Acoustic ecology of tawny owl *(Strix aluco)* in the Greek Rhodope Mountains using passive acoustic monitoring methods

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Abstract

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Passive acoustic monitoring is a wildlife monitoring method used especially for the study of vocally active species which are difficult to observe directly. The tawny owl (*Strix aluco*, Linnaeus 1758) is such a species, and has not been previously studied in Greece. The aim of the study was to provide a first insight into the species' acoustic ecology in the Rhodope Mountains by describing its calling activity at four sites over a period of 3–6 months, and to examine possible correlation with natural and climatic parameters. Based on 24,937 calls, we report a significant increase in the number of calls per night (18:00 pm to 9:00 am) as the length of the night increased, as well as a negative relation with wind speed. We did not observe a relationship between calling frequency and the phase of the moon.

Keywords

acoustic ecology, acoustic sensors, Strigiformes, vocal activity

Introduction

Within the animal kingdom, communication is a key mechanism for keeping animal societies together (Smith, 1977), which for many species – especially insects, amphibians, birds, and some mammals – includes vocal signals (calls) (Colafrancesco and Gridi-Papp, 2016; Chaverri et al., 2018; Rand et al., 2022; Soulsbury et al., 2022). The call recipients could be either conspecific (e.g. to advertise reproductive status and territory of an individual; Naguib et al., 2022) or allospecific (e.g. to inform predators that they have been spotted or to alert sympatric species of danger; Sabol et al., 2022). While the study of animal sounds is a long established method for obtaining information on the ecology and status of species (Bradbury et al., 1998; Garcia and Favaro, 2017), lower acquisition and operational costs of autonomous sound recording units (ARUs) and increased computational power of personal computers have led to a rapid increase in the number of researchers using passive acoustic monitoring (PAM) (Sugai et al., 2019).

The vocal communication of owls (Strigiformes) has been widely studied, as direct behavioral observations of many species is particularly difficult due to their cryptic nature and mostly nocturnal activity. The tawny owl (*Strix aluco*, Linnaeus 1758) is a widely distributed and relatively common Eurasian nocturnal raptor typical of woodlands, whose calls have been studied for individual, geographical and temporal variations (Shekhovtsov and Sharikov, 2015; Choi et al., 2019; Agostino et al., 2020). The three note territorial call (hooting) of a tawny owl is audible up to 1.5–2.0 km in open areas (Peri, 2018), and it is used not only for asserting territorial ownership, but also to attract breeding partners and to synchronize activities with conspecifics (Shekhovtsov and Sharikov, 2015) (Fig. 1). Additional types of calls are made during aggressive interactions, which are characterized by irregular sounds (Peri, 2018). Since the tawny owl is a sedentary species that uses the same nesting sites for many years (Cramp, 1985), both sexes strongly defend their territory (Peri, 2018). This is why the species is especially amenable to acoustic population surveys and monitoring of breeding pairs (Peri, 2018; Gryz et al., 2019; Zuberogoitia et al., 2019).

The tawny owl is one of the ten owl species occurring in Greece, for all of which there have been few acoustic ecology studies. As part of the first acoustic grid deployed to

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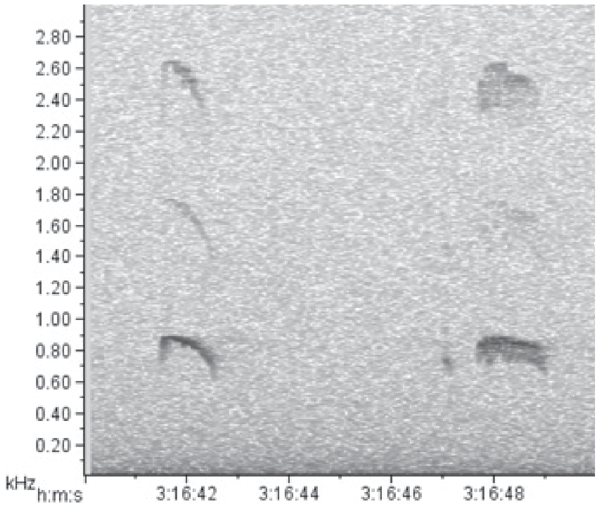

Fig. 1. Spectogram of a male tawny owl *(Strix aluco)* call.

