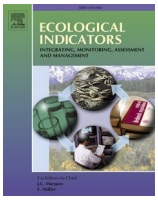
Ecological Indicators 142 (2022) 109158

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Original Articles

Passive acoustic monitoring for estimating human-wildlife conflicts: The case of bee-eaters and apiculture

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ARTICLE INFO

Keywords:
ARUs
Vocal Activity Rate
Apiculture
Merops apiaster

ABSTRACT

In human-wildlife conflicts, it is crucial to develop accurate protocols for the reliable verification of the causative species and its relationship with potential damage claims. One of such conflicts is that occurring between apiarists and bee-eaters. In this work, we aim to assess the utility of passive acoustic monitoring (PAM) as an efficient methodology to measure European bee-eater (*Merops apiaster*) predation pressure at beehives and its impact on honeybees foraging activity. Using Autonomous Recording Units (ARUs) in apiaries, coupled to automated recognition methods for bee-eater calls identification, we found a positive relationship between Vocal Activity Rate (VAR) index and number of bee-eaters hunting attempts on honeybees. We also found that VAR varied over time, showing a lower predation pressure during midday hours and higher during the post-breeding migratory period. Honeybees flying activity was negatively associated with VAR and this relationship was conditioned by the hour of the day. Our study offers a new application of PAM and acoustic derived indices for the evaluation of potential damages caused by wildlife. We focused on the interaction between honeybees and the European bee-eater, but we expect PAM might be useful also to remotely monitor impacts to human activities produced by other vocally active species.

1. Introduction

Interactions between wildlife and humans have occurred for millennia (Graham et al., 2005, Redpath et al., 2015), but their frequency has widespread in the last decades due to the exponential increase in human population and the resultant expansion of human distribution range and activities (Sanderson et al., 2002, Anand and Radhakrishna, 2017). Negative interactions have usually been termed as human-wildlife conflicts (Graham et al., 2005) and arises due to competition between humans and wildlife for shared and limited resources (Young et al., 2010, Redpath et al., 2015). Human-wildlife conflicts are especially problematic when shared resources have economic value (Manral et al., 2016) and they are exacerbated when the conflicting species are protected or charismatic (Peterson et al., 2010, Athreya et al., 2011). As a result of these conflicts, some wildlife species have been catalogued as pests or human competitors, and historically a great effort has been dedicated to restrain their populations (Thirgood et al., 2000, Yodzis, 2001).

One of such human-wildlife conflicts is that occurring between apiarists and bee-eaters (Family Meropidae). On one side there is the apicultural industry, which has a big worldwide economic value producing honey, beeswax and other bee-related products from European honeybees (*Apis mellifera*) (e.g. Lee et al., 2010, Chauzat et al., 2013). In Europe, apiculture sector produced 280.000 tonnes of honey in 2018, making the EU the second largest honey producer after China, and being Spain the first EU country in number of beehives (EU Commission, 2019). On the other side there are the bee-eaters, which are generally protected bird species characterized for their ability to hunt flying insects, especially hymenopterans, including honeybees (Fry, 2001). Honeybees can constitute an important part of European bee-eater (*Merops apiaster*; hereafter bee-eater) diet depending on the geographical area and season, becoming between one third and one half of the

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https://doi.org/10.1016/j.ecolind.2022.109158
Received 16 May 2022; Received in revised form 6 July 2022; Accepted 8 July 2022
Available online 16 July 2022
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total Hymenoptera predated by bee-eaters (Galeotti and Inglisa, 2001, Yosef, 2004, Arbeiter et al., 2016, Farinós-Celdrán et al., 2016). Bee-eaters hunt almost entirely flying, either by making short flights from an elevated perch or by hunting in continuous flight, while uttering characteristic contact calls (Fry, 2001). Bee-eaters seem to preferably predate on domestic honeybees (Inglisa et al., 1993, Galeotti and Inglisa, 2001) due to its high nutritional value, short handling time, and because it is a stable and predictable food source around beehives (Krebs and Avery, 1985).

Beekeepers of Mediterranean basin and Africa have pointed bee-eaters as a pest for apiculture, jeopardizing honey production and honeybee colonies vitality (Galeotti and Inglisa, 2001, Alfallah et al., 2010, Farinós-Celdrán et al., 2016, Langowska et al., 2018, Floris et al., 2020). The impacts of bee-eaters on honeybees have been relatively well-studied in Europe and rely on both direct predation and through the inhibition of honeybees normal flying behaviour due to the high predation pressure around the apiary (e.g., Fry, 1983, Galeotti and Inglisa, 2001, Farinós-Celdrán et al., 2016, Moreno-Opo et al., 2018).

Even though the presence of bee-eaters around beehives is unquestionable, their direct negative impact on beehives is controversial. Several authors have pointed out that predation of honeybees by bee-eaters is usually far below the regeneration threshold of a single honeybee colony, and thus their impact on colonies' dynamic might be negligible (Fry, 1983, Laplaza and Albero, 1997, Alfallah et al., 2010, Farinós-Celdrán et al., 2016). Flight inhibition cause losses in beekeeping economy by reducing beehives' production (Galeotti and Inglisa, 2001, Langowska et al., 2018), although this phenomenon seems to be variable in its magnitude between regions (Langowska et al., 2018, Moreno-Opo et al., 2018) and may also differ among populations according to their breeding or migratory status (Yosef et al., 2006). While the extent of the impact of bee-eaters predation pressure on honeybees' production is still under discussion, the perception by beekeepers is clearly contrary to the presence of bee-eaters around beehives. Even though it is a protected species in many countries, illegal killing of bee-eaters has been often reported (e.g. Woldhek, 1979, Galeotti and Inglisa, 2001). In this context, the public administration of some countries, such as Italy or Spain, has economically compensated to beekeepers because of the damage caused by bee-eaters (Galeotti and Inglisa, 2001, Villero et al., 2017).

