

MAIN FUNCTIONS OF LOUD VOCALIZATION IN POPULATIONS OF EDIBLE DORMOUSE *GLIS GLIS*

MIROSLAW JURCZYSZYN

*Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University,
Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland
E-mail: jurc@amu.edu.pl; <https://orcid.org/0000-0003-2383-9979>*

The study aimed to determine when, during summer activity, males and females of the edible dormouse most often used loud calls. On this basis, an attempt was made to determine the main purpose of the emission of these calls. It was assumed that 1) if males have the most of loud calls in July, their emissions may be related primarily to the mating behaviour (which takes place during this period), and if they have the most of loud calls in August, their emissions are most likely concerned defence of food resources, 2) in females, most of this vocalization would occur in August due to the need to defend their food resources and 3) in both sexes, more vocalization would occur in the year of good beech fruit crop (when the dormice would reproduce) than in the year of no crop (when the dormice would not reproduce). To check these assumptions, the number of loud calls and “performances” (series of loud calls) emitted by the animals from two wild populations tracked by telemetry was noted. The mean number of “performances” and loud calls in males and females was higher in August than in July (when beech fruits ripen), but significant differences were found only for “performances”. Both males and females had significantly more “performances” and loud calls in the mast/breeding year than in the non-mast/non-breeding year. It seems that males and females use loud calls mainly to defend important resources and are, therefore, most often heard during the mast year.

Keywords: number of loud calls, beech mast, resources defence.

INTRODUCTION

Loud repeated acoustic signals (so-called loud or long-distance calls), which propagate over a considerable distance, have been found in various groups of animals including insects, fish, amphibians, birds, and mammals (RYAN & KIME 2002). In most cases, these signals are associated with mating behaviour, carrying information about body size, condition, fighting ability, and alarm functions (e.g. CLUTTON-BROCK & ALBON 1979, RYAN & KIME 2002, EY & FISCHER 2009). On the other hand, vocalization, like other communication channels, is a means of transmitting specific information and manipulating the behaviour of other individuals (SLATER 1983, OWINGS & MORTON 1998). Loud sounds are known in many species belonging to different orders of mammals, for example, in the wolf (*Canis lupus*) (HARRINGTON & MECH 1979), the red deer (*Cervus elaphus*) (CLUTTON-BROCK & ALBON 1979), elephants (*Elephas maximus* and *Loxodonta africana*) (GARSTANG 2004, SOLTIS 2010), marmots

(*Marmota* spp.), prairie dogs (*Cynomys* spp.), ground squirrels (*Spermophilus* spp.) (BLUMSTEIN & ARMITAGE 1997, MATROSOVA *et al.* 2012), yellow-bellied glider (*Petaurus australis*) (GOLDINGAY 1994) and others. Loud signals are often found in primates (ZIMMERMANN 1995, DA CUNHA *et al.* 2015), for which several of their functions are postulated, including those related to alerting, coordination of group behaviour, attracting a reproductive partner, defence of infants and mates, and defence of resources (OLIVEIRA & ADES 2004, VAN BELLE *et al.* 2014, KITCHEN *et al.* 2015, SPERBER *et al.* 2017, MANDL *et al.* 2019). The carrying distance of loud calls emitted in primates, mainly by males, is positively correlated with the size of the home range, which indicates their essential role in attracting mates and defending mates and resources (WILCH & NUNN 2002).

The edible dormouse (*Glis glis*) is a small arboreal rodent that can emit a range of different sounds (Vietinghoff-Riesch 1960, Storch 1978, my observations). One type is louder than the others. The peak of the intensity of this so-called loud call occurs mainly at frequencies around 2.2 kHz and 4 kHz, which was observed in captive animals (my observations). Loud calls (each of which lasts an average of 379 ms) are emitted primarily in series, the so-called "performances", ranging from 1 to 217 individual calls (my observations). Humans can hear them from a distance of several dozen meters (HOODLESS & MORRIS 1993) and, under favourable conditions, even more than a hundred meters (JURCZYSZYN 1998).

