JOURNAL OF
AVIAN BIOLOGY

Research article

Daily and seasonal use of vocalizations by nesting black-tailed godwits

Ondřej Belfín[1,2], Bart Kempenaers[3] and Theunis Piersma[1,2,4]

[1]Rudi Drent Chair in Global Flyway Ecology, Ecology and Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, the Netherlands
[2]BirdEyes, Centre for Global Ecological Change at the Faculties of Science & Engineering and Campus Fryslân, University of Groningen, Groningen, the Netherlands
[3]Department of Ornithology, Max Planck Institute for Biological Intelligence, Seewiesen, Germany
[4]Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Den Burg, the Netherlands

Correspondence: Ondřej Belfín (ondra.belfin@gmail.com)

Journal of Avian Biology
2024: e03362
doi: 10.1111/jav.03362

Subject Editor: Dominique Potvin
Editor-in-Chief: Jan-Åke Nilsson
Accepted 12 September 2024

Ground-nesting shorebirds must balance the need for acoustic communication at the nest with the constant threat posed by predators. Although it may seem likely that their calls are adapted to minimize detection by predators, little is known about how these birds communicate at the nest or whether they employ cryptic strategies to avoid predation. Using passive acoustic devices and software to analyse extensive acoustic data, we quantified and categorised the calls of black-tailed godwits *Limosa limosa limosa* recorded throughout the whole incubation at eight nests at a dairy farm in the Netherlands in March–June 2021. While incubating, godwits frequently use five main call types, with distinct diurnal patterns and high variation in the number of calls between breeding pairs. Birds used two quiet calls, one for communication at the nest and a second without an easily suggested meaning. Three loud calls were presumably used for predator alert, territory establishment, and long-range communication. Interestingly, although nests were close to each other and exposed to the same aerial predators, the involvement of incubating birds in predator alert calling consistently differed. Furthermore, we described the relationship between the number of predator alert calls and the probability of a godwit flying off the nest. Our findings show that incubating godwits predominantly use loud vocalizations during the day, with only a few calls at night, which were more frequent on nights with a full moon. These descriptive findings for a single godwit community should now be expanded to other contexts, experimental situations, and shorebird species.

Keywords: breeding, communication, cooperation, *Limosa limosa*, nest predation

Introduction

Predators of ground-nesting birds use a variety of cues to locate nests, including visual, olfactory, and acoustic signals. However, we have limited knowledge of the exact mechanism of how predators find nests (Vickery et al. 1992, Pelech et al. 2010,

NORDIC SOCIETY OIKOS
www.avianbiology.org

Ibáñez-Álamo et al. 2015). To counter these threats, shorebirds have developed several antipredation strategies – cryptic eggs and plumage, hiding nests in vegetation, change of odours during incubation, or using distraction displays to avoid predation (Gochfeld 1984, Reneerkens et al. 2005, Humphreys and Ruxton 2020, Hancock et al. 2023). Visual cues are often critical during the day, with predators such as raptors and corvids relying on sight to detect the movement of adult birds or the presence of eggs and chicks in exposed areas (Santisteban et al. 2002). Acoustic cues are also expected to be significant, especially at night, yet they have received only little attention with a focus on the sounds of chicks around hatching and during brooding (Seymour et al. 2003, Kostoglou et al. 2020).

Birds commonly use acoustic communication at nests in various contexts to promote successful fledging (Magrath et al. 2010). Communication at nests is, however, affected by the continuous danger of predation, which leads species to use specific warning signals or stay quiet (Caro 2005, Magrath et al. 2010, Haff and Magrath 2011). Little is known about the communication of shorebirds at nests except during parental incubation exchange when vocalizations seem more common (Miller 1992). For example, in semipalmated sandpipers *Calidris pusilla* breeding in the high Arctic under constant light, the incubating parent vocalized more often just before the arrival of its mate, and at least one parent vocalized in 90% of the exchanges (Bulla et al. 2022). In contrast, females of northern lapwings *Vanellus vanellus* in central Europe vocalized more than males during nest reliefs during daylight, but both tended to be quiet at night (Sládeček et al. 2019). Given the diverse life histories and the description of just a few but large repertoires of shorebirds (Burger and Olla 1984, Sung et al. 2005, Piersma 2007), their vocalizations used during nesting are expected to be similarly diverse. On the other hand, as ground-nesting species with a long incubation period and under the constant threat of predation, selection might have led to reduced communication at the nest.