In a context of human-wildlife conflict, it is crucial to develop accurate protocols for the reliable verification by the authority of the causative species and its relationship with damage claims to create public trust in the legitimacy of compensation programs (López-Bao et al., 2017). Verification protocols are essential since self-reporting of wildlife damage may result in overestimates of damage or fraudulent claims (Nyhus et al., 2005). In the case of bee-eaters conflict, a feasible, accurate and easy to use methodology is needed to estimate bee-eater predation pressure at beehives, on which a potential public compensation or mitigation program may be based. Verification is a vexing problem for many human-wildlife compensation programs because evidence from wildlife that can cause harm can be difficult to find and/or quickly disappear (Nyhus et al., 2005). In the case of bee-eaters conflict, this problem is further exacerbated as no direct identifiable trace of potential harm remain, so reliable and easy-to-measure indirect indicators are critical.

Some methodological approaches based on direct bird counts or developing bee-eater distribution models together with land apicultural suitability models have been implemented for compensating damage claims (Villero et al., 2017, Moreno-Opo et al., 2018). However, they are costly in time and human resources to obtain continuous data, and/or they are unable to measure the real presence of the species in a specific place and time. Passive acoustic monitoring (PAM), based on the placement of unattended and programmable Autonomous Recording Units (ARUs hereafter), is a recent technique commonly used for terrestrial wildlife monitoring (see review in Sugai et al., 2019). ARUs have been found a suitable alternative to traditional field surveys for detecting birds' species presence or estimating bird species richness or population densities around recorders (e.g., Darras et al., 2018, Pérez-Granados and Traba, 2021). The Vocal Activity Rate index (VAR; number of vocalizations detected per unit time of recording) is the most often applied and validated indicator for estimating bird abundance using PAM (see a review in Pérez-Granados and Traba, 2021). VAR is based on the assumption that number of vocalizations on recordings is associated to number of individuals vocalizing around recorders (Pérez-Granados and Traba, 2021). Indeed, the use of ARUs coupled with automated signal recognition software has proven to be able to infer abundance of bee-eaters flying around beehives and to define the migratory pattern of the species (Bota et al., 2020; Pérez-Granados et al., 2019). These findings suggest that VAR might be also useful to provide a reliable estimation of bee-eater predation pressure at beehives, which might be used as an index for compensating damage claims.

Development and use of new tools and technologies have been pointed out as a relevant future research need to solve and mitigate human-wildlife conflicts (Nyhus, 2016). In this context, PAM has already been used as a promising tool to generate indicators and early warning systems for law enforcement tool to reduce poaching (Astaras et al., 2017) or detection of damaging invasive species (Martínez et al., 2020). Therefore, the use of PAM may offer many possibilities within the field of human-wildlife conflict studies. We aim to assess the utility of PAM as an efficient tool to measure bee-eater predation pressure indicator at beehives and to assess its impact on honeybees foraging activity. Our first goal was to assess whether the VAR (number of bee-eater calls per recording) can be a good indicator of bee-eater predation pressure in beehives by assessing the relationship between VAR and the number of bee-eater hunting attempts estimated by human surveyors at different spatial scales. Based on prior findings, we expected that VAR will show a positive relationship with bee-eater predation pressure (Pérez-Granados et al., 2019).

We also aimed to describe the daily and seasonal patterns of bee-eaters predation pressure at beehives as it may be important to identify when it might be most necessary to apply potential damage prevention measures. Finally, we aimed to evaluate whether the bee-eater predation pressure has an impact reducing the flying activity of honeybees, since it is one of the main mechanisms behind the losses in the beekeeping economy. We expected that bee-eater predation pressure indicator, acoustically measured, will have a negative effect on honeybees activity.

2. Methods

2.1. Study area

The study area comprised a flat farmland area situated on the eastern edge of the Ebro Valley (41°46 N, 0°46 E), in western Catalonia (Lleida province, NE Spain). The study was conducted in 22 different apiaries separated by a minimum distance of 2 km covering around 900 km2 (Appendix S1). Each apiary comprised between 30 and 50 beehives and remained in the same place during the study period. Beekeeping activity in the study area is characterized by the exploitation mainly of summer flowering of alfalfa (*Medicago sativa*) fields, and some mass-flowering crops like sunflower (*Helianthus annuus*).

Field work was carried out from 1 July to 21 September 2017, period that corresponds to the end of the breeding period and the post-nuptial migration of the bee-eater in the region (Bota et al., 2020). Average annual rainfall ranges between 300 and 450 mm and average annual temperature is 14.5 °C, being this region classified as semi-arid (Calvet et al., 2004). Bee-eater abundance in the study area during the breeding period reaches the highest value for the species in Catalonia (Estrada et al., 2004).

2.2. Passive acoustic monitoring

We selected nine out of the 22 apiaries to be used as acoustic monitoring stations. In each acoustic monitoring station, we placed one ARU at around 4 m of distance from the central beehive on each apiary. Each ARU (model RECoti registered trademark) consisted of an USB Voice Recorder SK-001 with processor AC1517D72772-C and one integrated and single-channel microphone. This model performed as well as commercial costliest device (see more details of the ARU model used in Pérez-Granados et al., 2019b). ARUs were ground-located with microphones in an upward position with no sound blocking barriers by at least 50 cm (Rempel et al., 2013). We used a sample rate of 44.1 kHz and 16 bits in stereo mode for all recordings. The hunting activity of bee-eaters is diurnal (Fry, 2001) and varies greatly between daily time and months, with lower presence around beehives during midday hours and higher during the post-breeding migration period (Moreno-Opo et al., 2018, Bota et al., 2020). ARUs were programmed to record for 30 min starting at the following local (GMT + 2) times: 9:15, 11:15, 13:15, 15:15, 17:15 and 19:15. ARUs were fortnightly moved between the nine selected apiaries along the entire study period. Recordings obtained during moving day were excluded from the analysis since there were no data for the whole day. Each day we simultaneously acoustically monitored 3.2 ± 1.1 stations (Mean ± SD, range 2–5) during the whole study period.