The edible dormouse preferably inhabits deciduous and mixed woodland (KRYŠTUFEK 2010). In forest areas where beech is the dominant tree species, the basis of its diet is beech seed (e.g. BIEBER & RUF 2004, JURCZYSZYN 2018). In central Europe, the edible dormouse is perfectly adapted to the fluctuations in mast seeding of European beech (BIEBER 1998, SCHLUND *et al.* 2002, FIETZ *et al.* 2004, 2005, 2009, RUF *et al.* 2006). The number and proportion of reproductively active females and litter sizes are positively correlated with beech mast in a given year (KAGER & FIETZ 2009). There are years when the beech does not bear fruit, and these animals do not reproduce (e.g. BIEBER 1998, SCHLUND *et al.* 2002, KRYŠTUFEK *et al.* 2003). Thus, dormice use a strategy of reproducing only in the years of food abundance, when the young can find a sufficient amount of beech fruit on the trees, which are rich in fatty acids and proteins (FIETZ *et al.* 2005), allowing them to prepare adequately for hibernation. In the evolutionary sense, the reproduction adjustment to mast years could be influenced by the high reproductive costs incurred by both sexes (FIETZ *et al.* 2004, 2009).

Observations in natural conditions showed that dormice most often emitted loud calls in exceptionally attractive feeding places (MÜLLER-STIEß personal communication). The number of loud calls per night varies in dormice during the season. More can be heard in late summer, in August (JURCZYSZYN 1995) than in the earlier period of summer. Because in August, the

mating season is over, it seems that the loud calls of dormice are used more to defend the food resources (when the beech fruits ripen) than during mating. VIETINGHOFF-RIESCH (1960), who observed dormice in captivity, believed that loud calls occur mainly during the mating season and that their essential role is related to this phenomenon. Therefore, the results of his research on the vocal activity of dormice in captivity differ from the results of studies in natural conditions (JURCZYŹYŹYN 1995). This difference may be due to the fact that the basic resource that animals could strive for in a cage are mating partners and not food, to which both sexes had constant access.

The study aims to determine what functions are performed by loud calls in males and females of the edible dormouse and whether one of the sexes emits more of them. If we assume that loud calls are related primarily to the mating behaviour of males that compete for females, then: 1) during the mating period (July of the breeding year), males should have more vocalizations (namely "performances" and loud calls) than females, 2) males should have more vocalizations in July during the mating season than a few weeks later in August when the mating season is over. If, however, the loud calls are related primarily to the defence of food resources, then: 3) in the mast seeding year (when the dormice reproduce), males and females should vocalize more often in August (when ripe beechnuts have the highest fat content) than a few weeks earlier in July (when beechnut fat content is much lower), and also 4) in both sexes there should be more vocalizations in August of the mast year (when the dormice reproduce) than in August of the non-mast year (with no dormice reproduction).

MATERIAL AND METHODS

Studies were conducted in the Roztocze National Park (RNP) in southeast Poland (50°36' N, 22°57' E) and in the Sieraków Landscape Park (SLP) in western Poland (52°37' N, 16°06' E). Beech constituted more than 80% of the tree stands in the first locality mentioned above and nearly 30% of the tree stands in the second locality. The study was carried out in the years 2005 and 2006, which differed considerably in terms of the beech fruit crop. The first was a year almost without beechnuts on both study plots ("no crop" according to the classification of KANTOROWICZ (2000)), and the latter was a mast seeding year for beech ("good crop" – KANTOROWICZ (2000)). The term non-mast year will be used for 2005 and the mast year for 2006.

