Young Eurasian Scops Owls make individually distinctive vocalizations

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Abstract. Vocal distinctiveness is expected to occur more often in colonial-breeding species as parents need to recognize their offspring in a large group of conspecifics. In this study, I examined the calls of the young of a territorial nocturnal raptor, the Scops Owl both before and after fledging. Contrary to what is expected for a territorial species, the calls of young owlets showed a high degree of repeatability in many acoustic features, particularly call duration, spectral centre of gravity, and spectral skewness. Discriminant analysis assigned 52.5% of the calls to the correct individual, and 77.5% when restricting analysis within broods. Inter-individual differences appear before fledging and were stable for multiple days. The results suggest that the vocalizations of young Scops Owls could potentially act as identity signals. However, the functional significance of acoustic signatures remains unclear; a few hypotheses are discussed. Acoustic distinctiveness could merely reflect the development of vocal individuality that is typical of the adults, with no net benefit to parents and offspring. However, it could also play a role in parent-offspring communication, preventing misdirected parental care to unrelated young, or helping the parents feed preferentially specific young, as was suggested earlier for this species. Acoustic signatures could also help brood mates maintain contact after fledging or mediate competition for food between them. Further studies are needed to determine whether parents and offspring do assess identity signals in vocalizations.

Keywords: Acoustic signature, food-begging, fledglings, individuality, nestlings, Otus scops, parent-offspring communication, repeatability.

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INTRODUCTION

The ability to discriminate among conspecifics is an important characteristic in many animals and is often required for mate and kin recognition, and parent-offspring communication (Tibbetts & Dale, 2007). Studies of bird vocalizations have found a plethora of apparent adaptations to increase the distinctiveness of individuals (Falls, 1982; Lambrechts & Dhondt, 1995; Carlson et al., 2020) in contexts such as mate and kin recognition (e.g. Sharp et al., 2005; Vignal et al., 2008), neighbour-stranger discrimination (Stoddard, 1996), and parent-offspring communication ((Beer, 1971; Tibbetts & Dale, 2007). The latter case occurs often in bird species that breed in dense and noisy colonies, like penguins and seabirds (Buckley & Buckley, 1972; Lefevre et al., 1998; Jouventin & Aubin, 2002). In colonial swallow species, nestlings make individually distinctive calls that parents recognize (Beecher et al., 1981; Stoddard & Beecher, 1983; Loesche et al., 1991; Strickler, 2013). On the contrary, calls of nestlings of non-colonial species show weak or absent individuality (Medvin & Beecher, 1986; Medvin et al., 1992, 1993; Leonard et al., 1997 but see Barg & Mumme, 1994). The observation that parent-offspring recognition is better developed in colonial than in noncolonial species led to the hypothesis that coloniality is a strong selection pressure for the evolution and maintenance of the distinctiveness of calls (Beecher, 1990). In colonially-breeding species, the parents must identify their own young among many unrelated ones, particularly after their young leave the nest and become mobile, so that their location is an unreliable indicator of identity. In those cases, the risk of misdirected parental care is high.

Individual variation in vocalizations is a prerequisite for the ability to discriminate between conspecifics (Falls, 1982). Features of the signal that is sent out, like its dominant frequency, or duration, must show weak intra-individual variability combined with high inter-individual variability. However, vocal traits often vary along with physical or behavioural conditions of the individual. To be a reliable indicator of identity, a signal must also be temporally stable, that is, it must remain unaltered along significant time scales (Gilbert & McGregor, 1994; Peake et al., 1998; Lengagne, 2001; Grava et al., 2008; Klenova et al.,

2009, 2012). Among *Strigiformes*, vocal signatures have often been found in adult birds (e.g. Eagle owls: Lengagne, 2001; Great horned owls, Odom et al., 2013; Barred owls, Freeman, 2000; Tawny owls, Galeotti & Pavan, 1991; Pigmy owl: Galeotti et al., 1993; Western screech-owls, Tripp & Otter, 2006; Ural owl, Zhou et al., 2020; Northern spotted owl, Fitton, 1991; Eastern screech owl Cavanagh & Ritchison, 1987), but less often in nestlings and fledglings (Dreiss et al. 2014).

The Eurasian Scops Owl (*Otus scops*, hereafter 'Scops Owl') is a small (body length 19-20 cm), nocturnal, primarily insectivorous owl, that breeds in open habitats in the Mediterranean zone and Central-Eastern Europe (Mikkola, 1983; Cramp, 1985). The species is mainly territorial, although it sometimes forms "loose colonies" of breeding pairs with inter-nest distances as short as 15 m (Grieco 2018; for an overview see Cramp 1985). The advertising call of the adult is highly repeatable (Koenig, 1973; Dragonetti, 2007) and can be used to track individuals unobtrusively (Galeotti & Sacchi, 2001; Denac & Trilar, 2006; Grieco, 2018). The young owlets fledge at about 21 days from hatching and stay together while they are fed by their parents up to independence. The young owlets produce short (0.15 s) "tschp" calls at intervals of 0.5-1 second, interpreted as food solicitation calls, and thought to gradually evolve into the adult advertising call after independence (Koenig 1973). However, there is no quantitative data about their inter-individual variability and stability over time.

Because the species is predominantly territorial, and the fledged brood mates do not mix with other, unrelated fledglings (unpubl. data), the parents likely do not need to recognize their offspring individually. Therefore, the expectation is that the degree of individuality in the vocalizations of the young during the period of dependence on the parents would be low to moderate.

This observational study had two aims: (1) To provide the first detailed description of the food-begging calls of the young Scops Owls and their inter-individual variation based on spectrographic analysis; (2) To determine whether individuals produce calls that are consistently similar in their structure. For this purpose, I recorded the vocalizations of young owlets both before and after nest departure. Especially information about post-fledging behavior is important, since most of the studies of vocalizations and

begging behaviour of young birds have focused on nestlings, while the post-fledging phase is underrepresented (Draganoiu et al., 2006; Middleton et al., 2007), particularly for nocturnal bird species (Kouba et al., 2014).

METHODS

Study area and species

The study was carried out at the State Reserve Metaponto, Italy (40°22'24"N, 16°50'19"E), a reforested area dominated by Aleppo pine *Pinus halepensis* along the sea coast. Forest plots are mixed with human settlements, especially recreational resorts and camping parks. The Scops Owl is a primarily cavity-nesting species but because tree cavities are virtually absent in this area, breeding pairs occupy old twig nests, particularly those of Magpies (*Pica pica*). The young leave their nest about 21 days after hatching (Koenig, 1973), and on the following nights, they move further and further away from the nest. The parents keep feeding the young regularly up to 40 days after hatching, then increasingly less often. At 45 days the young are fully able to catch prey (Koenig 1973), and become gradually independent and disperse. Up to that time, the owlets are inseparable but they do not come in contact with other broods (pers. obs.).