Recordings were analysed using Song Scope 4.1.5 (Wildlife Acoustic, 2011), an efficient automated sound recognition software (Knight et al., 2017). Song Scope is able to create a target signal from the characteristics of the example signals used for training, which is used as a recognizer file to compare when a sound within a recording matches its characteristics (Waddle et al., 2009). We used the same recognizer developed in Pérez-Granados et al. (2019a), which was created using part of the dataset of the current study. The recall rate of the recognizer (estimated as the proportion of bee-eater calls detected by the recognizer divided by the total number of bee-eater calls on sound recordings) was of 46.4 % and the precision (events detected by recognizer that were correctly identified as bee-eater calls) was between 97.3 and 99.2 % (mean value of 98.8 %, Bota et al., 2020; Pérez-Granados et al., 2019). Because of the high precision of the recognizer, we therefore decided to consider all events identified by Song Scope as bee-eater calls (see similar approximation in Bota et al., 2020).

2.3. Bird data

Number of bee-eater hunting attempts at beehives has been previously used as an indicator of bee-eater predation pressure in apiaries (Moreno-Opo et al., 2018). To validate that acoustic data were reliable and thus a useful indicator of the predation pressure exerted by bee-eaters, we conducted paired sampling (or "double sampling", see Bart et al., 2002, Van Wilgenburg et al., 2017). We performed 35 sampling stations where we simultaneously used an ARU to record the VAR of the bee-eater and performed visual censuses, where a human observer counted the number of bee-eater hunting attempts (successful or not) of bees through pursuit in flight or stalking and capture from perches around beehives. The 35 sampling stations were evenly distributed along the study period. We only counted those bee-eater hunting attempts that occurred within a radius of 20 m around the recorder. Hunting attempts were counted continuously for 30 min, simultaneously while the ARU was recording. The average simultaneous bird census with ARU recording per apiary was 3.5 ± 1.1 (Mean ± SD, range 2–5).

Bird censuses were also carried out using the same methodology in 12 non-acoustically monitored apiaries to assess the relationship between the weekly estimated VAR in the limited number of acoustic monitoring stations (n = 9) and weekly bee-eater hunting attempts counted in non-acoustically monitored apiaries, located on a larger territorial scale. A total of 134 30-min censuses (11.4 ± 2.6 censuses per week, mean ± SD) were performed on selected apiaries along the study period (around one census per apiary and week) (see Appendix S1 for location of this apiaries). These censuses included apiaries no used as acoustic monitoring station, and thus data obtained by weekly human censuses were independent of acoustic data.

Table 1
Variables considered in the study, including variable name, type of variable (continuous, integer, categorical, count), and description.

Variable name	Type of variable	Description
VAR	Count	Total number of bee-eaters calls automatically detected by recognizer per recording (number of calls in 30 min)
BE-attempt	Count	Total number of bee-eaters hunting attempts (successful or not) around beehives (<20 m) in 30 min censuses
Apiary	Categorical	ID of the different apiaries included in the study
Hour	Categorical	Time of starting recording (9:15, 11:15, 13:15, 15:15, 17:15 and 19:15)
Fortnight	Categorical	Corresponding fortnight from 1st July to 21st September
Bee-flow	Count	Hourly number of entrances and exits of honeybees in the hive (recorded by MELIXA system).
Texternal	Continuous	Hourly environmental temperature (Celsius degrees) outside hive (recorded by MELIXA system)
Tinternal	Continuous	Internal beehive hourly temperature (Celsius degrees) (recorded by MELIXA system)
Rain	Categorical	Presence (1) or absence (0) of rainy events hourly (recorded by MELIXA system)

2.4. Honeybees flying activity

To monitor honeybee flying activity, we installed a Melixa system (Melixa S.R.L, Italy, https://www.melixa.eu/en) at one beehive per apiary (Appendix S2). The Melixa system is a commercially available hive remote monitoring system, which allows beekeepers to perform remote and real-time monitoring of the beekeeping activity and researchers to obtain detailed data about hives' dynamics (e.g., Gil-Lebrero et al., 2017, Flores et al., 2019). The vigour, health status and quantity of bees in the beehives monitored using the Melixa system were checked and verified by an expert apiarist at the beginning of the study, to exclude beehives with poor vitality condition. The foraging activity of honeybees is influenced by several environmental factors such as wind, temperature, humidity, cloud cover, rain or sunlight intensity (Szabo, 1980, Burrill and Dietz, 1981, Kumar and Singh, 2005, Ramírez and Davenport, 2013, Moreno-Opo et al., 2018). The Melixa includes a bee counter which counts the number of entries and exits of honeybees per hour (Bee-flow). The system also records hourly data (as an average of measurements every 15 min) of environmental temperature (Texternal), temperature inside the hive using a probe (Tinternal), and the presence of rain events thanks to a specific sensor (Rain) (see Table 1 for variables description). The Melixa system does not disturb the normal flying of access/exit of honeybees from the hive (Appendix S2). The entrance is composed by 14 holes of 8 mm of diameter, which corresponds to the bee space and allows movement with no impediment. All data recorded by each Melixa System (bee flow, temperatures, rain, etc.) were automatically transferred hourly via GSM transmission to an online webserver. The same hive was monitored every fortnight in each apiary and Melixa systems were moved between the ten selected apiaries along the entire study period together with the movement of ARUs between apiaries. A total of 256 days of monitoring beehives were obtained (25.6 ± 5.7 monitored days per beehive, Mean ± SD).

