estimated age (n = 104; 20.0–31.8 g); *E* — females and *F* — males of 0+ and 1+ years old (n = 19; 22.8–31.3 g; n = 44, 20.3–31.7 g).

Рис. 1. Распределение массы тела особей в зимовочной колонии *N. noctula* в Киеве: *A* — общая выборка (n = 270; 20,0–32,4 г); *B* — самки (n = 83; 21,2–31,.8 г); *C* — самцы (n = 187; n = 20,0–32,4 г); *D* — все особи с оценённым возрастом (n = 104; 20,0–31,8 г); *E* — самки и *F* — самцы возрастом 0+ и 1+ лет (n = 19; 22,8–31,3 г; n = 44, 20,3–31,7 г).

Males clearly dominated in all age classes in the interval 0–3 years, except 1+. The difference of frequencies between males and females (observed vs. expected as to be 1 : 1) was significant ($p < 0.05$). In the age class 1+, there was no significant difference between males and females: the percentage of females was unusually large (40 % vs 29 % in the total sample).

Three year old bats of both sexes were found in higher proportions than expected (in comparison to both 1+ and 2+ age classes, $p < 0.05$).

Discussion

P. P. Strelkov (2002) summarised data on sex ratios of common noctule bats in winter in Europe and reported the general tendency: the percentage of females in winter aggregations grew southward and southwestward. P. P. Strelkov interpreted the prevalence of males in winter aggregations with the marginal positions of the localities in the winter range and the male tendency to remain closer to their summer areas. As well, males dominated in the winter colony in Rostov-on-Don in December, 1976 (68 %); whereas the sex ratio was close to 1 : 1 in Krasnodar and Maikop, south to Rostov-on-Don (Gazaryan, Kazakov, 2002). Males also dominated in winter aggregations in Kharkov (Vlaschenko, 2008).

Winter colonies of common noctule bats in Kyiv followed the northern pattern of sex distribution described by P. P. Strelkov (2002). They had quite stable sex structure: male dominance was recorded from year to year. The percentage of males varied within 59–77 % (samples with n > 25 were considered). In total, in addition to the colony examined here, 455 males and 254 females were recorded in winter in a few localities in Kyiv in 2001–2014 (Godlevska, unpublished data; Kravchuk, Godlevska, unpublished data). Thus, the male-biased ratio can be explained by the northern position of Kyiv as the wintering locality on the margin of the expanding range of *N. noctula* (Godlevska, 2014).

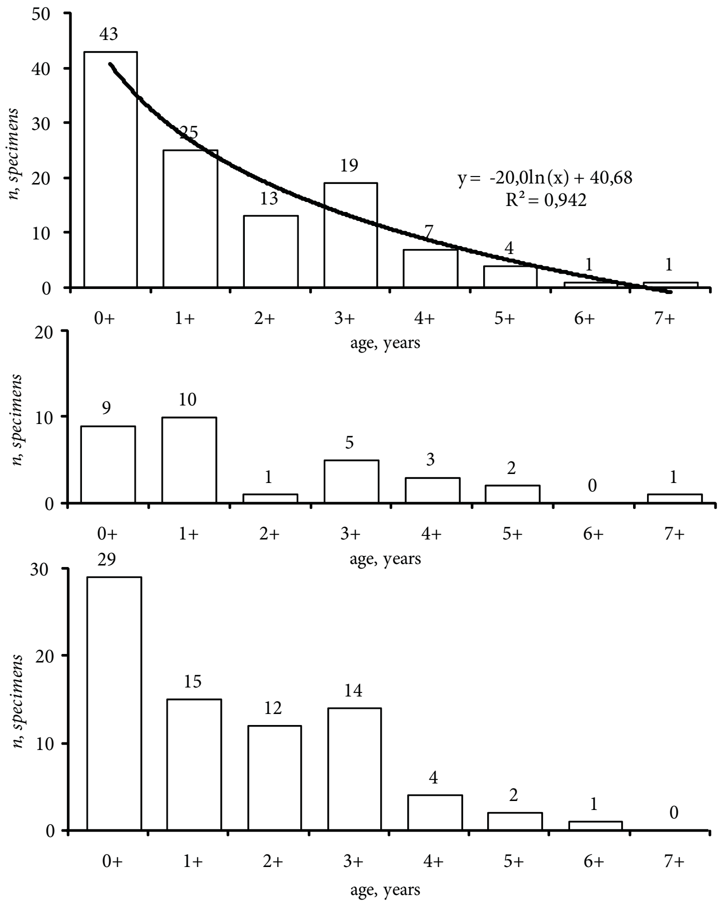

Fig. 2. Age of common noctule bats in the examined sample: *A* — total sample, n = 113, the model of the logarithmic regression is indicated with the line; *B* — females, n = 31; *C* — males, n = 77.