Adult overwintered edible dormice were caught in live traps and fitted with radio transmitters (made by Titley Electronics, Australia) around their neck, which amounted to no more than 5 % of the animal's body mass. Each year, from 1 to 21 July and from 4 to 24 August, six individuals (three males, three females) were radio-tracked in RNP and an equal number of males and females in SLP. The same individuals were studied in July and August in a given year, but in 2005 and 2006, different individuals were studied. Every animal was radio-tracked for four nights in July and four nights in August each year. Con-

tinuous observation was conducted by persons equipped with directional antennas and telemetry receivers (Australis 26k, Titley). Three dormice were simultaneously tracked. The order in which individuals were tracked was randomly determined prior to its commencement in each month of the study. The loud vocalization emitted by telemetrically tracked individuals heard by the investigator was noted in a notebook. The nights in July and August vary in length. In order to be able to quantify the vocalization of dormice in these two months, only six hours of radio-telemetry tracking of these animals during each night were taken into account. Therefore, in July, the listening to vocalizations lasted from the beginning of the night to more or less its end, and in August, only for part of the night (six hours of radio-telemetry from its start at the beginning of the night). Studies were not conducted during rainy or overly windy nights. In 2005, such bad weather prevented surveys during one night in July and one in August in SLP and during 2 nights in July at RNP. In 2006, it prevented surveys during one night in July in both SLP and RNP.

The total number of loud calls emitted by the tracked individuals and the number of "performances" were noted. "Performance" was defined as a series of calls emitted by the animal continuously, one after another, in short intervals of 1.4 seconds on average (my observation). The intervals between individual "performances" are noticeably longer than the intervals between individual loud calls within a "performance" (in the present study, the shortest interval between the performances was 3 minutes). The analysis considers both loud calls and performance numbers, as they both reflect the intensity of edible dormice vocal activity, but in a slightly different way. The performance numbers indicate how many times the animal decides to start vocalizing. Moreover, the number of calls seems to correspond to the animal's involvement in a particular performance.

To test the differences in calls and performances between years, sexes, and months, generalized linear mixed models (GLMMs) implemented via *glmmTMB* package in R was used (Brooks *et al.* 2017). I report the results of two models with either calls or performances as the response. In each model, fixed factors included year, sex, and month as categorical variables. I also constructed models with two-way interaction terms, but these interactions were not significant and thus removed from the final models. In each model, I used animal ID and site as random intercepts. In the case of a model that includes calls as a response, I used negative binomial family error term (as the Poisson model was overdispersed), whereas, in the case of a model that included performances as a response, I used Poisson family error term. I tested for statistical significance of fixed factors using Type II Wald test.

The studies were approved by the Local Ethical Commission (14/2005) and the Polish Ministry of the Environment (DOPog-4201-04-44/05/aj).

RESULTS

Prediction 1. On the study plots in July of the mast/breeding year, no significant difference was found between males and females in the number of "performances" (β (SE) = 0.16 (0.13), $p = 0.21$), (Fig. 1), but it turned out that males emitted more loud calls than females (β (SE) = 0.35 (0.10), $p < 0.001$).

Prediction 2–3. Animals emitted significantly less "performances" in July than in August (β (SE) = 0.34 (0.13), $p = 0.009$), irrespective of year or sex. However, no such difference was found for loud calls (β (SE) = 0.09 (0.10), $p = 0.36$).

Prediction 4. Both males and females had significantly more “performances” and loud calls in August (and July) of the mast/breeding year than in August (and July) of the non-mast/non-breeding year (performances: β (SE) = 1.42 (0.15), $p < 0.001$, loud calls: β (SE) = 1.11 (0.13), $p < 0.001$).