2.5. Statistical analyses

To estimate bee-eater VAR per recording, we used the total number of bee-eater calls automatically detected by the recognizer by recording length (30 min) (Oppel et al., 2014; Pérez-Granados et al., 2019). To determine the relationship between VAR and the number of bee-eaters'

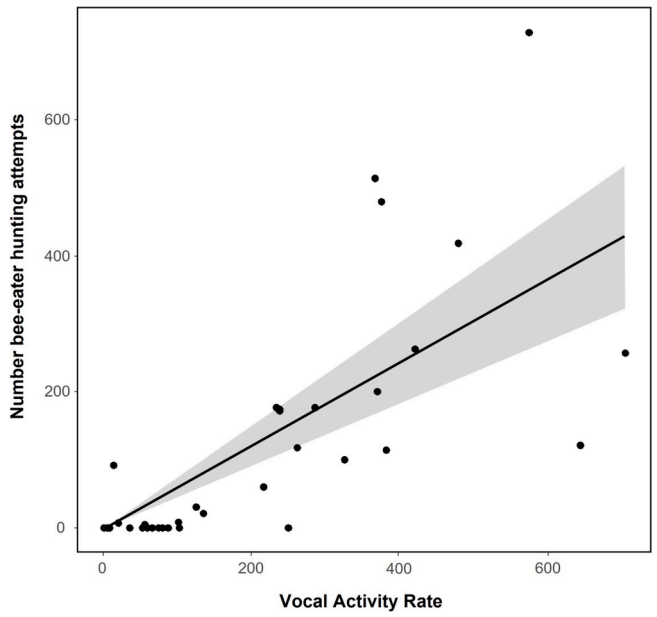

Fig. 1. Linear relationship between Vocal Activity Rate (number of calls in 30 min) index and number of European bee-eaters hunting attempts counted by human surveyors ($F_{1,34} = 72.44$, $R^2 = 0.68$, $P < 0.0001$). The observed values (dots) fitted linear regression (black line) and 95 % confidence interval (grey area) are depicted.

hunting attempts visually counted by human surveyors (BE-attempt), we fitted a linear regression. We also assessed whether the use of ARUs in a relatively small number of beehives might be useful to infer bee-eater predation pressure at a larger spatial scale. For this purpose, we estimated the Pearson rank correlation between mean VAR detected per week in apiaries monitored by ARUs (n = 9) and mean number of hunting attempts detected by human surveyors in the rest of non-acoustically monitored apiaries (n = 12).

To determine if bee-eater predation pressure (using the VAR as a surrogate of predation pressure) significantly varied between hours and fortnights, we fitted a Generalized Linear Mixed Model (GLMM). Preliminary analysis showed overdispersion of the data, so we used a negative binomial distribution error and log-link function to account for overdispersion (Ver Hoef and Boveng, 2007). The GLMM was fitted using VAR index as response variable and Hour (six categorical levels) and Fortnight (six categorical levels) as fixed effects. Acoustic monitoring station (Apiary) was included as random effect (Table 1). When a fixed effect was found to be significant, a Tukey's post hoc test was performed to assess whether there were differences among levels.

We also fitted a GLMM to assess the relationship between flying activity of honeybees (Bee-flow) and bee-eaters' predation pressure (using the VAR as a surrogate). The distance between beehives equipped with Melixa and the position where ARUs were located slightly varied among apiaries but did not exceed 20 m in any case, allowing to assess the relationship between VAR index with honeybees flying activity. The GLMM (Gaussian distribution error and an identity-link function) was fitted using log transformed hourly Bee-flow as response variable and log transformed VAR as fixed effect. We also included other environmental and temporal factors that may also affect the flying activity of honeybees, and so the variables Hour, Fortnight, environmental temperature (log transformed Texternal), internal temperature of the hive (log transformed Tinternal) and presence of rain events (Rain; categorical, presence/absence) were included as fixed factors (Table 1). Since bee-eater predation pressure around beehives varies depending on daily hour and moment of the season, Hour*VAR and Fortnight*VAR interactions were also included in the model as fixed effects, while Apiary was also included as random effect (Table 1). Model performance was