passively monitor wildlife and human activities within a protected area in Greece, we examined tawny owl vocal activity at four sites within the Rhodope Mountain Range National Park over a period of 3–6 months (July–January). Beyond providing a first description of the species' acoustic ecology in Greece, we also tested whether previously reported diel and seasonal variations in calling patterns of the species due to weather (wind, rain) applied in our study area. Specifically, we hypothesized that, as reported by Zuberogoitia et al. (2019), tawny owl vocal activity would be lower in nights with higher rainfall and wind speeds. Moreover, we tested whether the vocal activity of tawny owls was positively correlated with moonlight, as such a pattern has previously been reported for nocturnal birds such as nightjars (Caprimulgidae; Pérez-Granados et al., 2022) and the Ferruginous pygmy-owl (*Glaucidium brasilianum*; Pérez-Granados et al., 2021). The above knowledge of tawny owl acoustic ecology will help design effective and efficient survey protocols for the species at the landscape level.

Materials and methods

The acoustic dataset analyzed for the purposes of this study was collected within the Rhodope Mountain National Park (RMNP; 41.4°N, 24.5°E, 7,006 km^2) in northern Greece, from July 2019 to January 2020. As part of a larger acoustic survey of the protected area, four SWIFT sensors (rugged version, Cornell University) were installed at approximately 1.8 m on the trunk of trees located away from streams, where flowing water would result in high background noise levels. The sensors were powered by 12 D alkaline batteries and were scheduled to record continuously at 8 KHz sample rate and with a 33 dB gain (medium). The sample rate was selected for reasons relating to the broader project, but is sufficient for capturing tawny owl calls, which have a mean fundamental frequency range below 1 KHz (Fig. 1; Agostino et al. 2020). Data (1.3 Gb day^{-1} sensor^{-1}) were stored on 128 GB SD cards (Class 10, U3, V30 type). The cards and batteries were replaced once during the study period.

The first sensor (RP13) was placed in an oak forest at 751 m asl, 2.5 km north of the village Kallikarpo (Fig. 2). The second sensor (RP14) was placed in a sparse cluster of oak and juniper trees at 467 m asl, 4 km northwest of the village Potamoi. This site was under moderate grazing pressure by cattle. The third sensor (RP16) was located in a beech forest on the northern slopes of Mount Falakro at 855 m asl, 8 km east of the village Volakas. The fourth sensor (RP17) was placed in a mixed beech and oak forest at 1,022 m asl, 2 km north of the village Livadero. The sites were not selected specifically for recording tawny owl calls, but with the intent of recording the soundscape of typical RMNP habitats.

Using the RavenPro acoustic analysis software (v.1.5,

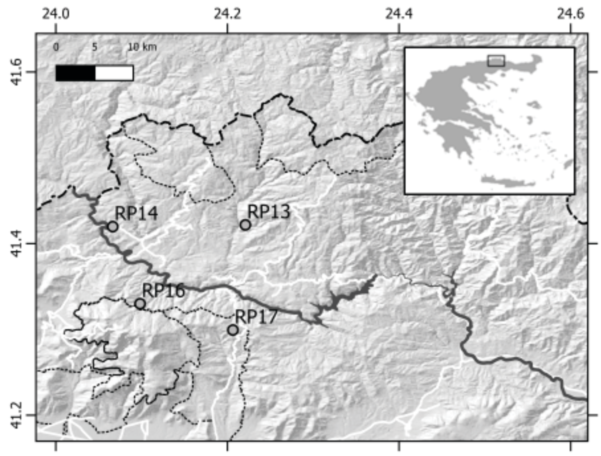

Fig. 2. Location of acoustic sensors (RP13, RP14, RP16, RP17) of the acoustic grid within the Rhodope Mountains National Park (overlayed over topographic relief). The main road (tar) network is depicted as white lines, the Nestos River is dark grey, dotted lines denote the boundaries of Natura 2000 areas, and the dash line the Greek-Bulgarian border.