Sound recording and call selection

I recorded vocalizations of 20 Scops Owl nestlings and fledged young from six broods between July and August 2021 and July 2022. Recording sessions were carried out between 19:30 and 21:30 and between 00:00 to 04:30 and were made opportunistically. The study area was actively searched for nests and fledged broods. To find active nests, Magpie twig nests were watched in the evening and in the morning for at least half an hour to detect adult owls bringing food (see also Grieco 2018). Fledged young were found by listening to their calls at a distance. To record sound, I used a Telinga Pro 8 MK2 stereo

microphone mounted on a parabolic dish with a diameter of 52 cm, and a Marantz PMD 661 MK2 digital sound recorder. Each recording lasted at least one minute and was stored in a WAV file at a sampling rate of 44.1 kHz, and with 16-bit depth. In most cases, recordings were made a few meters from the nest tree or the fledged young.

Among all the recordings available, I selected those that contained the calls of all the individuals of the brood that could be measured: brood 1-3 (3 individuals, 1 recording each); brood 4 (4 individuals, 2 recordings); brood 5 (4 individuals, 5 recordings), and brood 6 (3 individuals of which one disappeared; 13 recordings in total). An additional recording was selected for broods 5 and 6 to illustrate the changes in the calls' structure during the visits by the adults. The total length of the audio analyzed was 30996 s (8 h 36 min 36 s). Recordings lasted on average 1291 ± 812 (SD) seconds (n = 24).

Because hatching was not observed directly, the exact age of the nestlings was unknown. For four of the six broods, the fledging date was known, and the first recording was made 7 days before fledging (brood 6) to 10 days after fledging (brood 2). For the other two broods with an unknown fledging date, their behavior suggests that they were recorded at least one week after fledging.

For each of the 20 young owlets and each recording, I selected the 10 loudest calls that were free of background noise and did not overlap calls of their mates or adults. This resulted in the main data set of 490 calls. It is important to state that calls were assigned based on the visual appearance of their spectrogram, that is, two calls with similar spectrograms were assumed to be from the same individual. The entire work is based on this assumption. Because the owlets were not individually marked, the assumption could have produced overestimates of distinctiveness. However, when the young owls were clearly separated from their brood mates – and consequently the position of the caller could not be mistaken – the spectrograms of the calls given by a specific individual were of the same type, and that consistency could be verified for as long as half an hour of continuous calling (e.g. Figure 4 in Results).

In a second analysis, I tested whether vocal differences between brood mates were stable over days. For this purpose, I selected recordings of brood 6 that covered the longest period of time, i.e., 10 days (July 20 to July 29, 2022). This second data set only includes the calls of two young out of three, because one disappeared shortly after leaving the nest (July 22).

Sound analysis

Sound analysis was carried out in Audacity 2.1 (https://www.audacityteam.org), Praat 6.0 (https://www.fon.hum.uva.nl/praat/), and Sound Analysis Pro (http://soundanalysispro.com/) depending on the acoustic features examined (see below). Recordings were first filtered with a 1000 high-pass filter in Praat 6.0 to remove low-frequency background noise. The following FFT settings were used: FFT window size 2048 samples, Hanning window, temporal resolution 46 ms, frequency resolution 21.5 Hz. Two temporal features and eight spectral features were measured:

1. Call duration (s). The time from the onset to the end of the call, measured from the waveform in Praat.
2. Time from the previous call (s). The interval between the onset time of the previous call and that of the current call, measured from the waveform in Praat.
3. Peak frequency(Hz). The frequency at maximum amplitude. To measure it, the entire call duration was selected in Audacity and the function Plot Spectrum was used with the following settings: algorithm Spectrum, function Hanning window, window size 2048.
4. Peak frequency 1/3 (Hz). The frequency at maximum amplitude within the first third of the call duration, measured the same way as Peak frequency.
5. Peak frequency 3/3 (Hz). The frequency at maximum amplitude within the last third of the call duration, measured the same way as Peak frequency. Peak frequency 1/3 ad Peak Frequency 3/3

were chosen because the initial and the ending parts of the calls were often very different - whereas the initial part is generally noisy, the ending part is more structured.

6. Centre of gravity (Hz). The average frequency over the entire frequency domain, weighted by the sound amplitude. It was measured in Praat by selecting the call waveform and calling the function Spectrum > View spectral slice, then Query > Get centre of gravity, with power setting 2.
7. Pitch (Hz). The average pitch across the call duration. It was measured in Praat by selecting the waveform and calling the function Pitch > Get Pitch, with the following settings: frequency range 1000-10000, Analysis method Autocorrelation, Silence threshold 0.03, Voicing threshold 0.1. The intended use of Pitch was to describe the perceived tone of a sound.
8. Average entropy. The average Wiener entropy across the call duration, measured with Sound Analysis Pro. Entropy measures the extent to which the sound contains a mixture of frequencies, as opposed to a single frequency or tone. The noisier a sound is, the more energy is smeared within a wide range. Entropy is a pure number and varies between 0 to 1, but in this work it is reported on a logarithmic scale, ranging between minus infinite (pure tones, complete order) and zero (white noise, complete disorder).
9. Minimum entropy. The minimum Wiener entropy within the call duration (see Average Entropy above for details). Minimum Entropy aims at capturing the more structured sound, usually at the end of the call (see an example in Online Resource S1).
10. Spectrum skewness. A measure of the symmetry of the spectrum, that is. It was measured in Praat by selecting the waveform and calling the function Spectrum > View spectral slice, then Query > Get skewness, with power setting 2. Skewness is a pure number; it is negative when frequencies are concentrated on the right of the spectrum, and positive when the frequencies are concentrated on the left of the spectrum. If skewness is zero, the spectrum is perfectly symmetrical.