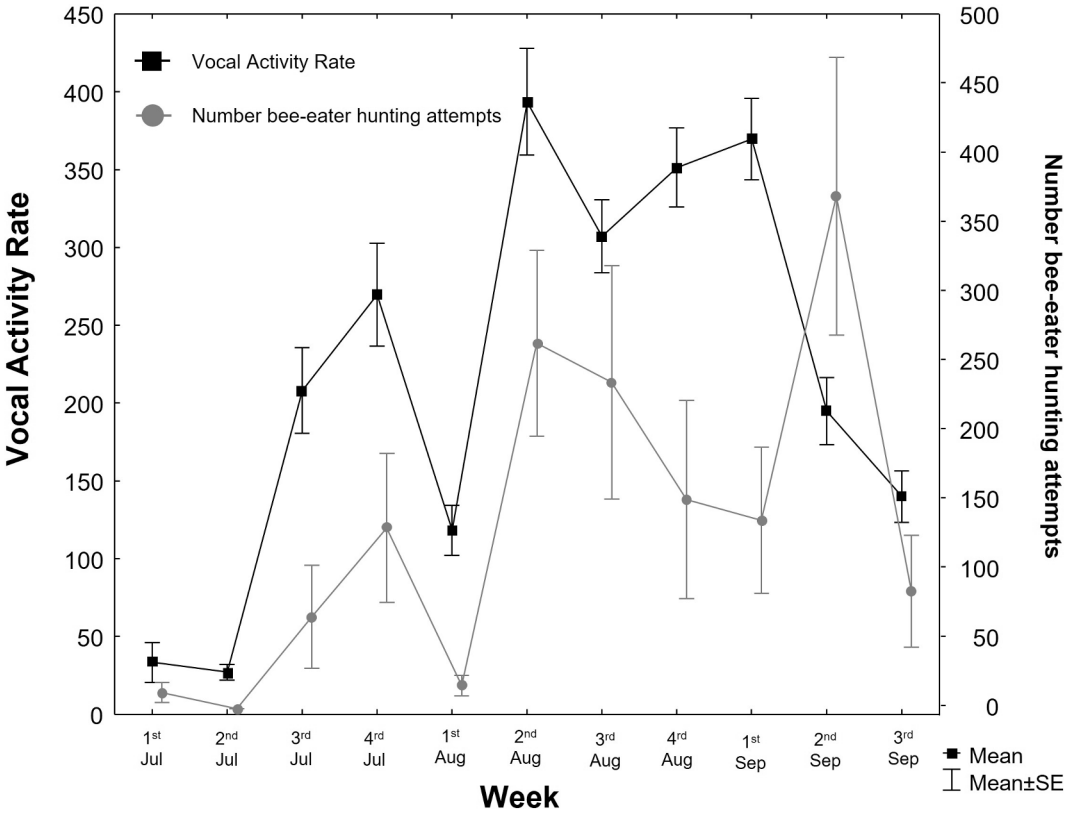

Fig. 2. Weekly pattern of Vocal Activity Rate (number of calls in 30 min) and number of European bee-eater hunting attempts at beehives during the monitoring period.

Table 2
Summary table of the results of a Generalized Linear Mixed Model (GLMM; Negative binomial error and log-link function) testing the relationship between Vocal Activity Rate per recording (VAR; number of bee-eater calls of each 30 min recording) and Hour (six categories) and Fortnight (six categories). Number of European bee-eater calls were monitored trough PAM. Acoustic monitoring station (Apiary) was included as random effects. Estimates are expressed as the differences from the intercept, which was estimated using the recordings made at 9:15 and during the first fortnight of July as reference values.

Fixed effects	*Estimate*	*Std. Error*	*z-value*	*P*	
(intercept)	3.581	0.219	16.333	<0.0001	**
Hour (11:15)	−0.493	0.128	−3.849	<0.0001	**
Hour (13:15)	−0.906	0.129	−7.021	<0.0001	**
Hour (15:15)	−0.610	0.128	−4.747	<0.0001	**
Hour (17:15)	−0.024	0.127	−0.188	0.8506	
Hour (19:15)	0.197	0.127	1.547	0.1211	
Fortnight (2nd Jul)	1.790	0.200	8.947	<0.0001	**
Fortnight (1st Aug)	2.261	0.152	14.873	<0.0001	**
Fortnight (2nd Aug)	2.372	0.199	11.914	<0.0001	**
Fortnight (1st Sep)	2.295	0.190	12.034	<0.0001	**
Fortnight (2nd Sep)	1.479	0.234	6.312	<0.0001	**

evaluated by plotting standardised residuals versus fixed variables, normal QQ-plots and histogram of residuals. No concrete pattern was found in any case.

All analyses were performed using the software R (v. 3.5.3) and packages "nlme" (Pinheiro et al., 2021), "lme4" (Bates et al., 2015) for GLMM models and "multcomp" (Hothorn et al., 2008) for post-hoc comparison tests.

3. Results

We collected 1,531 30-mins recordings (765.5 h of recording) during the study period. Recordings were scanned in about 74 h and a total of 361,479 acoustic events were identified by Song Scope recognizer and used as bee-eater calls in posterior analyses.

We found a positive significant relationship between VAR recorded by ARUs and number of bee-eaters hunting attempts counted by human surveyors ($F_{1,34} = 72.44$, $R^2 = 0.68$, $P < 0.001$, Fig. 1). We also found that mean weekly VAR detected by ARUs in nine acoustically monitored apiaries was strong and positively correlated to mean weekly number of bee-eaters hunting attempts counted by human surveyors in 12 different apiaries at a larger spatial scale (Pearson Rank correlation = 0.763, P = 0.006, Fig. 2). Despite this overall result, a mismatch between both variables was observed during the end of August and the beginning of September (Fig. 2).

Mean VAR (calls in 30 min) obtained for the entire study period and apiary was 237 ± 289 (Mean ± SD), with a wide range of average values per apiary (maximum 393 ± 362; minimum 104 ± 151, Mean ± SD).