This study on black-tailed godwits (*Limosa limosa limosa,* hereafter 'godwit'), once a very common breeding bird in the dairy farmland of the Netherlands (Kentie et al. 2016), builds on the only detailed study of their vocalizations (Lind 1961) and a few historical records (Huxley and Montague 1926, Richardson and Bishop 1968, Glutz von Blotzheim et al. 1977, Cramp and Simmons 1983, Bergmann et al. 2008). Using detailed observations of behaviour and written translations of calls, Lind described different call types and their 'meaning', especially in the context of aggression. In view of the enormous technological development over the past 60 years since Lind (1961) and the fact that his study did not focus on nest vocalizations, we re-examined the vocal behaviour of godwits using automatic sound recorders and advanced analysis of the recordings with a focus on communication at nests in another ecological setting.

In addition to the threat of mowing, godwits breeding in the human-altered landscapes of northwestern Netherlands frequently face predation from 14 primarily diurnal avian species and 11 predominantly nocturnal mammalian species (Teunissen et al. 2008, Hooijmeijer et al. 2024). Some predators, such as the carrion crow *Corvus corone*, the red fox *Vulpes vulpes*, and the European badger *Meles meles*, pose a significant risk to eggs, while others, like the western marsh harrier *Circus aeruginosus* and the common buzzard *Buteo buteo*, mainly target chicks. Additionally, several predators are known to kill adult godwits, particularly when they are incubating (Hooijmeijer et al. 2024). Godwits rely on visual detection of predators and respond to alarm calls from other godwits, collectively mobbing predators when they are spotted in the breeding area.

We aimed to describe and quantify the communication of godwits at the nest to examine how they use vocalizations yet stay cryptic for predators. We quantified and categorised calls used by adults at nests over the whole incubation period. Given the known nest behaviour of godwits and shorebirds in general (Burger and Olla 1984, Bulla et al. 2016), we expected vocalizations in at least three different contexts: calls during the exchange of partners at the nest (Sládeček et al. 2019, Bulla et al. 2022, Lee et al. 2023), a staccato call used in response to incoming predators (Lind 1961), and calls used to communicate with chicks around the time of hatching (Cramp and Simmons 1983). Besides these circumstances, we expected godwits to be mostly silent at or near their nest. Given the limited eyesight of birds at night (Martin and Piersma 2009, Martin 2012), which limits their abilities to fully engage in mobbing or other distraction displays (Seymour et al. 2003), we expect godwits to behave quietly, particularly in darkness (Yorzinski and Platt 2012).

Material and methods

Study site and species

We conducted the study in 2021 at the dairy farm of Murk Nijdam near the village of Wommels in the province of Fryslân, northwestern Netherlands (53°.092′N, 05°.565′E; gruttoland.nl). The farm has one of the highest densities of godwits in the Netherlands (Peeters 2023). In an area of 25 ha of meadows, around 70 pairs of godwits, 20 pairs of redshanks, 10 pairs of northern lapwings, 20 pairs of pied avocets *Recurvirostra avosetta*, and five pairs of Eurasian oystercatchers *Haematopus ostralegus* breed each year (Fig. 1). In addition to breeding species, many other shorebirds commonly visit the area, such as ruffs *Calidris pugnax*, Eurasian curlews *Numenius arquata*, and Eurasian whimbrels *Numenius phaeopus*.

Godwits usually arrive at the breeding area in the second half of March, with most clutches laid in the first half of April (Lourenço et al. 2011, Kentie et al. 2014, Hooijmeijer et al. 2024). In early April, the meadows are fertilised by spreading manure (Onrust and Piersma 2017), and mowing starts in the second half of June when most chicks can fly. In addition to the delayed mowing regime, the area has been provided with two permanent water pools of 5 ha in total and