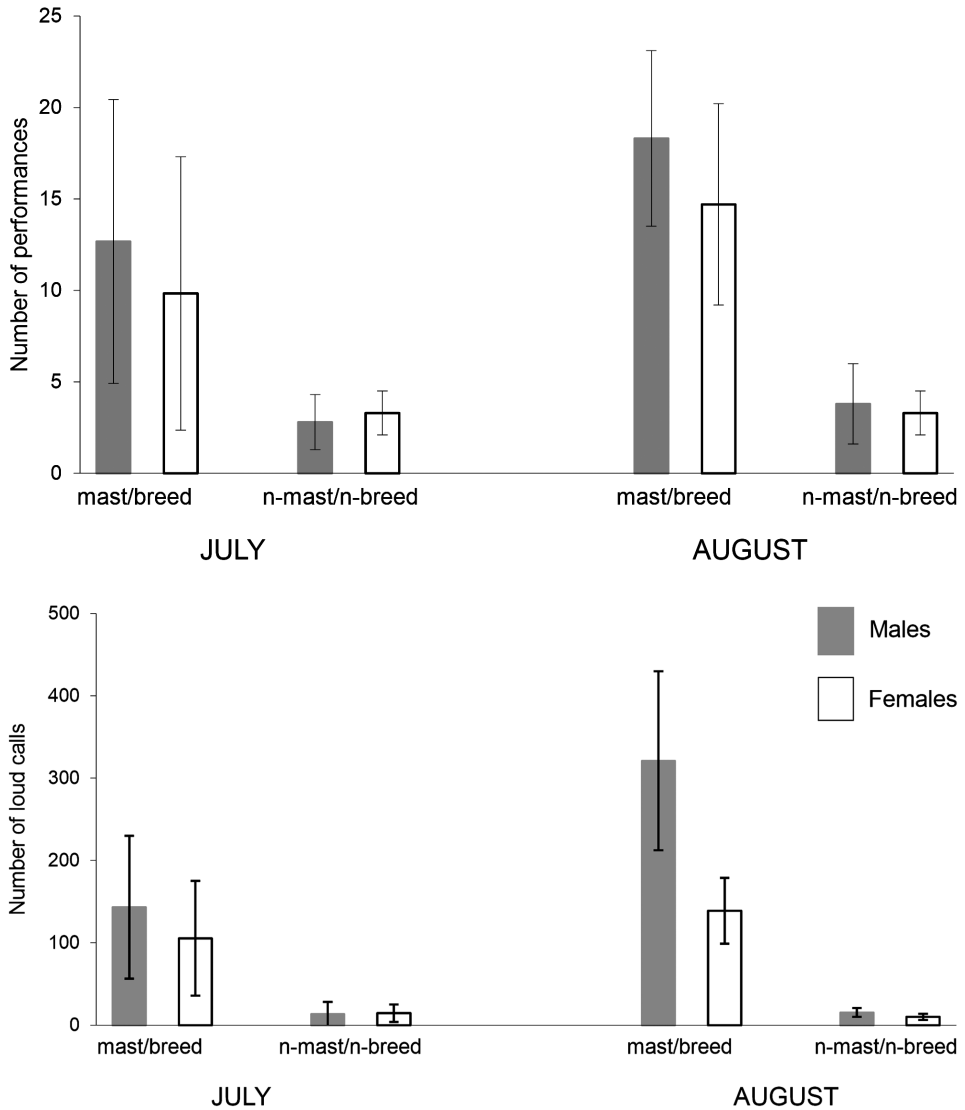


Fig. 1. Mean number of “performances” (a) and loud calls (b) found in all studied edible dormice (6 males and 6 females) in July and August in mast/breeding year and non-mast/non-breeding year. Abbreviations: mast/breed – mast and breeding year; n-mast/n-breed – non-mast and non-breeding year; whiskers represent SD

DISCUSSION

The results obtained in RNP and SLP do not indicate that edible dormice emit loud calls most often during the mating period, as suggested by the observations of VIETINGHOFF-RIESCH (1960). Mating in Central European dormice occurs in the second half of June and July (BIEBER 1998, FIETZ *et al.* 2004, ŚCIŃSKI & BOROWSKI 2008, LEBL *et al.* 2010, JURCZYSZYN 2020), while in males from RNP and SLP, the highest number of “performances” in the reproductive year was found in August when the mating behaviour expires. The mean loud call values for males were also higher in August, although these differences were not statistically significant. Moreover, in July, males did not have more “performances” than females, although these “performances” consisted of more loud calls than females. This may indicate that loud vocalization has some significance for males competing for females during the mating season.