Cornell University), we manually located all tawny owl three note (hoot) calls from 18:00 pm to 9:00 am. This time window was selected because preliminary analysis showed very low tawny vocal activity outside it. The manual detection of calls, while significantly more time consuming than using a semi-automated detection algorithm, ensured that all audible calls were used for our analysis, reducing possible biases due to unknown heterogeneity in detection probability of a call by a detection algorithm. For the purposes of our study, this was important. Not all calls were equally clear, as the tawny owls called from different areas within their territory. For our analysis we used all the calls, regardless of their intensity, since species identification was unquestionable. Moreover, while the hoot call of a male and a female tawny owl can be distinguished, with the latter being shorter in duration, tone and sometimes with a double second note (Peri, 2018), we compiled all calls of the territory's pair, as sex distinction for distant calls was not possible. Our assumption is that the calls recorded at each sensor were from the same pair of tawny owls; an assumption previously made in a similar passive acoustic monitoring study of the species (Choi et al., 2019).

To test for possible effect of weather and moon light on the vocal activity of tawny owls, we first aggregated the number of calls per night (count). Since the number of calls were not normally distributed (Shapiro-Wild Normality test $p < 0.001$) due to the many nights with no calls, we constructed a series of negative binomial generalized mixed effect models in R package lme4::glmer.nb (Bates et al., 2014) with temperature (°C; minimum, maximum or mean), precipitation (mm), wind speed (m s^{-1}), night length (proportion of 24 hr with daylight), and moon phase (0.00–1.00) as predictive variables, and site (acoustic sensor) as a nested random effect (fixed slope, random intercept). Using the R package DHARMa::testZeroInflation (Hartig and Lohse, 2022), we determined that zero-inflated negative binomial models were not necessary. Weather data were obtained from the closest available weather station at the city of Xanthi (40 m asl), which was located ~ 60–70 km southeast of the study area, and therefore describe weather patterns at the landscape/regional scale. We first run univariate models and compared them against the null (intercept only) model, in order to select an optimal set of informative variables while also managing model complexity. We used Akaike Information Criteria (AIC) for model selection (Burnham and Anderson, 2002). Variables were included in multivariate models only when they were informative (i.e., their univariate model had < AIC than the intercept only model). Among correlated variables, we kept for further consideration the one with the lowest univariate model AIC. Predictive variables were standardized when not in 0–1 scale (z-score, subtracting from each value the mean and dividing by SD). We examined the residual distribution and structure of the final model using informal diagnostics in R package DHARMa. The goodness-of-fit of the best model was assessed by calculating the coefficient of determination (R^2) using R code provided by Byrnes (2008), which calculates the correlation between fitted and observed values.

We used the R package overlap (Meredith and Ridout, 2018) to estimate the coefficient of activity overlap (Δ), as defined by Ridout and Linkie (2009), of tawny owl calling activity in nights of new (<10% moon face illuminated) and full (>90% moon face illuminated) moon. A Δ value of 0 denotes no overlap whereas 1 complete overlap. We used bootstrapping (n = 1,000) to estimate Δ confidence intervals.

Results

In total, we recorded 24,937 tawny owl three note hoot calls during 648 recording nights (185 days sensor^{-1}, except for RP16 sensor which recorded for 93 days) (Table 1). The majority of calls were recorded at sensor RP13 (66%) and RP17 (28%), which also had the highest number of nights with at least one call and highest call frequency per night (Table 1). Vocal activity was higher across all locations in autumn compared to summer, both in terms of hours per night with at least one call and in the total number of calls per hour, and it decreased in winter (Table 2, Fig. 3). Calling activity extended throughout the night for the two sensors with the most calls, with moderate peaks during late evening, early morning and before sunrise (RP13, RP17) (Fig 4). The calling activity of the other two sensors showed more pronounced calling peaks, especially in early morning hours. While the time of peak calling activity differed during nights with little or no moon (percent moon face illuminated ≤0.1) and those with near full or full moon (percent moon face illuminated ≥0.9), the overall calling activity overlap was high (D-hat = 0.86) (Fig. 5).

Of the climatic and natural factors we examined, night duration and the average wind intensity had a statistically significant predictive value for tawny owl vocal activity (i.e. count of calls) per night and were included in the final model (Table 3). Specifically, longer nights with less wind had significantly more tawny owl calls.

Discussion

Our findings provide a first insight on the vocal activity of a tawny owl population at the southern end of its range in Europe, adding to our overall understanding of the species' acoustic ecology. Nevertheless, given the duration of the study (185 days) and the number of surveyed sites (4), the results should be considered as preliminary.