Statistical analysis

For each of the acoustic features defined above, I tested whether the 10 measurements taken for each individual were more similar to each other than to those of the other brood mates. Data were first tested for normality. For each recording, I considered the residuals of the measurements after fitting the individual means (i.e., each measurement diminished by the mean within the recording). Kolmogorov-Smirnov tests were applied to the sets of measures in each recording (10 acoustic features and 23 recordings). After Bonferroni correction for multiple testing, where alpha was reduced by dividing 0.05 by the number of recordings, a few features showed signs of non-normality. The null hypothesis of normality was rejected in five out of 23 cases for Peak frequency and Peak Frequency 1/3 and in two out of 23 for Peak Frequency 3/3. Overall, the effects of non-normality should not be fatal for the ANOVA but the results of Peak Frequency and Peak Frequency 1/3 should be taken with caution.

To assess the repeatability of acoustic features, I performed a one-factor ANOVA for each recording and calculated the Repeatability (*R*) using the formula by Lessells & Boag (1987). In the main data set, each brood resulted in one to five values of R for each acoustic feature, depending on how many recordings were available for that brood. Furthermore, 95% Confidence intervals were calculated from the individual R values from the six broods using the method described by Nakagawa & Schielzeth (2010). Similarly, the second data set provided multiple values of R for each acoustic feature. For this data set, which should be considered illustrative as it was based on one brood (brood 6), the confidence intervals were not calculated.

Another way to look at individual differences in vocalizations is to use linear discriminant analysis (LDA) to test whether a specific call could be attributed to an individual based on its acoustic features. To keep a balanced design with an equal number of calls per individual, I selected one recording (10 calls) for each of the 20 owlets. Among the 10 acoustic features, seven were entered as explanatory variables. The other three features (Time from the previous call, Peak frequency, and Average entropy) were excluded because the former showed low inter-individual variation according to the Repeatability analysis (see Results) and

the other two were highly correlated with other features (Peak frequency correlated with Peak frequency 1/3 and Average entropy correlated with Minimum entropy). LDA was performed in XLSTAT for Excel (Lumivero, 2023). Classification accuracy was obtained with leave-one-out cross-validation, that is, each of the 200 calls was classified using a discriminant function computed from the remaining 199 calls.

RESULTS

The calls of young Scops Owls

Food calls of young Scops Owls showed marked variation in all the temporal and spectral features measured (Table 1). First, some calls exhibited a wide spectrum, with peak frequency around 4000-5000 kHz, while in others the spectrum was more asymmetric, with the loudest sound around 2000 Hz (Figure 1A). Second, the calls of the same form were also consistent in their duration and occurred sometimes with a consistent rhythm (Figure 1A, B). Third, fine-scale spectral structure, in the form of spots or scribbles in the spectrograms, could be easily detected through visual inspection (Figure 1C). Finally, calls that looked similar also did sound different to the human ear (Online Resource S6). Figure 2 shows a summary of the spectrogram types for each of the six broods examined.

Covariation between vocal features

Young owls that gave high-frequency calls also produced less skewed calls, that is, with a broader spectrum and less clear frequency peaks (Table 2 and Online Resource 2). The negative relationship between frequency and spectrum skewness was also apparent when considering individuals within broods (Online Resource 3), so it was not the result of fundamental differences in the spectral structure between broods. Frequency measurements co-varied in general with each other, as expected. However, Peak Frequency 3/3, which measured the dominant frequency at the end of the call, did not correlate significantly with any other measure. Call duration and time from the previous call did not co-vary with

spectral measures, although longer calls tended to be low-frequency and more skewed (Online Resource 2).

Distinctiveness of calls

Repeatability estimates within broods were significantly greater than zero for all the measured features (Table 3). Call duration showed the highest repeatability with the lowest uncertainty of the estimate, suggesting that it was the best indicator of individual distinctiveness. Frequency features and spectral skewness showed moderate to high repeatability, while average and minimum entropy were somewhat less repeatable. On the contrary, the time from the previous call, a measure of the calling rhythm, showed the lowest repeatability.

Discriminant analysis confirmed a substantial level of individuality in the calls. On average, 52.5% of the 200 calls were correctly assigned to an individual owl. Calls of some individuals were more distinctive than those of others, with individual-based classification accuracy ranging from 30% to 90% (n = 20). When LDA was repeated within broods, classification accuracy increased to 77.5%, with little difference between individuals in broods of three siblings and those in broods of four siblings (79.2% vs. 75.0%; range 50% to 100% in both cases).

Effect of parental visits on the call structure

Young owls in the post-fledging phase vocalized continually for a long time, also in the absence of the parents. Temporal changes in the acoustic structure occurred around the visits of the parents (Figure 3). At the arrival of the parent, the young generally tended to get closer to it, while their calls became more frequent and shorter. During the actual feeding event, which occurred a few seconds later, the calls

changed most profoundly: frequency measures and entropy tended to increase, while the spectral skewness decreased especially for the call types with a highly-skewed spectrum (Figure 3, bottom-right chart). In short, the young gave shorter, noisier, and less distinctive calls (see for example call duration in Figure 3 and S4). However, the spectral centre of gravity still differed between individuals in two broods (Figure 3 and S4).

Stability of between-siblings differences

Analysis of a separate dataset of vocalizations of brood mates recorded over multiple days revealed that individual differences in acoustic features emerged well before fledging. Peculiarities in the spectrograms appeared seven days before fledging (Online Resource 5), but a proper quantitative comparison between calls could not be done because of the low sound amplitude. Two days before fledging, and in the following 10 days, almost all call features exhibited significant inter-individual differences (Figure 4). The results were generally in line with the patterns found in the large data set with multiple broods. Call duration was the acoustic feature that showed consistently the highest repeatability (Figure 4, top-right). Inter-individual differences were also found in most of the recordings, particularly for minimum entropy, spectral skewness, centre of gravity, and peak frequency 3/3 (Figure 4). Therefore, inter-individual variability could be potentially used to discriminate between brood mates for several days, also after fledging.

DISCUSSION

The results of this study may be summarized as follows: (1) The main call of young Scops Owls is more complex than previously described (Koenig, 1973) as it exhibited larger variability (for example, in its duration) and marked spectral complexity. (2) Significant interindividual differences were found in almost all temporal and spectral features measured. (3) Individuality of vocal characteristics appeared before fledging and could be traced for ten days. (4) Calls were less distinctive when the young interacted with the provisioning parents, but the latter could have enough time to perceive differences immediately before the actual feeding event. Taken together, these findings suggest that vocalizations of young Scops allow not only discrimination, that is, telling whether two calls are from different individuals, but also identification, that is, labeling individuals, at least within broods.

