Received: 12 January 2021 | Revised: 15 July 2021 | Accepted: 10 August 2021

DOI: 10.1111/aje.12923

SHORT COMMUNICATION

African Journal of Ecology WILEY

Male impala (*Aepyceros melampus*) vocal activity throughout the rutting period in Namibia: daily and hourly patterns

Elena V. Volodina[1] | Ilya A. Volodin[1,2] | Roland Frey[3]

[1]Department of Behaviour and Behavioural Ecology of Mammals, A.N. Severtsov Institute of Ecology and Evolution, Moscow, Russia

[2]Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Moscow, Russia

[3]Department of Reproduction Management, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany

Correspondence
Ilya A. Volodin, Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Vorobievy Gory, 12/1, Moscow 119234, Russia.
Email: volodinsvoc@gmail.com

Funding information
Russian Foundation for Basic Research, Grant/Award Number: 19-04-00133

Keywords: passive acoustic monitoring, polygynous ruminant, rutting period, vocal activity

1 | INTRODUCTION

In polygynous ruminants, vocal activity represents an important part of male advertising behaviour in the rutting period (Briefer et al., 2010; Clutton Brock & Albon, 1979; Frey et al., 2007a, 2007b, 2011, 2012; Golosova et al., 2017; Jarman, 1979; Volodin et al., 2019). Impala (*Aepyceros melampus*) are polygynous ruminants with impressive male rutting displays including complex behaviour (Frey et al., 2020) and bouts of rutting calls including different types of roars and snorts (Volodin et al., 2021). In other studied polygynous ruminants, the rutting periods are known to have a strict seasonality (Rusin et al., 2019, 2021; Volodin et al., 2013, 2015, 2016; Yen et al., 2013). However, the timing of the rutting period and the daily and hourly vocal activity throughout the rut require investigation in male impala.

In impala, the timing of the rut differs between temperate and tropical climate zones. A clearly defined rutting period exists only in regions of Africa with prominent seasonal changes of temperature, day length and rainfall, as, for example, in Zimbabwe (Murray, 1982; Warren, 1974), South Africa (Oliver, 2002; Oliver et al., 2006) and Namibia (Frey et al., 2020; Volodin et al., 2021). In such a temperate climate, rutting male impala produce their bouts of rutting calls in May-June, depending on the latitude (Dasmann & Mossman, 1962; Fairall, 1983; Frey et al., 2020; Mason, 1976; Oliver, 2002; Oliver et al., 2006; Volodin et al., 2021). During the rutting period, males keep territories rich in food and/or water resources of about 34 ha (Oliver, 2002; Oliver et al., 2006) that attract females, and defend them against rival males (Anderson, 1972a, 1972b, 1975; Frey et al., 2020; Jarman, 1979; Leuthold, 1970; Murray, 1982; Oliver, 2002; Oliver et al., 2006; Volodin et al., 2021). But in the tropical climate of Eastern Africa, impala breed year-round and dominant impala males constantly herd females and defend them against rival males, at low levels of roaring activity (Leuthold, 1970; Schenkel, 1966). The aim of this study was to quantify male impala rutting vocal activity along the defined one-month rutting period in Namibia by conducting passive acoustic monitoring using an autonomous recording unit.

2 | MATERIALS AND METHODS

2.1 | Study site, population and dates

Audio recordings of bouts of rutting calls (hereafter 'bouts') (Figure 1) of an unknown number of rutting male common impala (*Aepyceros melampus melampus*) were conducted at the fenced 15,000-ha Okambara Elephant Ranch (22.68S, 18.16E), located about 130 km east of Windhoek, Namibia, during the rutting period from 1st to 28th of May 2015. This is a native Namibian habitat with approximately 60% bush cover and open areas around artificial watering places. In 2015, it accommodated about 800 free-ranging impalas originating from about 100 individuals released in 1994 (Frey et al., 2020; Volodin et al., 2021).