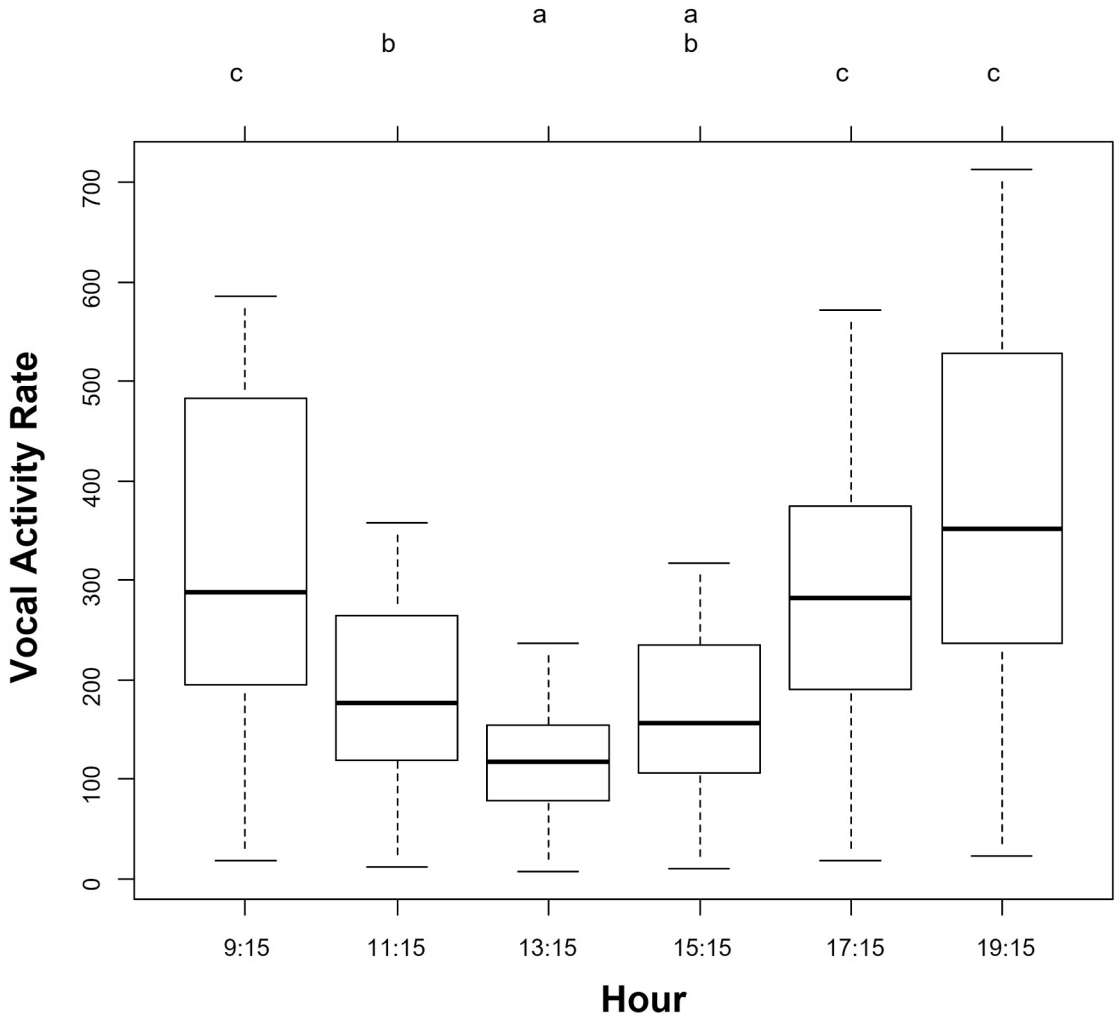

Fig. 3. Daily Vocal Activity Rate (number of calls in 30 min) of the European bee-eater. Boxplots show the mean (black horizontal line), twenty-fifth and seventy-fifth percentiles of the data (boxes), and the 95 % confidence interval (dashed lines).Different letters on the top indicate significant differences between recording times from Tukey's post hoc test.

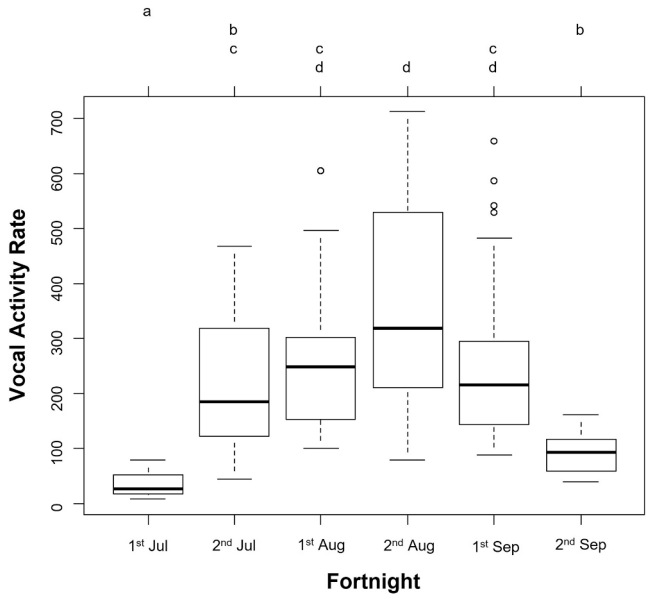

Fig. 4. Fortnightly Vocal Activity Rate (number of calls in 30 min) of the European bee-eater. Boxplots show the mean (black horizontal line), twenty-fifth and seventy-fifth percentiles of the data (boxes), and the 95 % confidence interval (dashed lines). Different letters on the top indicate significant differences between recording times from Tukey's post hoc test.

We found a significantly variable time pattern (daily and fortnightly) in the VAR, a surrogate of bee-eater hunting attempts (Table 2). Specifically, there was a significant higher VAR during early morning (9:15) and afternoon (17:15 and 19:15) in relation to late morning (11:15), midday (13:15) and early afternoon (17:15) (Fig. 3). Midday hour (13:15) presented the lowest values of all periods. Similarly, the VAR increased from early July until late August, when the highest VAR was detected, to later decrease until the end of September. Lowest VAR was detected during the 1st fortnight of July (Fig. 4).

Honeybee flying activity was negatively associated with VAR, with a lower bee flow during the hours with higher number of bee-eater calls detected (Table 3). The magnitude of the effect was conditioned by the hour, being the impact significantly lower in the central hours of the day and in the afternoon at equal intensity of VAR (Table 3, Fig. 5). Honeybee flying activity also decreased as the study period progressed and during rainy events, while it was positively associated with environmental and internal beehive temperature (Table 3).

4. Discussion

Our results have proven that PAM, coupled with automated signal recognition, is an effective and useful tool to provide estimates of bee-eater predation pressure at beehives, and in consequence to assess their impact on bees' foraging activity. The positive significant relationship between VAR and number of bee-eaters hunting attempts counted by human surveyors suggests that VAR could be used as a reliable indicator of bee-eaters abundance around beehives, in agreement with previous studies with that and other bird species (Pérez-Granados et al., 2019b; see review in Pérez-Granados and Traba, 2021). Furthermore, the strong temporal positive relationship between VAR and bee-eaters hunting attempts counted at independent and non-acoustically monitored apiaries suggest that VAR estimated at a local scale may perform as a good indicator of bee-eater predation pressure at a regional scale. Nonetheless, we detected a mismatch between VAR and bee-eaters hunting attempts during late August and early September (Fig. 2). This variation could be related to the migratory peak of the species. The defined period coincides with the maximum migratory bee-eater passage in the study area (Bota et al., 2020), so it is likely that the ARUs may have recorded bee-eaters calling in active migration flying above apiaries but non actively hunting.