In terms of the hypothesis that tawny owl calling activity would decrease with increasing rainfall (Lengagne and Slater, 2002; Zuberogoitia et al., 2019; Agostino et

Table 1. Tawny owl three note hoot call frequency per sensor during the study period

Sensor	Recording period	Nights recording	Calls	Nights with ≥1 call	Calls/night
RP13	10/7/2019–10/1/2020	185	16,098	177 (95.7%)	90.9 ± 87.5
RP14	10/7/2019–10/1/2020	185	1,064	43 (23.2%)	24.7 ± 19.7
RP16	10/7/2019–9/10/2020	93	794	30 (16.2%)	26.5 ± 20.3
RP17	10/7/2019–10/1/2020	185	6,981	141 (76.2%)	49.5 ± 49.5

Table 2. Mean number of hours with Tawny owl calls per night with >1 call (a) and number of calls per hour (b)

	July	August	September	October	November	December	January
a)							
RP13	2.1 ± 1.5	3.6 ± 2.3	5.1 ± 2.4	9.3 ± 2.8	9.1 ± 2.6	6.0 ± 2.2	5.4 ± 2.4
RP14	0.4 ± 0.7	0.2 ± 0.5	0.2 ± 0.4	1.3 ± 1.5	0.2 ± 0.6	0.1 ± 0.3	1.1 ± 3.0
RP16	0.6 ± 0.9	0.4 ± 0.8	0.9 ± 1.3	0.3 ± .7	–	–	–
RP17	1.8 ± 1.4	2.6 ± 1.9	4.2 ± 2.2	3.4 ± 2.5	2.0 ± 1.9	1.6 ± 2.1	1.6 ± 2.9
b)							
RP13	4.7 ± 4.8	5.7 ± 3.7	5.4 ± 2.3	18.6 ± 7.7	17.0 ± 7.9	13.9 ± 9.8	15.8 ± 9.8
RP14	2.6 ± 5.6	2.8 ± 13	0.2 ± 0.4	8.2 ± 10.7	1.2 ± 4.1	3.0 ± 11.0	2.1 ± 6.3
RP16	4.0 ± 8.5	2.5 ± 5.7	0.9 ± 1.3	8.6 ± 23.8	–	–	–
RP17	8.8 ± 10.4	7.9 ± 6.8	4.7 ± 2.2	16.6 ± 12.5	7.2 ± 10.5	3.4 ± 4.7	3.5 ± 5.5

Table 3. Estimates and significance of the fixed effect variables predicting tawny owl three note hoot calling activity, as measured in number of calls from 18:30 pm to 9:00 am ($R^2 = 0.38$; negative binomial generalized mixed-effect model with site as random (intercept only) effect [Variance 1.029 ± 1.014 St. Dev.])

Variables	β coefficient	Standard Error	z-value	Pr(>|z|)
Intercept (βo)	–0.085	0.907	–0.094	0.925
Night hours	0.285	0.064	4.418	< 0.001
Mean wind speed	–0.074	0.026	–2.812	0.005