2.2 | Audio recording

Stereo audio recordings of male impala rutting calls were collected automatically using one Song Meter SM2+ (Wildlife Acoustics Inc., Maynard, MA, USA) at sampling rate 22.05 kHz, amplitude resolution 16-bit, wav format. The device was equipped with two omnidirectional microphones SMX-II, fixed horizontally at 180° to each other. The device was set at maximum sensitivity and potentially captured male impala rutting calls within about 300 m around at sufficient quality for spectrographic and aural detection. The device was placed on the ground within a large wire-mesh cage, protecting it from damage by baboons *Papio ursinus*, at a rutting hot spot, identified by multiple fresh impala tracks and faeces, in the vicinity of an impala watering place. At this location, several impala passes crossed in dense vegetation on a hill slope. The position of the device remained unchanged throughout the entire survey period. The device was checked every 2–3 days during daytime for replacing memory cards and batteries.

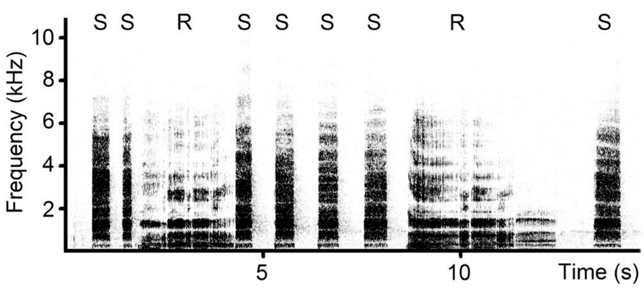

FIGURE 1 Spectrogram of a representative bout of rutting calls of an impala male. (R) roars, (S) snorts. The Audio file is available at Audio S1. The spectrogram was created with a Hamming window; 22.05 kHz sampling rate; FFT 1024 points; frame 50%; and overlap 75%

The device was set to 9-min recording, interrupted by 1 min pause (the minimum possible pause for this device), providing 120 audio wav-files of 9 min length (total duration 1080 min = 18 h) for each 20-h study cycle (hereafter 'study night') starting from 14:00 of the current day throughout the night to 10:00 of the next day. Recording excluded the four midday hours when the animals were assumed to be less active. In total, our analysis included 27 study nights: night #1 corresponded to the night from 1st to 2nd May 2015, and night #27 corresponded to the night from 27th to 28th May 2015. During the 27 study nights, a total of 3240 9-min wav-files (486 h of recording time) were collected.

2.3 | Acoustic analysis

All wav-files were inspected using Avisoft SASLab Pro software (Avisoft Bioacoustics, Germany, Berlin) main window, with sampling rate 22.05 kHz, Hamming window, FFT (Fast Fourier Transform) 512, frame 100%. The number of bouts in each wav-file irrespective of quality was counted (Figure 1). In total, we registered 3176 bouts.

Although the automated recordings did not allow identifying individuals, the bouts belonging to different males could be recognised by different intensities resulting from different distances of males to the device or by overlapping bouts. At the same time, successive same-intensity emissions probably coming from the same individual were commonly separated by intervals of at least a few minutes. In all wav-files, we counted all bouts irrespective of how many males might have produced them.

We calculated the number of bouts/h for each hour of recording as the total number of bouts, divided by 0.9 (54 min). Then, we calculated the mean number of bouts/h for each study night, averaged across the 20 h. For evaluating the hourly vocal activity patterns of males, we calculated the mean number of bouts/h for each hour of recording, averaged across the 27 study nights.