Acoustic distinctiveness in parent-offspring communication

The results of this study are in contrast with what one would expect if vocal signatures develop primarily to make the offspring recognizable in a large group of fledglings, as it occurs in colonial-breeding species. The Scops Owl is to a large extent territorial (Cramp, 1985), and fledged brood mates tend to stick together and do not intermingle with other, unrelated ones. Therefore, it is unlikely that vocal signatures in fledglings serve the function to prevent misdirected parental care. In the study population, however, breeding density is unusually high: nests can be as close as 12 m from one another and males defend partially overlapping territories (Grieco, 2018, 2022). Fledgled broods have sometimes been observed moving outside their natal territory, even entering other males' territories (pers. obs.), which suggests that unrelated fledglings may sometimes be at a short distance from each other. A semi-colonial organization of breeding pairs is poorly known but probably occurs frequently in the South-European distribution

range of the species where local breeding density can be high. Some degree of intermingling of young could provide some selection pressure for vocal distinctiveness in this species. A similar mechanism has been suggested by Barg and Mumme (1994) to explain the apparent contradictory finding that in the Florida Scrub Jays, a highly territorial species with some limited intermingling of young after fledging, the parents can discriminate between offspring and nonoffspring (Barg and Mumme, 1994).

There are a few possible alternative explanations for the occurrence of acoustic signatures in young Scops Owls. First, the acoustic structure in young birds' calls could merely reflect the development of individuality at later stages. In several species, including the Scops Owl (Koenig 1973), begging calls gradually transition to adult calls (Redondo & Exposito, 1990; Brittan-Powell et al., 1997; Marques et al., 2011). Young owlets might not "broadcast" their individuality, and their voice would simply reflect their individuality in adulthood, with no net advantage early in life for parents and offspring. Second, parents could use acoustic signatures to discriminate between their own nestlings and alien (parasitic) nestlings, as found in other species (Colombelli-Négrel et al., 2012; Yang et al., 2015). However, Scops Owls are not subject to any known brood parasites (Mikkola, 1983; Cramp, 1985), and laying eggs by multiple females in the same nest is a rare event (Bavoux et al., 1991). Therefore, the acoustic distinctiveness of nestlings is unlikely to be of adaptive value in the context of the rejection of unrelated nestlings.

There is another, intriguing scenario where parents may be using acoustic signatures of their offspring to feed preferentially some individuals over others, as suggested earlier for this species (Parejo et al., 2010). Theory (Lessells, 2002) and an increasing number of empirical studies suggest that in some circumstances the parents do not distribute food equally among nestlings, based on nestling size, body condition, sex, or age (Krebs, 2001; Smiseth et al., 2003; de Ayala et al., 2007; Dickens & Hartley, 2007; Dugas, 2009; Avilés et al., 2011; Ersoy et al., 2021). For example, females and male parents differ in the amount of care given to the smallest nestlings (Slagsvold, 1997), although it is not always clear whether nestling size is the primary cue used in this discrimination. Condition-dependent parental favouritism mediated by visual cues has been suggested to occur in several species (Jourdie et al., 2004; Bize et al., 2006; Galván

et al., 2008; Avilés et al., 2011), including nocturnal raptors (Avilés & Parejo, 2013). In an experimental study on Scops Owls, Parejo et al. (2010) found that when the ultraviolet reflectance of the cere (i.e., the skin above the beak) of the nestlings was experimentally reduced, thereby simulating lower body condition, those nestlings gained more weight than their control siblings. The authors concluded that the parents somehow perceived the lower brightness of the cere and fed preferentially those nestlings over the untreated siblings. The study suggested that parent Scops Owls do attend to cues of quality of nestlings. Discriminating between offspring by sight only is efficient in the nestling-rearing phase, where both parent and offspring are confined in the small environment of the nest. However, when the offspring leave the nest and become mobile, a recognition system based on visual cues of limited size like the beak cere could could be aided by acoustic distinctiveness (Draganoiu et al., 2006). The parents could learn to associate cues of quality in the offspring, like their body size, sex, or hatching order, with the vocal signatures learnt during the nestling-rearing phase so that they could adjust their food-provisioning decisions. With an important limitation though - this mechanism could only work if the cues of quality remain stable in the short/medium term (i.e. over days to weeks) so that they can be associated with an individual's voice.

Why vocalize in the absence of parents?

In contrast with what occurs in many bird species, the young Scops Owls spent significant time calling when the parents were absent (Figure 3, Figure S4). This behavior has often been described as "parent-absent begging" (Budden & Wright, 2001) or "secondary begging" (Leonard & Horn, 2001). Vocalizations in the absence of parents are known in other owl species, both during the nestling (Roulin et al., 2000, 2009) and in the post-fledging stage (Olsen et al., 2020). Prolonged vocalizing is presumably costly, in terms of energy requirements (Kilner & Johnstone, 1997), predation risk (Magrath et al., 2010),

and vigilance costs (Roulin, 2001). Because any begging signal that does not elicit any parental responses is wasteful, one may wonder what other benefits of this behavior could be. First, because the fledglings are mobile, by continually vocalizing they could inform the parents about their location and need. A second possibility is that siblings may need to recognize each other to keep contact after they leave the nest (Ligout et al., 2016). In this scenario, vocal distinctiveness would play a role in sib-sib communication. Furthermore, repeated calling may be a “quick on-trigger” strategy to attract the attention of the parents. This behavior presumably results in many false alarms (that is, soliciting a parent that is absent at that time) but at the same time reduces costly misses if the parent is in the vicinity (Dor et al., 2007). The high cost of misses could be particularly important after fledging when each individual does not know whether the parent will arrive next to it or its siblings. Finally, vocal individuality could be advantageous in another, interesting scenario of sibling competition. Through repeated calling, the siblings could be displaying their willingness to compete for the next food item delivered by the parents - a form of negotiation known in another nocturnal raptor, the Barn Owl (Roulin et al., 2000; Roulin, 2002). Each individual could recognize which mates are more motivated to compete, and thereby adjust its competitive behavior accordingly (Roulin et al., 2009; Dreiss et al., 2014).

Concluding, this work has revealed that vocalizations of juvenile Scops Owls potentially carry individual information, at least within broods. This should encourage researchers to address the many unanswered questions outlined above and gain insights into the relationships between nesting ecology, social/territorial organization, and communication in this still poorly known species.

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TABLES

Table 1

Descriptive statistics of ten acoustic variables of 670 vocalizations of 20 young Scops Owls after they left the nest. The standard deviation (SD) represents the inter-individual variation. (*) Minimum and maximum of individual averages. (**) Minimum and maximum of the single measurements (n=670).