However, it seems more likely that this vocalization is mainly related to competition for food resources during the ripening of beech nuts. During an earlier study in the beech woods of RNP (JURCZYSZYN 1995), more loud calls of the edible dormouse (vocalization of unknown individuals) were found in August, when the beechnuts were almost ripe than in July, when they were unripe. Direct observations of the behaviour of these animals suggest that loud calls are emitted in order to keep away other individuals from the place where vocalizing dormice are feeding (JURCZYSZYN 1995). Similar observations were made by MÜLLER-STIEß (personal communication), who found that dormice vocalized most often in places with particularly attractive food. The results obtained in captivity (VIETINGHOFF-RIESCH 1960) were most likely the effect of the conditions created by man there, in which edible dormice were regularly fed, and also benefited from other advantages not considered in this study (e.g. numerous hiding places, safety from predation). In this situation, the emission of loud calls was primarily related to the mating function.

During the present study, it was observed that individuals of both sexes vocalized the most in the same periods. The highest number of “performances” was found in edible dormice in August of the mast/breeding year when the beech seeds reach their full nutritional value (SUSZKA 1990, BIEBER & RUF 2004). The number of loud calls, however, did not differ significantly between July and August of the breeding year, although in both sexes, higher mean values were found in August. It is difficult to determine the reason for such a difference between “performances” and loud calls. It is possible that the number of “performances” more accurately characterizes the degree of dormice involvement in the defence of food resources than the number of loud calls because it indicates how often the animal decides to defend resources through vocalization. However, it should be taken into account that beechnuts constitute a certain part of the food of these animals already in the first half of sum-

mer (FIETZ *et al.* 2005, BIEBER & RUF 2009, JURCZYSZYN 2018), so the use of loud vocalizations to protect food resources can also be expected in July.

Since the loud calls of edible dormice can be used to detect the presence of this species in forests (e.g. MORTELLITI *et al.* 2009, CIECHANOWSKI & SACHANOWICZ 2014, ADAMIK *et al.* 2019), as well as to estimate population densities (HOODLESS & MORRIS 1993, JURCZYSZYN 1995, KUREK *et al.* 2007, JURCZYSZYN *et al.* 2018), it is worth considering what results from this work in practice. The outcomes obtained clearly indicate that the above type of research is best carried out in beech mast years when these animals (males and females) emit calls much more often than in non-mast years. This applies to both August and July of the mast year. In the beech mast year, the best period for research using dormice calls is the second half of summer (August), because then males and females generate much more “performances” and emit a little more loud calls.

*

Acknowledgements – This study was supported by the Adam Mickiewicz University, Eko-Fundusz Foundation, the management of the Roztocze National Park and the directorate of the Landscape Park Complex of the Province of Greater Poland. I would like to thank students of the Adam Mickiewicz University in Poznań for their help in field work. I am grateful to David Orwin for his comments and English proofreading and to Prof. Michał Bogdziewicz for his valuable advice on the statistical analyses. I would like to thank two anonymous reviewers for taking the time and effort necessary to review the manuscript.

REFERENCES

- ADAMÍK, P., POLEDNÍK, L., POLEDNÍKOVÁ, K. & ROMPORTL, D. (2019): Mapping an elusive arboreal rodent: Combining nocturnal acoustic surveys and citizen science data extends the known distribution of the edible dormouse (*Glis glis*) in the Czech Republic. – *Mammalian Biology* **99**: 12–18. <https://doi.org/10.1016/j.mambio.2019.09.011>
- VAN BELLE, S., ESTRADA, A. & GARBER, P. A. (2014): The function of loud calls in Black Howler Monkeys (*Alouatta pigra*): Food, mate, or infant defense? – *American Journal of Primatology* **76**: 1196–1206. <https://doi.org/10.1002/ajp.22304>
- BIEBER, C. (1998): Population dynamics, sexual activity, and reproduction failure in the fat dormouse (*Myoxus glis*). – *Journal of Zoology* **244**: 223–229. <https://doi.org/10.1111/j.1469-7998.1998.tb00027.x>
- BIEBER, C. & RUF, T. (2004): Seasonal timing of reproduction and hibernation in the edible dormouse (*Glis glis*). Pp. 113–125. In: BARNES, B. M. & CAREY, H. V. (eds): *Life in the cold: evolution, mechanisms, adaptation, and application*. – Institute of Arctic Biology, University of Alaska, Fairbanks, Twelfth International Hibernation Symposium. Biological Papers of the University of Alaska.
- BIEBER, C. & RUF, T. (2009): Habitat differences affect life history tactics of a pulsed resource consumer, the edible dormouse (*Glis glis*). – *Population Ecology* **51**: 481–492. <https://doi.org/10.1007/s10144-009-0140-x>