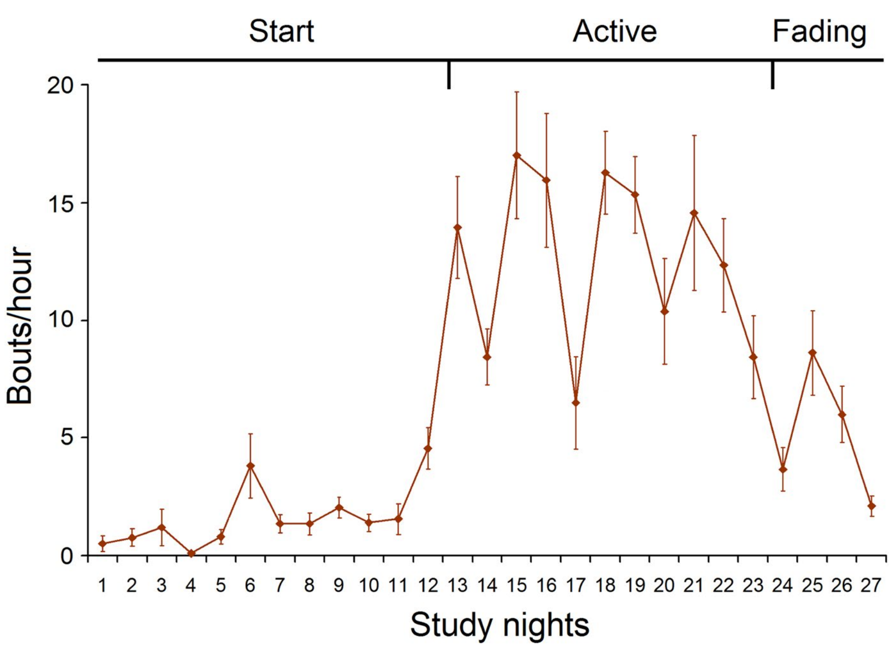

FIGURE 2 Daily pattern of male impala rutting vocal activity across the 27 study nights of the rutting period. Start, Active, Fading = the three phases of the rut. Points indicate the mean numbers of rutting bouts per hour per study night, whiskers indicate *SE*

2.4 | Statistical analyses

All statistical analyses were made with STATISTICA v. 8.0 (StatSoft Inc., Tulsa, OK, USA). Means are given as mean ± SE, all tests were two-tailed, and differences were considered significant whenever $p < 0.05$. As most (21 of 27) distributions did not depart from normality (Kolmogorov–Smirnov test, $p > 0.05$) and because ANOVA is relatively robust to departures from normality (Dillon & Goldstein, 1984), we could apply the parametric tests. We used a GLMM (General Linear Mixed Model) with Tukey HSD (Honest Significantly Different) post hoc to estimate the effects of rut phase (start, active and fading), time of night (hourly), interaction between rut phase and time of night (hourly), and study night on the number of bouts per hour, taking rut phase and time of night (hourly) as fixed factors and study night as random factor.

3 | RESULTS AND DISCUSSION

From the total of 3240 analysed wav-files, 1287 contained bouts of male impala rutting calls. From these 1287 wav-files, 538 contained one bout per file, 302 contained two bouts per file, 276 contained 3–4 bouts per file, 161 contained 5–9 bouts per file and 10 files contained 10–15 bouts per file. This indirectly indicates that vocal duels between two or more males were infrequent.

The number of bouts/h was different in different study nights throughout the recording period (Figure 2). Based on rutting activity, the rutting period was subdivided into three phases, Start (study nights #1-12), Active (study nights #13-23) and Fading (study nights #24-27). During the Start phase, the rutting vocal activity ranged from 0.09 to 4.56 (1.62 ± 0.40) bouts/h. During the Active phase, the vocal activity ranged from 6.50 to 17.0 (12.65 ± 1.10) bouts/h. At the Fading phase, the vocal activity decreased to 2.11–8.61 (5.10 ± 1.42) bouts/h (Figure 2). On average, over the 27 study nights, male impala produced 6.63 ± 1.12 bouts/h.