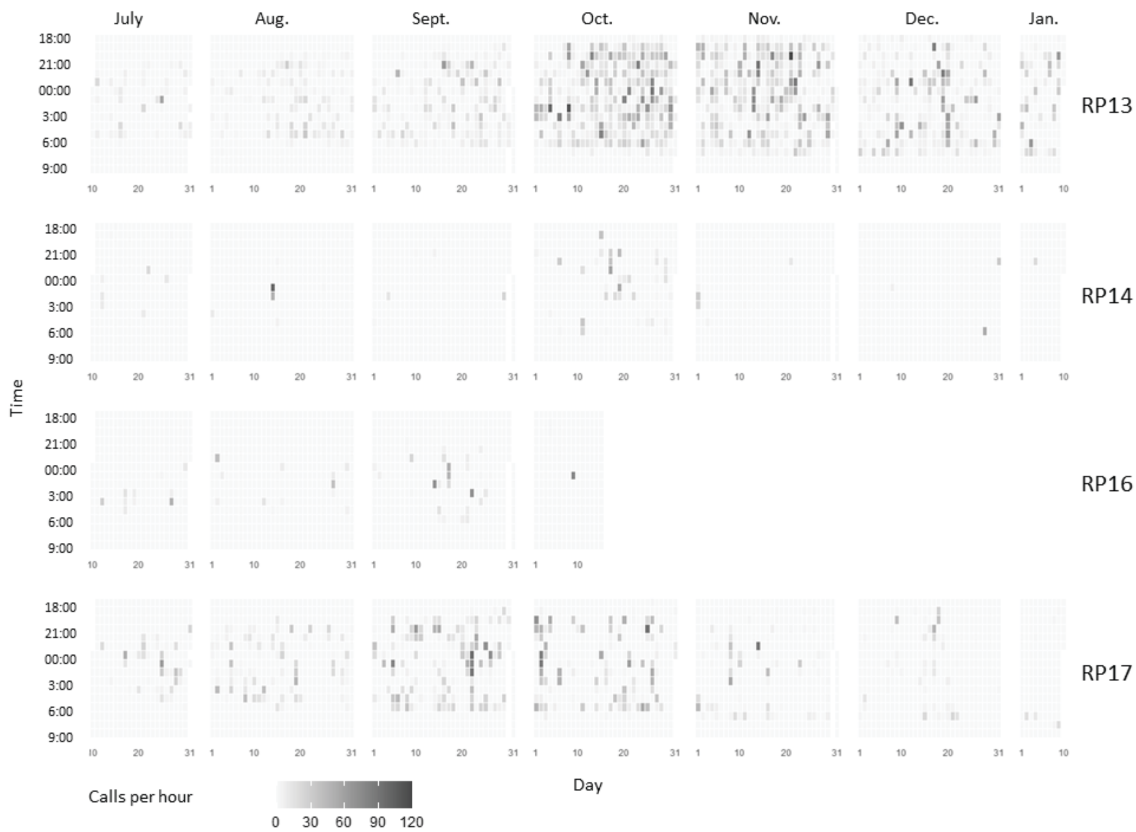

Fig. 3. Distribution of tawny owl *(Strix aluco)* three note hoot calls per hour, day (18:00 pm to 9:00 am), month and acoustic sensor.

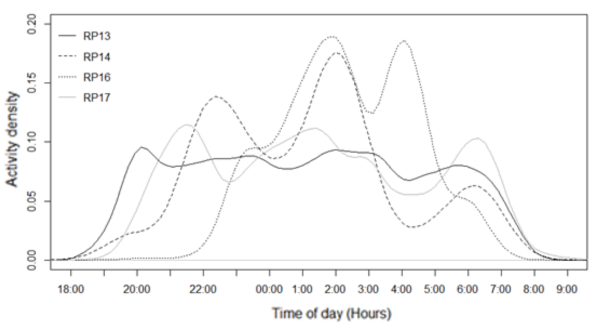

Fig. 4. Density plot showing tawny owl three note hoot calling activity pattern at the four acoustic recorder (RP13, RP14, RP16, RP17) for the duration of the study period.

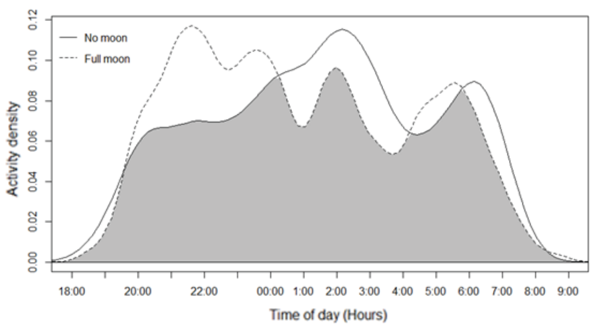

Fig. 5. Tawny owl three note hoot calling activity overlap across all acoustic recorders for days with full moon and no moon (percent moon face illuminated ≥0.9 and ≤0.1 respectively; coefficient of overlap D-hat = 0.86).