- BLUMSTEIN, D. T. & ARMITAGE, K. B. (1997): Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. – *American Naturalist* **150**: 179–200. <https://doi.org/10.1086/286062>
- BROOKS, M. E., KRISTENSEN K., VAN BENTHEM, K. J., MAGNUSSON, A., CASPER W. BERG, C. W., NIELSEN, A., SKAUG, H. J., MAECHLER M. & BOLKER, B. M. (2017): glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – *The R Journal* **9**: 378–400. <https://doi.org/10.32614/RJ-2017-066>
- DA CUNHA, R., DE OLIVEIRA, D., HOLZMANN, I. & KITCHEN, D. (2015): Production of loud and quiet calls in howler monkeys. Pp. 337–368. In: KOWALEWSKI, M., GARBER, P., CORTÉS-ORTIZ, L., URBANI, B. & YOULATOS, D. (eds): *Howler monkeys. Developments in primatology: progress and prospects* – Springer, New York.
https://doi.org/10.1007/978-1-4939-1957-4_13
- CIECHANOWSKI, M. & SACHANOWICZ, K. (2014): Fat dormouse *Glis glis* (Rodentia: Gliridae) in Albania: synopsis of distributional records with notes on habitat use. – *Acta Zoologica Bulgarica* **66**: 39–42.
- CLUTTON-BROCK, T. H. & ALBON, S. D. (1979): The roaring of red deer and the evolution of honest advertisement. – *Behaviour* **69**: 145–170. <https://doi.org/10.1163/156853979X000449>
- EY, E. & FISCHER, J. (2009): The “acoustic adaptation hypothesis” – a review of the evidence from birds, anurans and mammals. – *Bioacoustics* **19**: 21–48.
<https://doi.org/10.1080/09524622.2009.9753613>
- FIETZ, J., SCHLUND, W., DAUSMANN, K. H., REGELMANN, M. & HELDMAIER, G. (2004): Energetic constraints on sexual activity in the male edible dormouse (*Glis glis*). – *Oecologia* **138**: 202–209. <https://doi.org/10.1007/s00442-003-1423-0>
- FIETZ, J., PFLUG, M., SCHLUND, W. & TATARUCH, F. (2005): Influences of the feeding ecology on body mass and possible implications for reproduction in the edible dormouse (*Glis glis*). – *Journal of Comparative Physiology B* **175**: 45–55.
<https://doi.org/10.1007/s00360-004-0461-1>
- FIETZ, J., KAGER, T. & SCHAUER, S. (2009): Is energy supply the trigger for reproductive activity in male edible dormice (*Glis glis*)? – *Journal of Comparative Physiology B* **179**: 829–837. <https://doi.org/10.1007/s00360-009-0364-2>
- GARSTANG, M. (2004): Long-distance, low-frequency elephant communication. – *Journal of Comparative Physiology A* **190**: 791–805. <https://doi.org/10.1007/s00359-004-0553-0>
- GOLDINGAY, R. L. (1994): Loud calls of the Yellow-bellied glider, *Petaurus australis*: territorial behaviour by an arboreal marsupial? – *Australian Journal of Zoology* **42**: 279–293.
<https://doi.org/10.1071/ZO9940279>
- HARRINGTON, F. H. & MECH, L. D. (1979): Wolf howling and its role in territory maintenance. – *Behaviour* **68**: 207–249. <https://doi.org/10.1163/156853979X00322>
- HOODLESS, A. & MORRIS, P. A. (1993): An estimate of population density of the fat dormouse (*Glis glis*). – *Journal of Zoology* **230**: 337–340.
- JURCZYSZYN, M. (1995): Population density of *Myoxus glis* (L.) in some forest biotopes. – *Hystrix* **6**: 265–271.
- JURCZYSZYN M. (1998): Methods of detecting edible dormouse *Myoxus glis* (L.) in the field. – *Przegląd Przyrodniczy* **42**: 247–250. [in Polish]
- JURCZYSZYN, M. (2018): Food and foraging preferences of the edible dormouse *Glis glis* at two sites in Poland. – *Folia Zoologica* **67**: 83–90. <https://doi.org/10.25225/fozo.v67.i2.a5.2018>
- JURCZYSZYN, M. (2020): Radio-transmitters gnawed by edible dormice *Glis glis* in populations of different density. – *Mammalia* **84**: 493–496.
<https://doi.org/10.1515/mammalia-2019-0072>