GLMM revealed the effects of rut phase ($F_{2,456}$ = 121.48, $p < 0.001$) and hour of study night ($F_{19,456} = 2.43$, $p < 0.001$), but not the interaction effect of rut phase and hour of night ($F_{38,456} = 0.86$, $p = 0.70$) on the number of bouts/h. The Tukey post hoc showed that the number of bouts/h differed ($p < 0.001$) among all three rut phases. However, during a study night male vocal activity varied less strongly, from 4.32 to 14.11 bouts/h (Figure 3). A single significant maximum of vocal activity was found at 17:00 (compared to other hours 14:00, 15:00, 19:00–01:00, 03:00, 04:00; Tukey post hoc, $p < 0.05$) and a smaller peak (10.42 bouts/h) at 07:00. Thus, at our study site peaks of male vocal activity occurred at sunset and sunrise (Figure 3). Two periods of lowered vocal activity were identified, from 19:00 to 21:00 (4.32 bouts/h) and from 03:00 to 04:00 (4.81 bouts/h) (Figure 3).

The two peaks of male impala vocal activity are similar to those found in red deer (Rusin et al., 2021). Despite strongly different ecological conditions in geographically remote habitats, both species showed well-expressed peaks of rutting vocal activity at dusk and dawn. Probably, the feeding times of ruminants around sunset and around sunrise (Pagon et al., 2013; Tyler et al., 2016) entail more frequent encounters between individuals, thereby, provoking the production of higher numbers of rutting bouts.

We found that male impala roaring activity during the May rutting period in Namibia involved three phases (start, active and fading), similar to red deer *Cervus elaphus*, another ruminant with a strictly seasonal rutting period (Rusin et al., 2019, 2021). Although

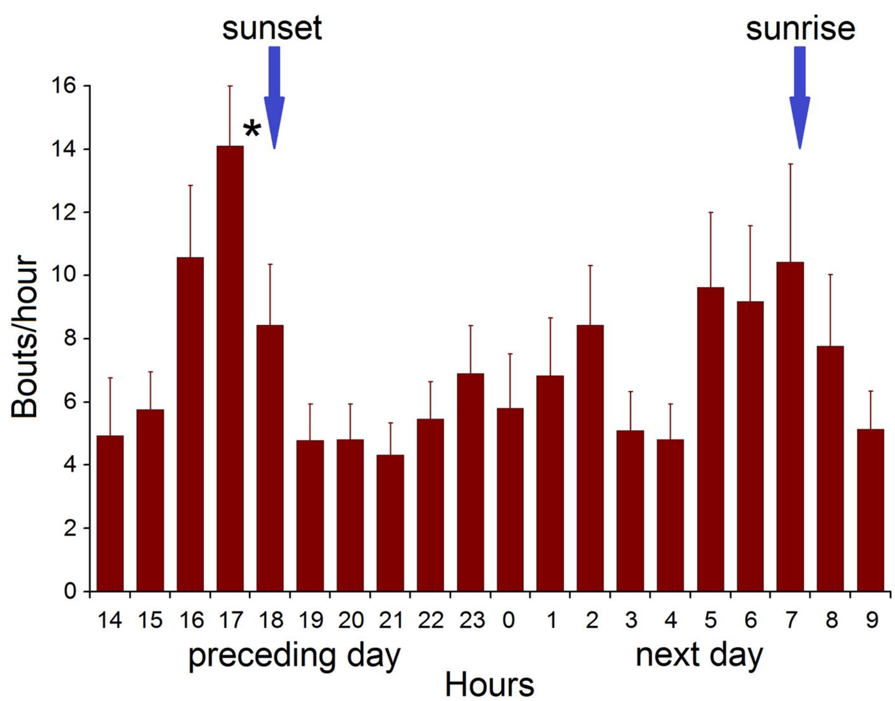

FIGURE 3 Hourly (by time of day) male impala rutting vocal activity averaged over 27 study nights of the rutting period. Bars indicate the mean number of bouts of rutting calls per hour of the 20-h study night averaged over the 27 study nights; whiskers indicate *SE*. The asterisk indicates the time (from 17:00 to 18:00) with maximum rutting vocal activity

we could not track the fading phase to the end because of limited time available for data collection, we assume a prolonged fading phase in impala similar to that in red deer.