al., 2020), our data do not support it. This is surprising given that Lengagne and Slater (2002) reported a 69-fold increase in the effective area in which a tawny owl call was audible in dry versus rainy conditions. So, during rainy nights, tawny owl calls – regardless of calling frequency – should have been less likely to be detected by our sensors. Moreover, that same study also showed a significant decrease of calling activity during rainy nights, albeit the overall survey duration was brief (four nights in total; two with and two without rain). Since the lack of calling activity during rainy nights was not universal across the 22 tawny owl pairs monitored by Lengagne and Slater (2002; 5% and 14% of the pairs called during rain), it is possible that the lack of a similar pattern in our data is a due to the small sample size of tawny owl pairs surveyed. Also, our weather data were obtained from a single station located >60 km away from the acoustic grid, and therefore describe landscape level weather patterns, rather than site (acoustic sensor) specific ones. Moreover, Lengagne and Slater's study only included windless nights with heavy rain (>23 mm within 12 hours). So, their finding may describe a behavioral response of tawny owls to specific rain intensity and season conditions, where as our analysis included data ranging from summer to winter, and a wide range of daily rainfall (range 0–82.6 mm day^{-1}; mean 3.2 ± 6.8 mm). Finally, beyond calling intensity, tawny owls have been reported to vary their vocalizations diurnally and seasonally at the temporal scale of minutes and seconds – i.e. in terms of the overall duration of a call (three notes of the hoot call) and the interval between successive calls (Agostino et al., 2020). We were unable to conduct such an analysis as we used all calls recorded by each sensor, regardless of quality and number of notes detected or the calling individual.

Our findings do support our original hypothesis that tawny owl calling activity would decrease during windy nights as per the report of Zuberogoitia et al. (2019). However, while significant, the effect was small. We are unable to determine whether this pattern is due to wind limiting the detection probability, or due to an actual decrease in calling activity. To be able to confidently identify the cause of the lower number of recorded calls during windy nights, we would need acoustic data from sensors placed at varying distances of known tawny owl perches. This was not possible in our study, unlike with Zuberogoitia et al. (2019), where most calls were of radio-tagged birds.

As far as we are aware, no published study has examined the potential relation of the phase of the moon on overall tawny owl night calling activity (but see unpublished British Trust of Ornithology report based on volunteer data analysis, which showed increased calling during full moon; www.bto.org/our-science/projects/project-owl/tawny-owl-calling-survey/about-tawny-owl-calling-survey; cit. 2022-01-31). Such a relation has been reported for tropical nocturnal birds (Pérez-Granados et al., 2021, 2022). Since the duration of our study was across several moon cycles, we are confident that for the tawny owl pairs observed such a pattern is not significant for summer, autumn and winter – periods which tawny owls are known to be more vocally active (Zuberogoitia et al., 2019).

The discontinuous calling activity at sensors RP14 and RP16 probably suggests that these were not occupied by a resident tawny owl pair. Instead, the calls during September and October could be due to dispersing non-resident individuals. This interpretation is supported by the fact that August-October has been reported as the post-breeding dispersal period for juveniles (Zuberogoitia et al., 2019). Increased calling activity during autumn months in the two sites with resident pairs (RP13, RP17) is probably due to increased hooting by the pairs to warn off juveniles trying to establish territories (Southern, 1970; Balčiauskienė et al., 2005; Chaverri et al., 2018).

In addition to the acoustic ecology information on a previously unstudied tawny owl population in the Greek Rhodope Mountains, our study adds to the increasing evidence recognizing passive acoustic monitoring (PAM) as a tool for studying hard to observe – yet vocal – species at a large temporal and spatial scale (Shonfield and Bayne, 2017; Gibb et al., 2019). Medium to long-duration PAM surveys can be only achieved with the use of autonomous sound recording units (ARUs), which are becoming increasingly more affordable (Sugai et al., 2019). The information obtained from such large datasets does not only provide the spatiotemporal resolution needed for detecting ecological patterns not discernible with smaller duration studies, but also inform the design of cost-effective monitoring protocols for rare and or cryptic species such as nocturnal birds. For example, the use of PAM for spotted owls (*Strix* occiddentalis, Xántus de Vésey, 1860) – a congener of tawny owl occurring in western North America – is gradually enabling a shift in northern California from spatially-limited mark-recapture studies to regional-scale population monitoring protocols which account for non-resident animals occasionally calling in unoccupied territories, which would otherwise inflate occupancy estimates (Reid et al., 2021). While in our case manual detection of calls was possible, despite the long survey duration because of the small number of survey sites, this would not have been possible for larger acoustic grids. It is important therefore that species-specific semi-automated or fully-automated detection algorithms are developed for vocal species of conservation and/or management concern at a national level, to facilitate the wider adoption of PAM as a wildlife monitoring tool by front line conservationists. Existing tools (e.g. cluster analysis function of Kaleidoscope Pro, Wildlife Acoustics) or pattern matching of the Rainforest Connection Arbimon on-line platform (https://arbimon.rfcx.org) are promising for confirming presence of species and could therefore be used for occupancy monitoring of target species. Nevertheless, custom made algorithms with very high recall rate would be needed for acoustic ecology studies.