- JURCZYŚYŹN, M., KOZIK, B., DONARSKA, A. & CZAPRACKA A. (2018): Edible dormouse *Glis glis* in Pieniny National Park. – *Chrońmy Przyrodę Ojczystą* **74**: 173–180. [in Polish]
- KAGER, T. & FIETZ, J. (2009): Food availability in spring influences reproductive output in the seed–preying edible dormouse (*Glis glis*). – *Canadian Journal of Zoology* **87**: 555–565. <https://doi.org/10.1139/Z09-040>
- KANTOROWICZ, W. (2000): Half a century of seed years in major tree species of Poland. – *Silvae Genetica* **49**: 245–249.
- KITCHEN, D., DA CUNHA, R., HOLZMANN, I. & DE OLIVEIRA, D. (2015): Function of loud calls in howler monkeys. Pp. 369–399. In: KOWALEWSKI, M., GARBER, P., CORTÉS-ORTIZ, L., URBANI, B. & YOULATOS, D. (eds): *Howler monkeys. Developments in primatology: progress and prospects*. – Springer, New York. https://doi.org/10.1007/978-1-4939-1957-4_14
- KRYŠTUFEK, B. (2010): *Glis glis* (Rodentia: Gliridae). – *Mammalian Species* **42**: 195–206. <https://doi.org/10.1644/865.1>
- KRYŠTUFEK, B., HUDOKLIN, A. & PAVLIN, D. (2003): Population biology of the edible dormouse *Glis glis* in a mixed montane forest in central Slovenia over three years. – *Acta Zoologica Academiae Scientiarum Hungaricae* **49** (Suppl. 1): 85–97.
- KUREK, P., SKOWRON, B. & ŚWIĘCIAK, T. (2007): Records of *Glis glis* (L., 1766) in the vicinity of Olsztyn and Złoty Potok in the Wyżyna Częstochowska Upland (S Poland). – *Chrońmy Przyrodę Ojczystą* **63**: 91–96. [in Polish]
- LEBL, K., KÜRBIĆH, K., BIEBER, C. & RUF, T. (2010): Energy or information? The role of seed availability for reproductive decisions in edible dormice. – *Journal of Comparative Physiology B* **180**: 447–456. <https://doi.org/10.1007/s00360-009-0425-6>
- MANDL, I., SCHWITZER, C. & HOLDERIED, M. (2019): Sahamalaza Sportive Lemur, *Lepilemur sahamalaza*, vocal communication: call use, context and gradation. – *Folia Primatologica* **90**: 336–360. <https://doi.org/10.1159/000493939>
- MATROSOVA, V. A., SCHNEIDEROVÁ, I., VOLODIN, I. A. & VOLODINA, E. V. (2012): Species-specific and shared features in vocal repertoires of three Eurasian ground squirrels (genus *Spermophilus*). – *Acta Theriologica* **57**: 65–78. <https://doi.org/10.1007/s13364-011-0046-9>
- MORTELLITI, A., SANTULLI SANZO, G. & BOITANI, L. (2009): Species' surrogacy for conservation planning: caveats from comparing the response of three arboreal rodents to habitat loss and fragmentation. – *Biodiversity and Conservation* **18**: 1131–1145. <https://doi.org/10.1007/s10531-008-9477-2>
- OLIVEIRA, D. A. G. & ADES, C. (2004): Long-distance calls in Neotropical primates. – *Anais da Academia Brasileira de Ciências* **76**: 393–398. <https://doi.org/10.1590/S0001-37652004000200031>
- OWINGS, D. H. & MORTON, E. S. (1998): *Animal vocal communication: A new approach*. – Cambridge University Press, Cambridge, 289 pp. <https://doi.org/10.1017/CBO9781139167901>
- RUF, T., FIETZ, J., SCHLUND, W. & BIEBER, C. (2006): High survival in poor years: life history tactics adapted to mast seeding in the edible dormouse. – *Ecology* **87**: 372–381. <https://doi.org/10.1890/05-0672>
- RYAN, M. J. & KIME, N. M. (2002): Selection on long distance acoustic signals. Pp. 225–274. In: SIMMONS, A., FAY, R. R. & POPPER, A. N. (eds): *Acoustic communication*. – Springer, New York. https://doi.org/10.1007/0-387-22762-8_5
- SCHLUND, W., SCHARFE, F. & GANZHORN, J. U. (2002): Long-term comparison of food availability and reproduction in the edible dormouse (*Glis glis*). – *Mammalian Biology* **67**: 219–232. <https://doi.org/10.1078/1616-5047-00033>
- SLATER, P. J. B. (1983): The study of communication. Pp. 9–42. In: HALLIDAY, T. R. & SLATER, P. J. B. (eds): *Animal behaviour. Vol. 2*. – Blackwell Scientific, Oxford.