Рис. 2. Возраст рыжих вечерниц в исследованной выборке: *A* — все особи, n = 113, линией обозначен график логарифмической регрессии; *B* — самки, n = 31; *C* — самцы, n = 77.

However, the examined aggregation in Kyiv, as shown by this study, was characterised not only by minor percentage of females but also by its unusual age structure. In males, percentages in 0+ and 1+ age classes were in concordance with the known life tables of common noctule bats and other bat species: due to the high mortality of weaning juveniles, individuals of 0+ age class significantly dominate over 1+ year old ones (e. g. Funakoshi, Uchida, 1982; Heise, Blohm, 2003). On the contrary, the female age structure cannot be explained by demography: its most distinct trait is the particularly low ratio of 0+ and 1+ year old animals: 1+ year old bats even tended to dominate in number over the first wintering animals. Another unusual (and unexplained) trait is the relatively high proportion of 3 year old bats of both sexes.

There is little information on the age structure of hibernating common noctule bats in other geographical regions. However, detailed data on the age and sex structure have been published for hibernating common noctule bats in Almaty, Kazakhstan: among 146 animals, females contained 45 %, and they also significantly differed from males in the ratio of 0+ and 1+ age classes: respectively, females, 17 and 17, vs. males, 43 and 19, just as in this study (Butovsky et al., 1985: 199). Interestingly, Almaty is located in the region with quite severe winters. However, Butovsky et al. (1985) indicated that the sex ratio strongly fluctuated across years, and later Butovsky and Shaimardanov (1988) provided different data on the age structure: it is still unclear which samples were used in both cases and if these samples were homogenous in terms of time and place. In Krasnodar and Maikop ("southern type" of the sex structure), on the contrary, the proportion of nulliparous females with sharp teeth (hypothetically, 0+ age class) was notably high, 36 %, whereas sharp-toothed mature females (hypothetically, 1+ age class) contained only 6 %, and rounded-toothed females (hypothetically, the mix of 1+, 2+ and possibly 3+ age classes), 21 % (Gazaryan, Kazakov, 2002).

An apparent explanation for the skewed female composition is that Kyiv, with its comparatively long and cold winters, may be considered as the risk zone for wintering noctule bats. The smaller percentage of females would be the result of the press of natural selection: females have more demanding requirements to the wintering environment than males. Therefore, adult females would prefer to migrate further southwards and choose the regions with shorter and milder winters and earlier springs. On the contrary, young females may choose northern roosts, which are closer to breeding localities, due to lower energy costs for migration on shorter distances. This would also explain their prevalence in the winter colony in Kyiv. However, the unusually high percentage of 1+ year old bats in northern roosts remains unexplained under this scenario. Furthermore, the young females (0+ and 1+ age categories) in this study were in as good body condition, as adults, so their presence in the colony was owing to their individual preferences, rather than inability for a distant migration.

A possible explanation of this phenomenon could be the difference between wintering colonies in sex and age structure. Possibly other colonies could have different age structures. However, the overall sex structure of noctules wintering in Kyiv matches the structure of the colony reported here (Godlevska, unpublished data). Thus, the age structure is also suggested to be the same as in other wintering aggregations in Kyiv.

Another explanation is the mating strategy of *N. noctula*. The common noctule bat is characterised by promiscuous mating system with the sperm competition (Racey, 1974; Wilkinson, McCracken, 2003). Mating usually occurs in late summer and autumn, before or during migration, and a female can copulate with a few males and even give birth to twins with different paternity (Mayer, 1995). However, the common noctule bat is characterised by highly diverse mating strategies and behaviour patterns, and some of them involve mating in winter time, in wintering roosts; sometimes males even wake hibernating females (Gebhard, 1995; Dietz et al., 2011). Notably, winter copulations and mating behaviour were reported from Almaty, from the colonies with the same age structure, as in Kyiv (Butovsky et al., 1985). In these conditions, a female wintering in a roost together with a great number of males considerably increases the chance for the reproductive success. Common noctule bats usually attain the sexual maturity by the first winter of life (Gaisler et al., 1979), but many yearlings remain resting (Kleiman, 1969) or give birth to one young, whereas the older females often bear twins (Dietz et al., 2011). Thus, wintering in a northern roost can be an advantage for less competitive young females, particularly those who failed to mate a year ago or mating first, i. e. for 1+ year old bats. While the adult females copulate and leave for a long distance migration, the younger and less successful females can stay in a northern locality for a winter. The females of 0+ age class can prefer the southern wintering localities, but for the next year they may stay in the northern roosts if they did not mate during their first winter. Thus, the great percentage of 1+ year old females (especially in comparison to 0+ bats) is better explained by their reproductive behaviour.

In conclusion, the possible factor increasing the portion of young females in northern winter colonies is the lower energy costs of their migration on shorter distances, and the important potential advantage for 1+ year old females is their increasing reproductive success.

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