In conclusion, our passive acoustic monitoring (PAM) based study of tawny owl calling activity in the Greek Rhodope Mountains is the first from southeastern Europe and one of the longest – in terms of continuous recording days – for the species. While limited by the number of sites surveyed, and therefore preliminary in nature, the findings provide useful information both on the acoustic ecology of the species in relation to climatic and natural variables, as well as the potential of PAM for the study of nocturnal birds of prey. As more sites are surveyed acoustically across the region, it is our hope that the study will serve as the basis for more extensive multi-species occupancy surveys of nocturnal birds of prey.

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References

Agostino, P.V., Lusk, N.A., Meck, W.H., Golombek, D.A., Peryer, G., 2020. Daily and seasonal fluctuation in Tawny Owl vocalization timing. *PLOS ONE*, 15: e0231591. https://doi.org/10.1371/journal.pone.0231591

Balčiauskienė, L., Juškaitis, R., Atkočaitis, O., 2005. The diet of the Tawny Owl (Strix aluco) in South-Western Lithuania during the breeding period. Acta *Zoologica Lituanica*, 15: 13–20.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting linear mixed-effects models using lme4. *arXiv*: 1406.5823 [stat], June.

Bradbury, J.W., Vehrencamp, S.L., 1998. *Principles of animal communication*. Sunderland: Sinauer Associates. 882 p.

Burnham, K.P., Anderson, D.R. (eds), 2002. Statistical theory and numerical results. In *Model selection and multimodel inference: a practical information-theoretic approach.* New York, NY: Springer, p. 352–436.

Byrnes, J., 2008. *[R-sig-ME] Coefficient of determination (R^2) when using lme()*. [cit. 2022-3-22]. https://stat.ethz.ch/pipermail/r-sig-mixed-models/2008q2/000713.html

Chaverri, G., Ancillotto, L., Russo, D., 2018. Social communication in bats. *Biological Reviews*, 93: 1938–1954. https://doi.org/10.1111/brv.12427

Choi, W., Lee, J.-H., Sung, H.-C., 2019. A case study of male tawny owl (Strix aluco) vocalizations in South Korea: call feature, individuality, and the potential use for census. *Animal Cells and Systems*, 23: 90–96. https://doi.org/10.1080/19768354.2019.1592022

Colafrancesco, K.C., Gridi-Papp, M., 2016. Vocal sound production and acoustic communication in amphibians and reptiles. In Suthers, R.A., Fitch, W.T., Fay, R.R., Popper, A.N. (eds). *Vertebrate sound production and acoustic communication*. Handbook of Auditory Research, 53. Cham: Springer International Publishing, p. 51–82.

Cramp, S., 1985. *Handbook of the birds of Europe, the Middle East and North Africa*: *terns to woodpeckers*. Oxford: Oxford University Press. 960 p.

Garcia, M., Favaro, L., 2017. Animal vocal communication: function, structures, and production mechanisms. *Current Zoology*, 63: 417–419. https://doi.org/10.1093/cz/zox040

Gibb, R., Browning, E., Glover-Kapfer, P., Jones, K.E., 2019. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods in Ecology and Evolution*, 10: 169–185. https://doi.org/10.1111/2041-210X.13101

Gryz, J., Chojnacka-Ożga, L., Krauze-Gryz, D., 2019. Long-term stability of Tawny Owl (Strix aluco) population despite varying environmental conditions – a case study from Central Poland. *Polish Journal of Ecology*, 67: 75–83. https://doi.org/10.3161/15052249PJE2019.67.1.006

Hartig, F., Lohse, L., 2022. *DHARMa: residual diagnostics for hierarchical (multi-level /mixed) regression models*.v. [cit.2022-03-18]. https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html

Lengagne, T., Slater, P.J.B., 2002. The effects of rain on acoustic communication: tawny owls have good reason for calling less in wet weather. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 269: 2121–2125.