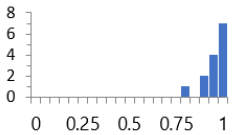
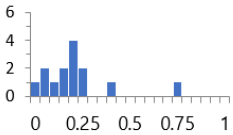
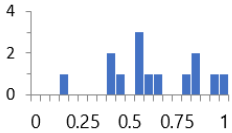
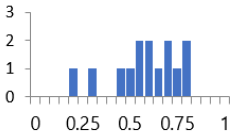
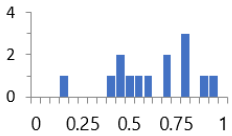
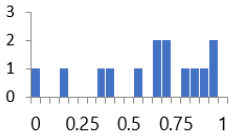
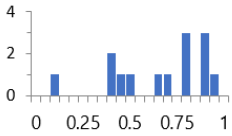
	Average	SD	Range (individuals)*	Range (calls)**
Call duration (s)	0.182	0.045	0.117 – 0.279	0.094 – 0.423
Time from previous call (s)	1.775	0.244	1.410 – 2.302	0.770 – 6.490
Peak frequency (Hz)	1924.9	701.7	1316.4 – 4082.1	1112 – 5963
Peak frequency 1/3 (Hz)	1984.6	690.1	1321.8 – 3937.6	1113 – 5393
Peak frequency 3/3 (Hz)	1577.6	235.0	1221.5 – 2093.6	1074 – 5459
Centre of gravity (Hz)	2296.6	560.2	1722.7 – 3717.9	1468 – 4924
Pitch (Hz)	1820.3	484.2	1334.8 – 3551.0	1202 – 5046
Average entropy	-2.73	0.50	-3.92 – -1.80	-4.80 – -1.18
Minimum entropy	-3.89	0.73	-5.12 – -2.39	-7.25 – -1.45
Spectrum skewness	2.24	1.13	-0.04 – 4.11	-1.04 – 9.36

Table 2

Pearson's correlation coefficients of temporal and acoustic variables in calls of 20 young Scops Owls, based on the per-individual averages. Values in bold indicate a significant correlation after Bonferroni correction (P < 0.0011). * P < 0.05; ** P < 0.0001; *** P < 0.00001. See also Online Resource 2.

	Time from previous call	Peak frequency	Peak frequency 1/3	Peak frequency 3/3	Centre of gravity	Pitch	Average entropy	Minimum entropy	Spectrum skewness
Call Duration	0.27 ns	-0.43 ns	-0.43 ns	0.06 ns	-0.52 *	-0.37 ns	-0.24 ns	-0.41 ns	0.47 *
Time from previous call		-0.002 ns	-0.08 ns	0.42 ns	-0.09 ns	-0.14 ns	-0.07 ns	-0.18 ns	0.34 ns
Peak frequency			**0.99** ***	0.52 *	**0.93** ***	**0.84** **	0.38 ns	0.43 ns	**-0.77** **
Peak frequency 1/3				0.50 *	**0.92** ***	**0.85** **	0.38 ns	0.42 ns	**-0.77** **
Peak frequency 3/3					0.48 *	0.56 *	-0.05 ns	-0.17 ns	-0.22 ns
Centre of gravity						**0.84** **	0.49 *	0.55 *	**-0.90** ***
Pitch							0.14 ns	0.17 ns	-0.66 *
Average entropy								**0.92** ***	-0.50 *
Minimum entropy									-0.61 *

Table 3. Estimates of repeatability of acoustic features within six Scops Owl broods. Significance refers to the F tests for each of the 14 recordings. Some broods are represented more often than others (see Methods). *P* values are adjusted after Bonferroni correction ($P < 0.0036$).

	Average	CI	Significant	
Call duration (s)	0.91	0.87 – 0.96	14 out of 14	
Time from previous call (s)	0.16	0.06 – 0.26	2 out of 14	
Peak frequency (Hz)	0.60	0.41 – 0.79	11 out of 14	
Peak frequency 1/3 (Hz)	0.54	0.48 – 0.61	12 out of 14	
Peak frequency 3/3 (Hz)	0.55	0.36-0.74	13 out of 14	
Centre of gravity (Hz)	0.56	0.22 – 0.91	11 out of 14	
Pitch (Hz)	0.59	0.37 – 0.81	12 out of 14	

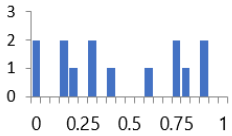
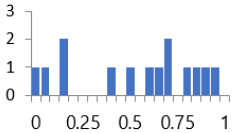
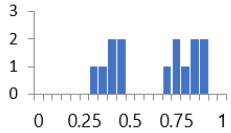
Average entropy	0.36	0.05 – 0.68	7 out of 14	
Minimum entropy	0.39	0.08 – 0.71	10 out of 14	
Spectrum skewness	0.62	0.41 – 0.83	11 out of 14	

FIGURE LEGENDS

Fig. 1

Example of spectral and temporal variation in vocalizations of young Scops Owls. **A**. Spectrogram of the calls of two young one week after leaving the nest. (a) Short call with many frequency components (see the spectrum on the left). (b) Longer call with a narrower bandwidth, and a main component around 2 kHz (see the spectrum on the right). **B**. Spectrogram of a train of calls by the same two young owls as in A. The symbols below indicate the intervals between subsequent calls, which may show some regularity as in this example. **C**. Spectrogram of the calls of two owlets and b in another brood. The arrows indicate individually-repeatable frequency peaks, usually captured with Peak frequency 1/3 and Peak frequency 3/3; see Methods. The time bar represents one second. The vertical axis scale is in kHz

Fig. 2

Representative spectrograms of the calls of young Scops Owls of six broods (1-2 from 2021, 3-6 from 2022). The letters indicate features that help recognition of individuals. (a) Differences in call duration. (b) S-shape patterns, usually at the lower end of the frequency range. (c) Wider frequency band in the first part of the call, resulting in a higher centre of gravity and lower spectral skewness. (d) Mass of frequency concentrated at specific points, especially at the end of the call (the “dots” in the spectrograms indicated with arrows). (e) The dominant frequency is generally lower than in calls of other brood mates. (f) More structured sound, with high spectral skewness