Table 3
Summary table of the results of a Generalized Linear Mixed Model (GLMM; Gaussian distribution error and an identity-link function) testing the relationship between hourly Bee-flow (log transformed) and Vocal Activity Rate per recording (VAR log transformed), Recording time (Hour, 6 categories), External temperature (Texternal log transformed), Internal temperature (Tinternal log transformed), Rain (2 categories), Fortnight (6 categories) and the interactions Hour*VAR and Fortnight*VAR as fixed effects. Apiary was included as random effect. Total number of hourly Bee-flow counts: 1,526. Estimates are expressed as the differences from the intercept, which was estimated using the recordings made at 9:15 and during the first fortnight of July as reference values.

Fixed effects	*Estimate*	*Std. Error*	*Df*	*t-value*	*P*	
(intercept)	−10.025	1.920	1492	−5.220	<0.0001	**
VAR	−1.488	0.403	1492	−3.685	0.0002	**
Hour (11:15)	0.363	0.058	1492	6.248	<0.0001	**
Hour (13:15)	0.171	0.058	1492	2.919	0.0036	*
Hour (15:15)	0.015	0.063	1492	0.244	0.8072	
Hour (17:15)	−0.008	0.068	1492	−0.129	0.8969	
Hour (19:15)	0.174	0.065	1492	2.684	0.0073	*
Texternal	2.620	0.215	1492	12.142	<0.0001	**
Tinternal	6.186	1.312	1492	4.712	<0.0001	**
Rain	−0.243	0.064	1492	−3.792	0.0002	**
Fortnight (2nd Jul)	−0.261	0.070	1492	−3.721	0.0002	**
Fortnight (1st Aug)	−0.303	0.055	1492	−5.426	<0.0001	**
Fortnight (2nd Aug)	−0.187	0.072	1492	−2.572	0.0102	*
Fortnight (1st Sep)	−0.519	0.071	1492	−7.283	<0.0001	**
Fortnight (2nd Sep)	0.056	0.086	1492	0.686	0.5117	
VAR: Hour (11:15)	−0.706	0.202	1492	−3.487	0.0005	**
VAR: Hour (13:15)	0.154	0.225	1492	0.686	0.4926	
VAR: Hour (15:15)	0.451	0.214	1492	2.105	0.0354	*
VAR: Hour (17:15)	1.037	0.191	1492	5.415	<0.0001	**
VAR: Hour (19:15)	1.343	0.177	1492	7.560	<0.0001	**
VAR: Fortnight (2nd Jul)	0.041	0.405	1492	0.101	0.9194	
VAR: Fortnight (1st Aug)	−0.707	0.402	1492	−1.758	0.0788	
VAR: Fortnight (2nd Aug)	−0.431	0.405	1492	−1.062	0.2880	
VAR: Fortnight (1st Sep)	−0.813	0.417	1492	−1.947	0.0517	
VAR: Fortnight (2nd Sep)	−0.652	0.517	1492	−1.259	0.2081	

We found that VAR (bee-eater predation pressure) varied over time. Predation pressure was lower during midday hours and higher during post-breeding migratory period. These results agree with previous studies that showed that the predation pressures of bee-eaters in the hives is not constant over time, but rather is highly concentrated at post-breeding period (especially during August) and in certain hours of the day within this period (Farinós-Celdrán et al., 2016, Moreno-Opo et al., 2018). Despite this general pattern, we detected a high variability among apiaries, thus suggesting variability of predation pressure on beehives at a local scale. PAM allowed us to quantify these variations efficiently and continuously between nearby localities, which would be useful to fine-tune and adjust possible compensations to beekeepers in a more accurate and fairer way.

Honeybees flying activity was negatively associated with VAR (bee-eaters predation pressure). Our results are in agreement with a previous study that also found a significant negative relationship between bee-eaters predation pressure and the number of bees going in and out of the hives (Moreno-Opo et al., 2018), though this study was based on a very limited sample size (around one field census counting bee-eaters per month and apiary). In our case, and thanks to the use of ARUs together with a remote monitoring system located in a hive, we were able to cost-efficiently monitor both the bee-eater predation pressure and the bees flying activity in a continuous way over long periods of time. Our results are similar to those described by Monceau et al. (2018), who found that the Asian hornet (*Vespa velutina*), an invasive honeybee

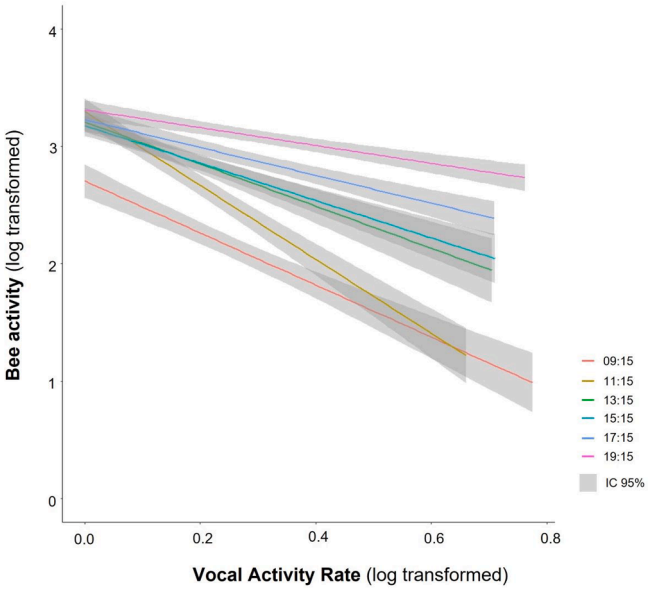

Fig. 5. Linear relationship between Vocal Activity Rate (number of calls in 30 min; log transformed) index and Bee activity (hourly number of entrances and exits of honeybees in the hive; log transformed) in different hours. Fitted linear regression (one colour by hour sampled) and 95 % confidence interval (grey area) are depicted.