Meredith, M., Ridout, M., 2021. *Overview of the overlap package: May 17, 2021*.[cit. 2021-08-08]. https://cran.r-project.org/web/packages/overlap/vignettes/overlap.pdf

Naguib, M., Titulaer, M., Waas, J.R., van Oers, K., Sprau, P., Snijders, L., 2022. Prior territorial responses and home range size predict territory defense in radio-tagged great tits. *Behavioral Ecology and Sociobiology,* 76: 35. https://doi.org/10.1007/s00265-022-03143-3

Pérez-Granados, C., Schuchmann, K.-L., Marques, M.I., 2021. Vocal activity of the Ferruginous pygmy-owl (Glaucidium brasilianum) is strongly correlated with moon phase and nocturnal temperature. *Ethology Ecology & Evolution*, 33: 62–72. https://doi.org/10.1080/03949370.2020.1820582

Pérez-Granados, C., Schuchmann, K.-L., Marques, M.I., 2022. Addicted to the moon: vocal output and diel pattern of vocal activity in two Neotropical nightjars is related to moon phase. *Ethology Ecology & Evolution*, 34: 66–81. https://doi.org/10.1080/03949370.2021.1886182

Peri, A., 2018. A comparison of three methods for planning a census of Tawny Owl (Strix aluco) populations living at high territorial density. *Bioacoustics*, 27: 245–260. https://doi.org/10.1080/09524622.2017.1326164

Rand, Z.R., Wood, J.D., Oswald, J.N., 2022, Effects of duty cycles on passive acoustic monitoring of southern resident killer whale (Orcinus orca) occurrence and behavior. *The Journal of the Acoustical Society of America*, 151: 1651–1660. https://doi.org/10.1121/10.0009752

Reid, D.S., Wood, C.M., Whitmore, S.A., Berigan, W.J., Keane, J.J., Sawyer, S.C., Shaklee, P.A., Kramer, H.A., Kelly, K.G., Reiss, A., Kryshak, N., Gutiérrez, R.J., Klinck, H., Peery, M.Z., 2021. Noisy neighbors and reticent residents: distinguishing resident from non-resident individuals to improve passive acoustic monitoring. *Global Ecology and Conservation*, 28: e01710. https://doi.org/10.1016/j.gecco.2021.e01710

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14: 322–337.

Sabol, A.C., Greggor, A.L., Masuda, B., Swaisgood, R.R., 2022. Testing the maintenance of natural responses to survival-relevant calls in the conservation breeding population of a critically endangered corvid (Corvus hawaiiensis). *Behavioral Ecology and Sociobiology*, 76: 21. https://doi.org/10.1007/s00265-022-03130-8

Shekhovtsov, S.M., Sharikov, A.V. 2015. Individual and geographical variation in the territorial calls of tawny owls Strix aluco in Eastern Europe. *Ardeola*, 62: 299–310. https://doi.org/10.13157/arla.62.2.2015.299

Shonfield, J., Bayne, E., 2017. Autonomous recording units in avian ecological research: current use and future applications. *Avian Conservation and Ecology*, 12: 14. https://doi.org/10.5751/ACE-00974-120114

Smith, W.J., 1977. *The behavior of communicating: an ethological approach*. Cambridge, MA: Harvard University Press. 558 p.

Soulsbury, C., Montealegre-Z, F., Elias, D,O., 2022. Evolutionary biomechanics of sound production and reception. *Frontiers Ecology and Evolution*, 9: 788711. https://doi.org/10.3389/fevo.2021.788711

Southern, H.N., 1970. The natural control of a population of Tawny owls (Strix aluco). *Journal of Zoology*, 162: 197–285. https://doi.org/10.1111/j.1469-7998.1970.tb01264.x

Sugai, L.S.M., Silva, T.S.F., Ribeiro Jr., J.W., Llusia, D., 2019. Terrestrial passive acoustic monitoring: review and perspectives. *BioScience*, 69: 15–25. https://doi.org/10.1093/biosci/biy147

Zuberogoitia, I., Burgos, G., González-Oreja, J.A., Morant, J., Martínez, J.E., Albizua, J.Z., 2019. Factors affecting spontaneous vocal activity of Tawny Owls Strix aluco and implications for surveying large areas. Ibis, 161: 495–503. https://doi.org/10.1111/ibi.12684

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