Fig. 3

Temporal variation of the calls’ acoustic features in two fledglings (brood 5, compare with Figure 3, last

two spectrograms) during a 31-minute recording, which included two visits of one of their parents (indicated by the owl symbols). During this period the owlets were always separated, so it was possible to accurately tell where the caller was. Time is expressed as the time remaining to the first visit (0 s). Each point represents the loudest call selected in a 30-second interval. The thin lines represent the running average calculated with three values per data point. The five figures on the right show representative spectrograms at five time points spread over the recording time; the numbers indicate the time points on the top-left chart. In each figure, the first spectrogram refers to the individual represented with open circles in the charts. Note the effect of the parental visits on call duration, time from the previous call, spectral centre of gravity and spectral skewness of both individuals

Fig. 4

Temporal stability of the ten acoustic variables of the calls of two young scops owls (triangles and circles) in 13 sets of measurements over 10 nights. The young left the nest on July 22. The squares indicate the resulting repeatability *R*. Filled squares indicate statistically significant *R* after Bonferroni correction for multiple tests ($P < 0.00385$)

Figure 1

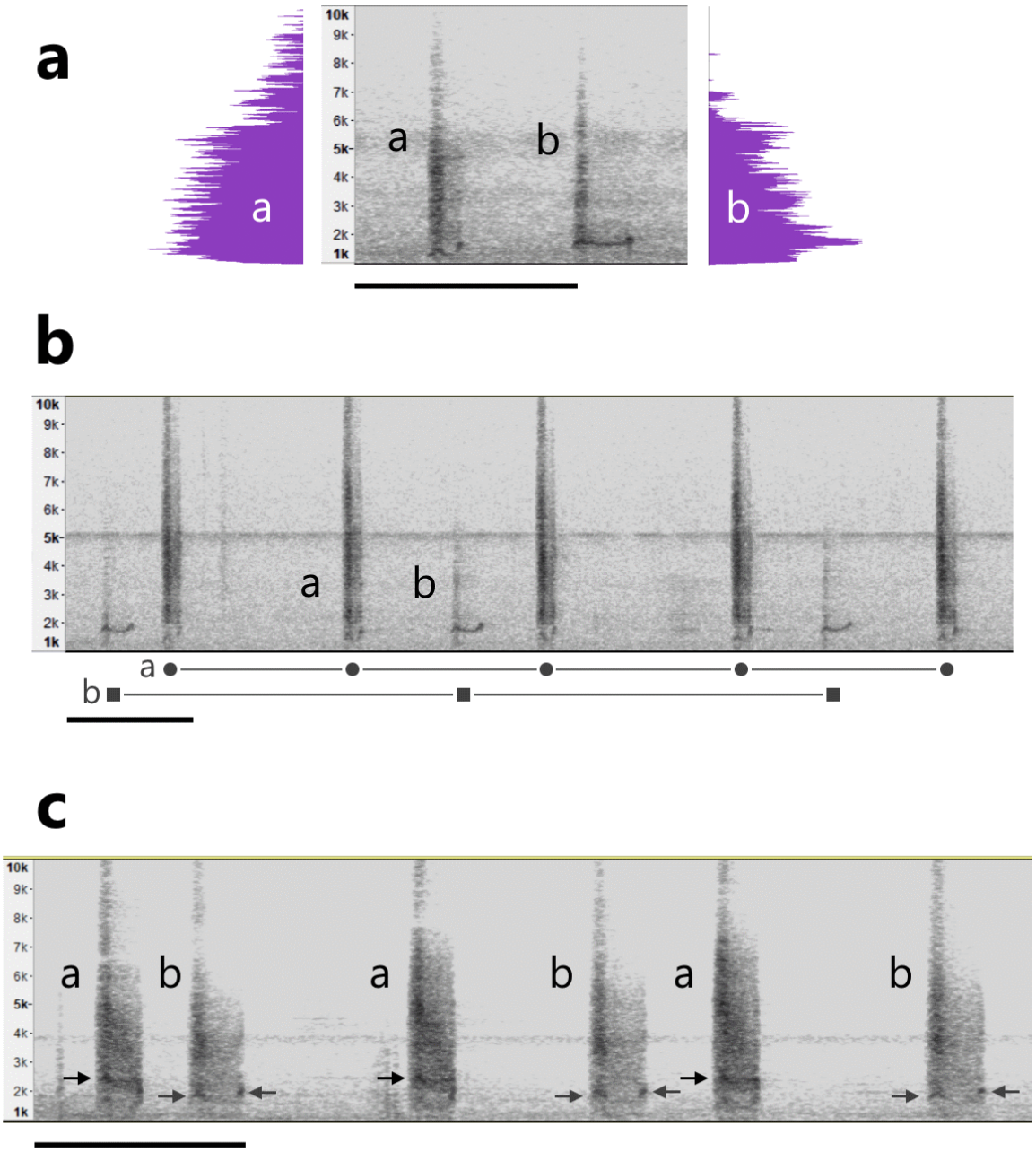


Figure 2

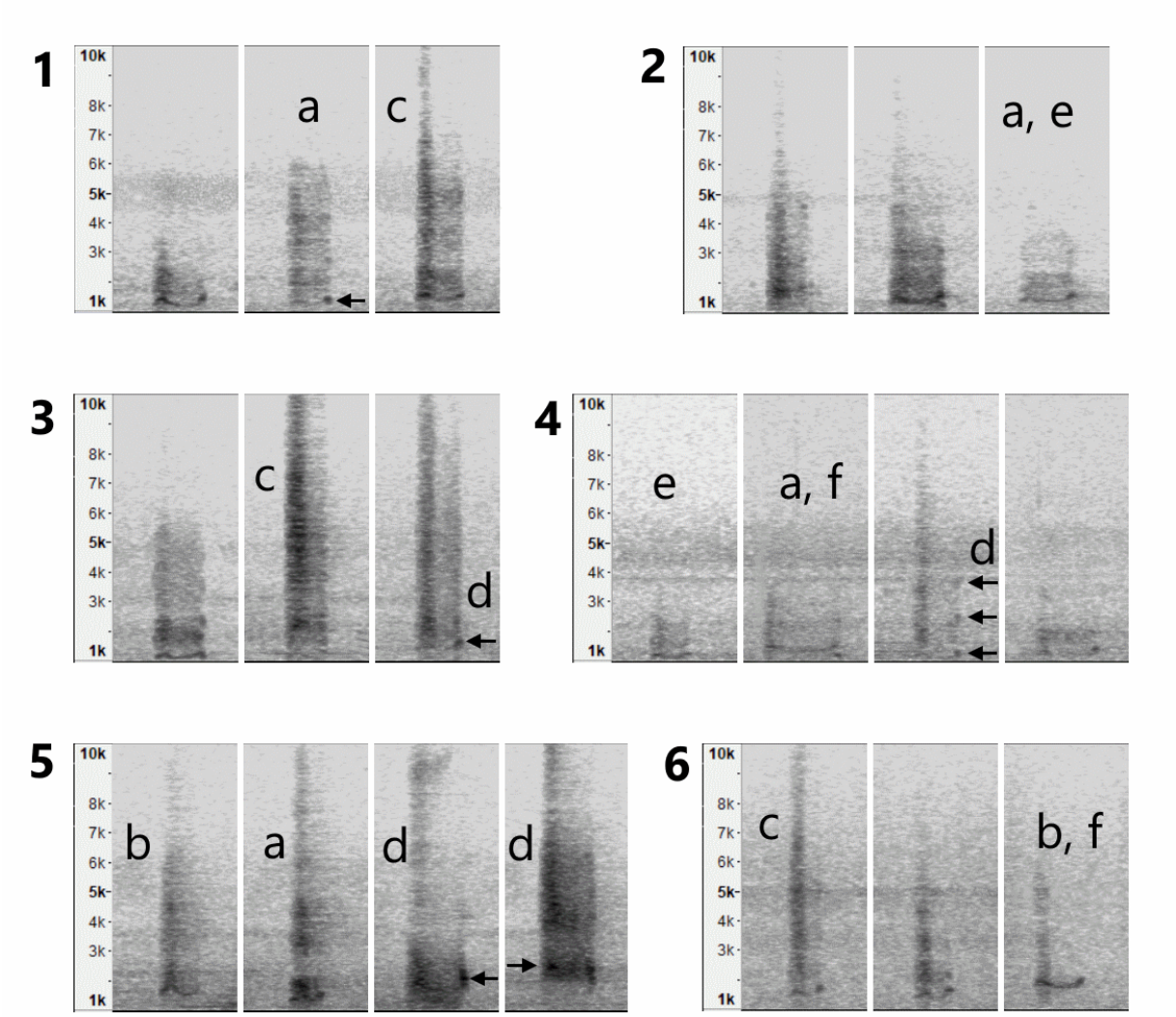


Figure 3

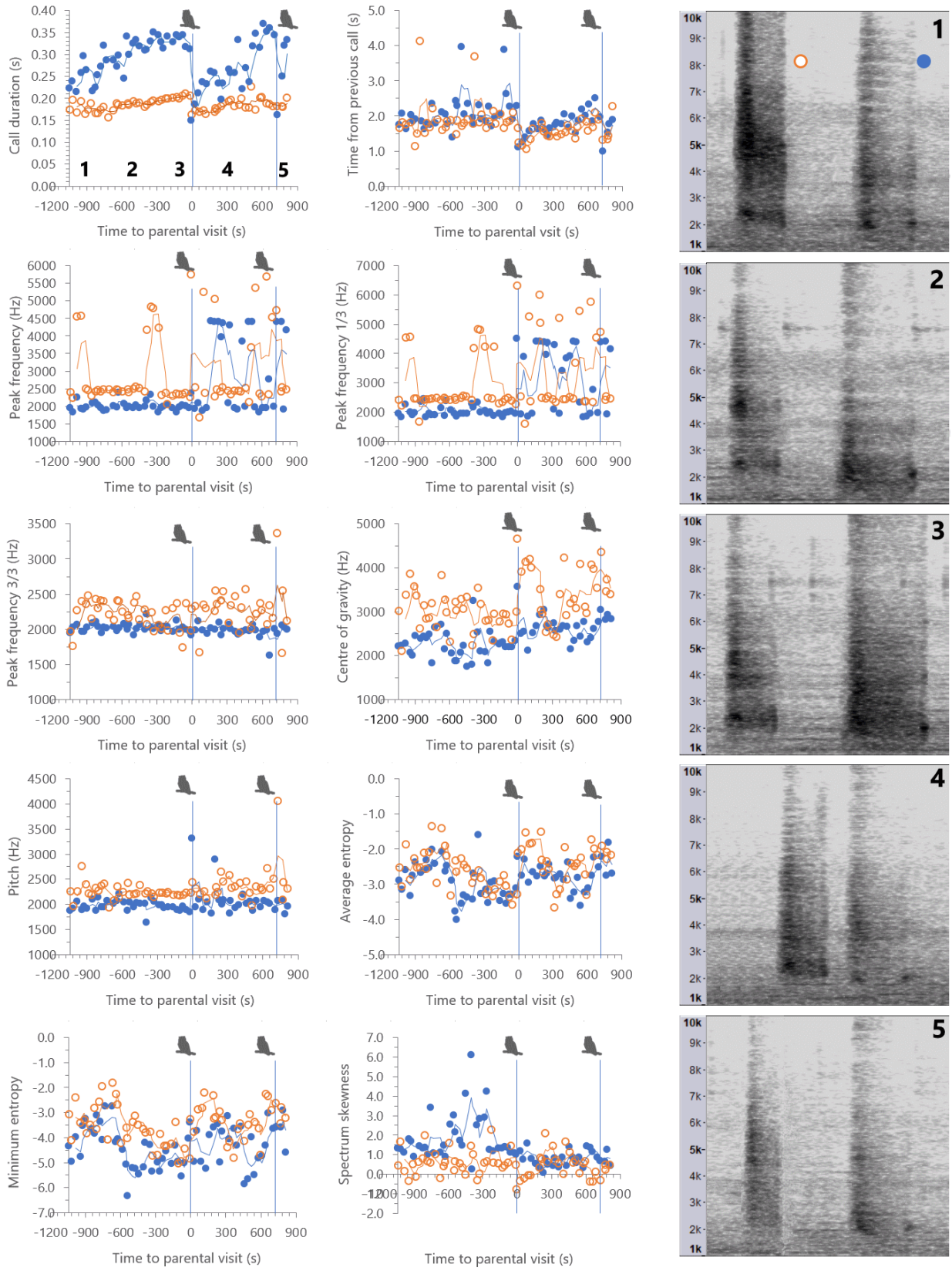
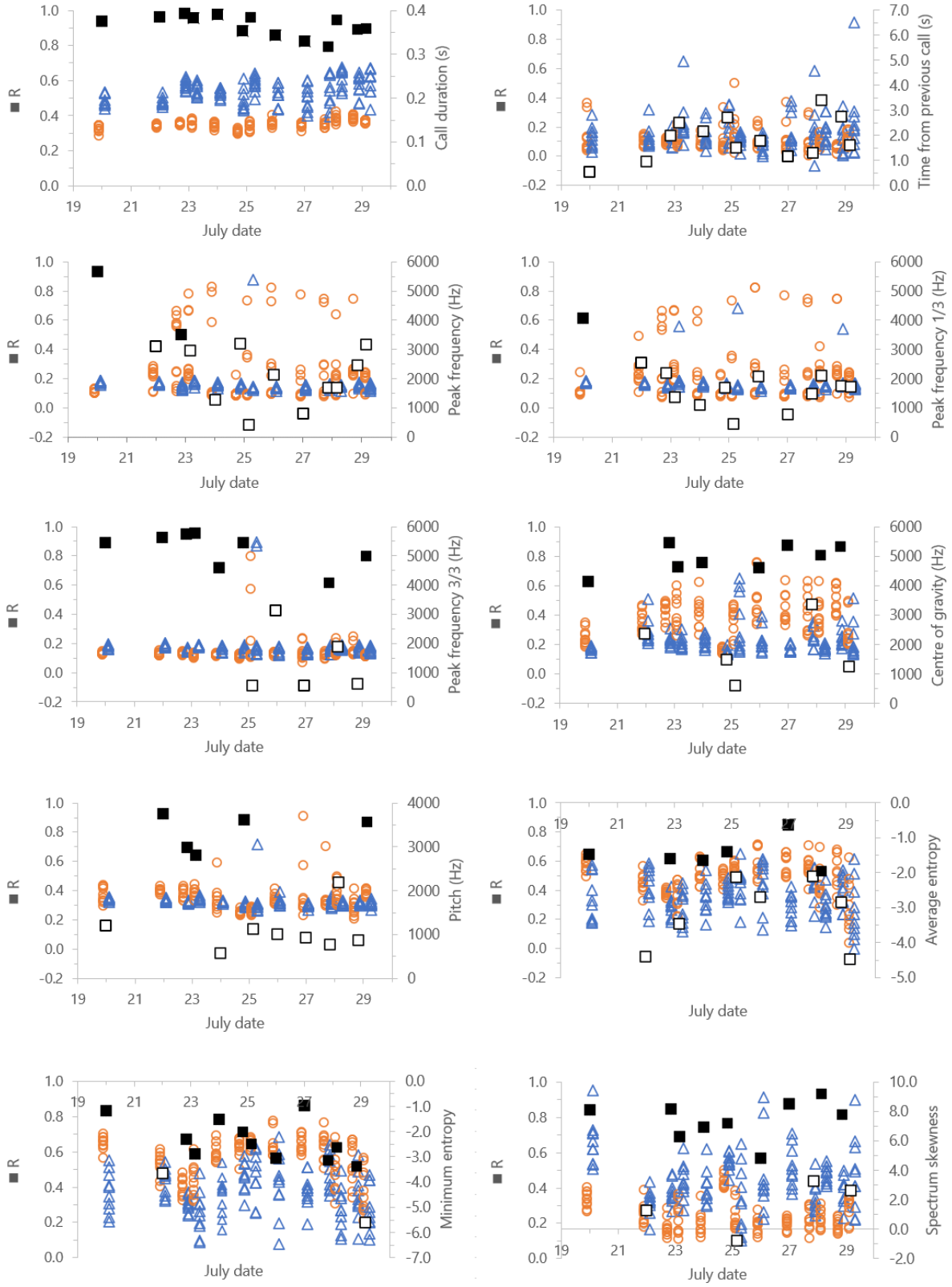