This study used state-of-the-art methods enabling documentation of reproductive activity in impala, a highly vocal and charismatic species. These methods are currently widely applied for monitoring daily and seasonal activity of diverse mammals, from ruminants (Rusin et al., 2019, 2021) to bats (Hanrahan et al., 2021). Human observers can only work during a limited time per day, whereas the automated recording system can be programmed to work day and night throughout the entire rut, thus providing full-scale data on the roaring activity without disturbing the animals. Consequently, results obtained with automated recorders are better reproducible and comparable across seasons and study sites than those based on censuses by ear (Volodin et al., 2016). We used only one recording site to track the dynamics of rutting vocal activity of male impala involving limitations to the conclusions of this study. However, as shown in red deer, one recording site provides already a reliable estimation of rutting activity per population (Rusin et al., 2019, 2021). This probably also applies to impala, yet further studies using several recording sites per population are necessary to confirm our conclusions.

This study suggests that in the temperate climate of Namibia, the impala rutting period is restricted to about one month in May. We showed that the active phase of the rut is relatively short, lasting for about ten days. These pioneering results concerning male rutting vocal activity in a bovid species may serve as referential data for further comparisons with year-round breeding impala populations of tropical zones (Leuthold, 1970; Schenkel, 1966) and for projects of ecoacoustical monitoring of landscapes and animal populations (Krause & Farina, 2016).

ACKNOWLEDGEMENTS

We thank the owner of the Okambara Elephant Ranch, Namibia, Christian Schmitt, for providing the possibility to investigate impala on his farm, for his interest in our work and continuous support. We thank Vera Mendes, Ruben Portas, Jörg Melzheimer and Jakob HaiHáb for their invaluable help and advice while we were conducting our research at the Okambara Elephant Ranch, Namibia. This work was supported by the Russian Foundation for Basic Research to IAV and EVV, grant 19-04-00133.

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Elena V. Volodina https://orcid.org/0000-0001-9755-4576
Ilya A. Volodin https://orcid.org/0000-0001-6278-0354
Roland Frey https://orcid.org/0000-0002-6759-761X

REFERENCES

Anderson, J. L. (1972a). Seasonal changes in the social organisation and distribution of the impala in Hluhluwe Game Reserve, Zululand. *Journal of South African Wildlife Management Association*, *2*, 16–20.

Anderson, J. L. (1972b). The impala rut. *African Wildlife*, *27*, 78–82.

Anderson, J. L. (1975). The occurrence of a secondary breeding peak in the southern impala. *East African Wildlife Journal*, *13*, 149–151.

Briefer, E., Vannoni, E., & McElligott, A. G. (2010). Quality prevails over identity in the sexually selected vocalisations of an ageing mammal. *BMC Biology*, *8*(35), 1–15. https://doi.org/10.1186/1741-7007-8-35

Clutton-Brock, T. H., & Albon, S. D. (1979). The roaring of red deer and the evolution of honest advertising. *Behaviour*, *69*, 145–170. https://doi.org/10.1163/156853979X00449

Dasmann, R. F., & Mossman, A. S. (1962). Population studies of impala in Southern Rhodesia. *Journal of Mammalogy*, *43*, 375–395. https://doi.org/10.2307/1376947

Dillon, W. R., & Goldstein, M. (1984). *Multivariate analysis: Methods and applications* (pp. 1–608). Wiley.

Fairall, N. (1983). Production parameters of the impala, *Aepyceros melampus*. *South African Journal of Animal Science*, *13*, 176–179.