- SOLTIS, J. (2010): Vocal communication in African elephants (*Loxodonta africana*). – *Zoo Biology* **29**: 192–209. <https://doi.org/10.1002/zoo.20251>
- SPERBER, A. L., WERNER, L. M., KAPPELER, P. M. & FICHTEL, C. (2017): Grunt to go – Vocal coordination of group movements in redfronted lemurs. – *Ethology* **123**: 894–905. <https://doi.org/10.1111/eth.12663>
- STORCH, G. (1978): *Glis glis* (Linnaeus, 1766) – Siebenschläfer. Pp. 243–258. In: NIETHAMMER, J. & KRAPP, F. (eds): *Handbuch der Säugetiere Europas. Band 1.* – Akademische Verlagsgesellschaft, Wiesbaden.
- SUSZKA, B. (1990): Rozmnażanie generatywne [Sexual reproduction of beech]. Pp. 375–498. In: BIAŁOBOK, S. (ed.): *Buk zwyczajny Fagus sylvatica L.* [European beech *Fagus sylvatica L.*] – PWN, Poznań. [in Polish]
- ŚCIŃSKI, M. & BOROWSKI, Z. (2008): Spatial organization of the fat dormouse (*Glis glis*) in an oak-hornbeam forest during the mating and post-mating season. – *Mammalian Biology* **73**: 119–127. <https://doi.org/10.1016/j.mambio.2007.01.002>
- WILCH, S. A. & NUNN, C. L. (2002): Do male “long-distance calls” function in mate defence? A comparative study of long-distance calls in primates. – *Behavioral Ecology and Sociobiology* **52**: 474–484. <https://doi.org/10.1007/s00265-002-0541-8>
- VIETINGHOFF–RIESCH, A. FRHR VON (1960): Der Siebenschläfer (*Glis glis L.*). Pp. 1–196. In: MÜLLER–USING, D. (ed.): *Monographien der Wildsäugetiere.* – Gustav Fischer Verlag, Jena.
- ZIMMERMANN, E. (1995): Loud calls in nocturnal prosimians: structure, evolution and ontogeny. Pp. 47–72. In: ZIMMERMANN, E., NEWMAN, J. D. & JÜRGENS, U. (eds): *Current topics in primate vocal communication.* – Plenum Press, New York. https://doi.org/10.1007/978-1-4757-9930-9_3

Revised version submitted September 23, 2022; accepted November 7, 2022; published February 28, 2023