Call duration (s)
Time from previous call (s)
Peak frequency (Hz)
Peak frequency 1/3 (Hz)
Peak frequency 3/3 (Hz)
Centre of gravity (Hz)
Pitch (Hz)
Average entropy
Minimum entropy
Spectrum skewness
Time to parental visit (s)
Time to parental vsit (s)
1
2
3
4
5

Figure 4


R
Call duration (s)
Time from previous call (s)
Peak frequency (Hz)
Peak frequency 1/3 (Hz)
Peak frequency 3/3 (Hz)
Centre of gravity (Hz)
Pitch (Hz)
Average entropy
Minimum entropy
Spectrum skewness
July date

ELECTRONIC SUPPLEMENTARY MATERIAL

Online Resource 1 – ESM_1.tiff

Spectrogram of the calls of two young Scops Owls: a low-frequency, longer call (a) and a high-frequency, shorter call (b). The line indicates the temporal changes of the Wiener entropy.

Online Resource 2 – ESM_2.tiff

Correlation matrix for the ten acoustic variables measured in 20 young Scops Owls. A line indicates a significant correlation after Bonferroni correction (n= 45 correlation tests; $P < 0.0011$)

Online Resource 3 – ESM_3.tiff

Spectrum skewness plotted against the spectrum centre of gravity of young Scops Owl calls. Points represent individuals' averages; symbols indicate the broods those individuals belong to. The insets show examples of spectrograms of calls at the two extremes of the range. Top: low-frequency, highly skewed calls. Bottom: calls with less skewed spectrum and frequencies distributed on a wider range. The width of the spectrograms represents a one-second interval. Pearson correlation, r = -0.896, n = 20, $P < 0.00001$

Online Resource 4 – ESM_4.tiff

Temporal variation acoustic features of the calls of two brood mates (Figure 3, brood 6, last two spectrograms) over two minutes preceding the visit by an adult. The arrival of the adult is indicated by the owl symbol; Time is expressed as the time to the feeding event (0 s). The thin lines represent the running

average calculated with three values per data point. After one fledgling was fed, the other keeps calling with longer, lower-frequency, lower-entropy calls

Online Resource 5 – ESM_5.tiff

Call spectrograms of young Scops Owls seven days before fledging. The first fragment includes three calls, the others two calls each. The arrows indicate the call with a more structured sound, similar to that detected later in the same brood (compare Figure 2, brood 6), suggesting that it could have been from the same individual.

Online Resource 6 – ESM_6.m4v

Fragment of recording of alternated vocalizations of two brood mates (brood 6 in Figure 2). Although the call spectrograms are similar, the two young make distinctive sounds. The sequence is as follows (a and b indicate the two individuals, b slightly low-pitched than a): 15:07 a-b-a-b-a, 15:11 b-a-b-a-b-a, 15:16 b-a-b-a-b-a. Note the “dots” in the spectrograms at specific frequencies. In the background, calls of adult Scops Owls and crickets. This fragment was not included in the analysis because of the pervasive background noise