Frey, R., Gebler, G., Fritsch, G., Nygrén, K., & Weissengruber, G. E. (2007a). Nordic rattle: the hoarse vocalization and the inflatable laryngeal air sac of reindeer (*Rangifer tarandus*). *Journal of Anatomy*, *210*, 131–159. https://doi.org/10.1111/j.1469-7580.2006.00684.x

Frey, R., Volodin, I. A., & Volodina, E. V. (2007b). A nose that roars: Anatomical specializations and behavioural features of rutting male saiga. *Journal of Anatomy*, *211*, 717–736. https://doi.org/10.1111/j.1469-7580.2007.00818.x

Frey, R., Volodin, I. A., Volodina, E. V., Carranza, J., & Torres-Porras, J. (2012). Vocal anatomy, tongue protrusion behaviour and the acoustics of rutting roars in free-ranging Iberian red deer stags (*Cervus elaphus hispanicus*). *Journal of Anatomy*, *220*, 271–292. https://doi.org/10.1111/j.1469-7580.2011.01467.x

Frey, R., Volodin, I. A., Volodina, E. V., Efremova, K. O., Menges, V., Portas, R., Melzheimer, J., Guido, F., Gerlach, C., & von Dörnberg, K. (2020). Savannah roars: The vocal anatomy and the impressive rutting calls of male impala (*Aepyceros melampus*) - highlighting the acoustic correlates of a mobile larynx. *Journal of Anatomy*, *236*, 398–424. https://doi.org/10.1111/joa.13114

Frey, R., Volodin, I. A., Volodina, E. V., Soldatova, N. V., & Juldaschev, E. T. (2011). Descended and mobile larynx, vocal tract elongation and rutting roars in male goitred gazelles (*Gazella subgutturosa* Güldenstaedt, 1780). *Journal of Anatomy*, *218*, 566–585. https://doi.org/10.1111/j.1469-7580.2011.01361.x

Golosova, O. S., Volodin, I. A., Isaeva, I. L., & Volodina, E. V. (2017). Effects of free-ranging, semi-captive and captive management on the acoustics of male rutting calls in Siberian wapiti *Cervus elaphus sibiricus*. *Mammalian Research*, *62*, 387–396. https://doi.org/10.1007/s13364-017-0322-4

Hanrahan, N., Turbill, C., Armstrong, K. N., Dalziell, A. H., & Welbergen, J. A. (2021). Ghost bats exhibit informative daily and seasonal temporal patterns in the production of social vocalisations. *Australian Journal of Zoology*, *67*, 305–315. https://doi.org/10.1071/ZO20055

Jarman, M. V. (1979). *Impala social behaviour, territory, hierarchy, mating and the use of space*. Parey, Hamburg, 1–93.

Krause, B., & Farina, A. (2016). Using ecoacoustic methods to survey the impacts of climate change on biodiversity. *Biological Conservation*, *195*, 245–254. https://doi.org/10.1016/j.biocon.2016.01.013

Leuthold, W. (1970). Observations on the social organisation of impala (*Aepyceros melampus*). *Zeitschrift für Tierpsychologie*, *27*, 693–721. https://doi.org/10.1111/j.1439-0310.1970.tb01896.x

Mason, D. R. (1976). Observations on social organisation, behaviour and distribution of impala in the Jack Scott Nature Reserve. *South African Journal of Wildlife Research*, *6*, 79–87.

Murray, M. G. (1982). The rut of impala: aspects of seasonal mating under tropical conditions. *Zeitschrift für Tierpsychologie*, *59*, 319–337. https://doi.org/10.1111/j.1439-0310.1982.tb00345.x

Oliver, C. M. (2002). *The role of the ram in the impala (Aepyceros melampus) mating system*. MSc. thesis, Faculty of Veterinary Science, University of Pretoria, Pretoria, 107 pp.