predator, inhibited or reduced the foraging and flying activity of European honeybees when predation pressure was exerted. Similarly, previous studies stated that honeybees were able to modulate their flying activity at moments when, with the same abundance of Asian hornet, the predator was less effective hunting bees (Monceau et al., 2013). Indeed, honeybees can assess predation risk and communicate this risk to the colony (Goodale and Nieh, 2012). In our case, the negative relationship between VAR and bees flying activity was conditioned by the hour. At equal intensity of bee-eaters pressure (VAR), the magnitude of the effect was significantly lower during midday and during the afternoon. This could be related to the natural foraging behaviour of the European honeybee workers since their flying activity peaks during afternoon in summer (Reyes et al., 2019). Indeed, using continuous temporal data from our hive remote monitoring system, we found maximum bees' flight activity between 8 and 9p.m. Therefore, it is likely that honeybees may be more prone to forage during midday and afternoon hours regardless of bee-eater predation pressure, which may partly explain the lower relationship between VAR and bee flow at these hours. We cannot discard the existence of a certain adaptative behaviour of honeybees to the hunting pressure of bee-eaters, since these two species have been living together for centuries. For example, populations of honeybees, where the Asian hornet is indigenous, have developed defence behaviours, while these behaviours are absent in the areas of recent colonization of this invasive wasp (Requier et al., 2019).

Further research is needed to understand the real impact and ecological mechanisms behind the relation between bee-eater predation pressure, bees flying activity inhibition and final beehive production and vigour parameters. Moreno-Opo et al. (2018) found that higher flying activity of bees did not influence the amount of honey, pollen, and brood produced despite that honey production and vigour hive parameters were negatively related to bee-eater predation pressure. These findings suggest that other factors beyond the presence of bee-eaters may be interacting in the total beehives production results. Protected wildlife usually takes more than its share of the blame (Nyhus et al., 2005) since their damages customarily are more obvious than those produced by more diffuse and complex environmental factors. This is the case of complex interactions between bee predation and environmental factors that affects apiculture production (Potts et al., 2010). If compensation programs for these damages need to be implemented, PAM would allow accurate, fully automated, comparable, and cost-efficient estimations of predation pressure exerted by bee-eaters across different apiaries, and thus, to adjust possible compensations.

The study of the human-wildlife conflicts requires fast and accurate protocols for the reliable estimation of potential competition between humans and protected species, aiming to provide realistic compensation through accuracy assessments of damage verification protocols (López-Bao et al., 2017). PAM based on the use of ARUs have proven to be a suitable and increasing used alternative to traditional field surveys for monitoring wildlife across many research areas (Sugai et al., 2019). Our study offers a new application of ARUs and new tools for the evaluation and quantification of damages caused by wildlife, a key element for the resolution or mitigation of human-wildlife conflicts. Here, we focused on the interaction between honeybees and the protected European bee-eater, but we expect that this technique might be useful to remotely monitor the predation or damage pressure caused by other vocally active species, such as birds or invasive species damaging agricultural crops (Hu et al., 2009, Gebhardt et al., 2011, Campbell et al., 2017). Similarly, this technique might be also useful for monitoring the predation pression caused by other conflict species with the beekeeping sector, such as the invasive Asian Hornet (see review about its impact on honeybees' colonies in Laurino et al., 2020), which might be feasible based on their flight buzzing sounds (Gradišek et al., 2017).

5. Open research statement

Raw data and code employed for statistical analyses in the current manuscript are provided as private-for-peer review and can be found in the following link: https://figshare.com/s/50c2a0addd7b586bac80.

CRediT authorship contribution statement

Gerard Bota: Conceptualization, Methodology, Data curation, Software, Writing – original draft. **Juan Traba:** Data curation, Software, Validation, Supervision, Writing – review & editing. **Francesc Sardà-Palomera:** Methodology, Data curation, Writing – review & editing. **David Giralt:** Methodology, Data curation, Writing – review & editing. **Cristian Pérez-Granados:** Data curation, Software, Validation, Supervision, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

A clear statement is included in the text

Acknowledgements

European bee-eater monitoring was funded by the Department of Territory and Sustainability of the Generalitat de Catalunya. Marc Pérez-Osanz, Joan Rodríguez and Josetxo Rodríguez contributed significantly to bee-eater field work and data preparation. Fina Gonell contributed to reviewing beehive vitality for hive selection. We also wish to thank Josep Albarracín for his close collaboration and help on building the ARUs, Ana Sanz-Pérez for her comments on statistical analysis and two anonymous reviewers whose comments helped to improve the manuscript. RECoti is an EU registered trademark (n° 18011408). ARUs conception and design were partially supported by Programa de Investigación y Conservación del Zoo de Barcelona within the project 'Nuevas tecnologías para viejos trabajos. Uso de grabadores automáticos para la detección y censo de especies raras y amenazadas. El caso de la alondra

ricotí en Lleida y otras poblaciones pequeñas'. CPG acknowledges the support from Ministerio de Educación y Formación Profesional through the Beatriz Galindo Fellowship (Beatriz Galindo – Convocatoria 2020). Finally, we would like to thanks to all apiarist involved in the project who let us work with their hives.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109158.

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