Oliver, C. M., Skinner, J. D., & Van der Merwe, D. (2006). Territorial behaviour in southern impala rams (*Aepyceros melampus* Lichtenstein). *African Journal of Ecology*, *45*, 142–148. https://doi.org/10.1111/j.1365-2028.2006.00687.x

Pagon, N., Grignolio, S., Pipia, A., Bongi, P., Bertolucci, C., & Apollonio, M. (2013). Seasonal variation of activity patterns in roe deer in a temperate forested area. *Chronobiology International*, *30*, 772–785. https://doi.org/10.3109/07420528.2013.765887

Rusin, I. Y., Volodin, I. A., Andronova, R. S., & Volodina, E. V. (2019). Passive acoustic monitoring of roaring activity in male wapiti *Cervus elaphus xanthopygus* in Far East of Russia: effects of recording site, ambient temperature and time of day. *Nature Conservation Research*, *4*, 34–44. https://doi.org/10.24189/ncr.2019.039

Rusin, I. Y., Volodin, I. A., Sitnikova, E. F., Litvinov, M. N., Andronova, R. S., & Volodina, E. V. (2021). Roaring dynamics in rutting male red deer *Cervus elaphus* from five Russian populations. *Russian Journal of Theriology*, *20*, 44–58. https://doi.org/10.15298/rusjtheriol.20.1.06

Schenkel, R. (1966). On sociology and behaviour in the impala (*Aepyceros melampus*). *Zeitschrift für Säugetierkunde*, *31*, 177–205. https://doi.org/10.1111/j.1365-2028.1966.tb00887.x

Tyler, N. J. C., Gregorini, P., Forchhammer, M. C., Stokkan, K.-A., van Oort, B. E. H., & Hazlerigg, D. G. (2016). Behavioral timing without clockwork: photoperiod-dependent trade-off between predation hazard and energy balance in an arctic ungulate. *Journal of Biological Rhythms*, *31*, 522–533. https://doi.org/10.1177/0748730416662778

Volodin, I. A., Nahlik, A., Tari, T., Frey, R., & Volodina, E. V. (2019). Rutting roars in native Pannonian red deer of Southern Hungary and the evidence of acoustic divergence of male sexual vocalization between Eastern and Western European red deer (*Cervus elaphus*). *Mammalian Biology*, *94*, 54–65. https://doi.org/10.1016/j.mambio.2018.10.009

Volodin, I. A., Volodina, E. V., & Frey, R. (2021). Rutting vocal display in male impala (*Aepyceros melampus*) and overlap with alarm context. *Frontiers in Zoology*, *18*(2), 1–15. https://doi.org/10.1186/s12983-020-00383-9

Volodin, I. A., Volodina, E. V., Frey, R., & Maymanakova, I. L. (2013). Vocal activity and acoustic structure of the rutting calls of Siberian wapiti (*Cervus elaphus sibiricus*) and their imitation with a hunting luring instrument. *Russian Journal of Theriology*, *12*, 99–106. https://doi.org/10.15298/rusjtheriol.12.2.06

Volodin, I. A., Volodina, E. V., & Golosova, O. S. (2016). Automated monitoring of vocal rutting activity in red deer (*Cervus elaphus*). *Russian Journal of Theriology*, *15*, 91–99. https://doi.org/10.15298/rusjtheriol.15.2.03

Volodin, I. A., Volodina, E. V., Sibiryakova, O. V., Naidenko, S. V., Hernandez-Blanco, J. A., Litvinov, M. N., & Rozhnov, V. V. (2015). Vocal activity and the acoustic structure of rutting calls in red deer in the Russian Far East. *Doklady Biological Science*, *462*, 144–147. https://doi.org/10.1134/S0012496615030114

Warren, H. B. (1974). Aspects of the behaviour of the impala male, *Aepyceros melampus* during the rut. *Arnoldia Rhodesia*, *6*, 1–9.

Yen, S.-C., Shieh, B.-S., Wang, Y.-T., & Wang, Y. (2013). Rutting vocalizations of Formosan sika deer *Cervus nippon* taiouanus - Acoustic structure, seasonal and diurnal variations, and individuality. *Zoological Science*, *30*, 1025–1031. https://doi.org/10.2108/zsj.30.1025

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Volodina, E. V., Volodin, I. A., & Frey, R. (2021). Male impala (*Aepyceros melampus*) vocal activity throughout the rutting period in Namibia: daily and hourly patterns. *African Journal of Ecology*, 00, 1–5. https://doi.org/10.1111/aje.12923