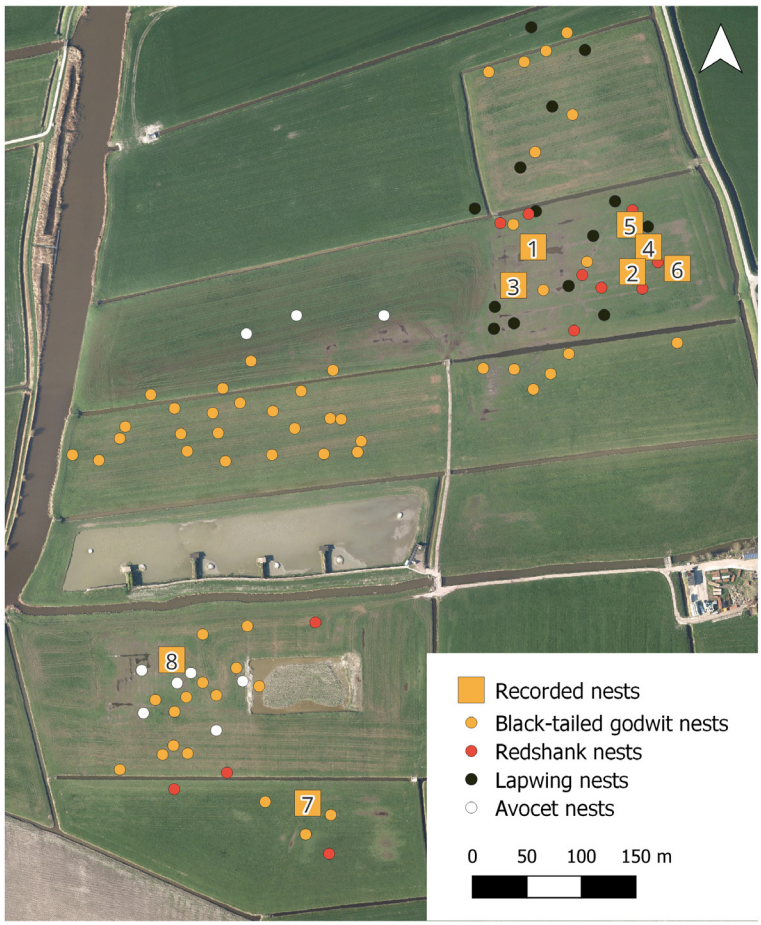

Figure 1. Map of the research area with marked recorded nests and other known shorebird nests. Generated using the ESRI Satellite base map (Beeldmateriaal.nl) in QGIS (ver. 3.28).

temporary water pools maintained by pumping water from dikes from March to May to enhance arthropod biodiversity (De Felici et al. 2019). Predator monitoring in 2021 confirmed the occurrence of five common predators: stoat *Mustela erminea*, carrion crow, common buzzards, western marsh harrier, and beech marten (*Martes foina*). There is no active predator control; however, a large canal isolates the area from the north, and red foxes are hunted annually in the region.

Field procedures and sound recording

We used SM2 recorders (Wildlife Acoustics) with omnidirectional microphones positioned 50 m away from the recorder via extended cables. Each recorder had two inputs and could thus capture recordings at two separate nests. Microphones were placed on the ground and 20 cm from the nest. Placing a microphone further from the nest failed to detect the quietest vocalizations (based on a test recording). Each cable and microphone were partially covered below old and dry manure or grass to reduce the potential risk of attracting predators.

Eight nests were recorded for most of the incubation period (on average 25.9 days ± 1.9 SD, range: 24–29 days), corresponding to known incubation times of 23–30 days (Verhoeven et al. 2020). However, some days were not fully recorded due to technical problems. Hence, the dataset consisted of 22, 24, 25, 21, 20, 21, 24, and 26 fully recorded days following the order of nest labels used in Fig. 1. The estimated first egg dates were 6, 7, 16, 14, 15, 14, 14, and 17 April. Recordings had a sampling rate of 44.1 kHz, a gain of + 48 dB, and a bit depth of 16 bits. All audio files were stored in uncompressed WAV format. The recorders were charged with 4 Varta Industrial PRO 1,5 V D Mono 17 000 mAh batteries and could record up to 8.5 days. We used two 64 GB cards for data storage that could save 96 h of recordings on average; thus, we replaced the cards every fourth day. At the latest, every eighth day, we synchronised the time at all recorders and checked the placement and sensitivity of microphones to ensure the quality of the recordings.

Nests of all shorebird species in the area were found based on observed nesting behaviour or by drone with a thermal camera operated by a team of volunteers at Nijdam's farm. After we deployed the microphones next to the focal nests, each nest was observed from a distance to check whether the birds accepted the microphones. All observed birds returned to their nest within a few minutes and seemed not to be disturbed by the nearby microphone.

In addition to audio recordings, we collected 22 h of video footage from five nests (8 h at each of two nests, 2 h at each of 3 nests, whereby each recording session lasted 2 h). Nests were recorded during afternoons across the incubation period (8–18 May) to help interpret the calling behaviour of individuals at their nests. To this end, we placed a GoPro Hero 6 camera with a wide-view angle lens approximately 50 cm from the nest and covered it with grass.

Extraction and categorisation of calls from recordings

We analysed 4392 h of recordings using a semiautomatic workflow.

1. We first divided the recordings into 3-s fragments of 1–3 kHz. Segmentation into 3-s fragments allowed for more efficient processing and more consistent amplitude measurement across the dataset. We then extracted all fragments with average power density above −69 measured in Raven Pro with window type Hann, window size 1020 samples, overlap 50%, and discrete Fourier transform (DFT) size of 2048 samples, using the Rraven library (Araya-Salas 2020). When applying this threshold of −69, 98% of all calls identified manually in a test dataset of two days (48 h or recording) were detected in the selected 3-s fragments. We extracted, on average, 158 879 3-s fragments per nest (± 52 880 SD, range: 106 663–240 390) with possible godwit vocalizations.
2. For each 3-s fragment, we created spectrograms using the warbleR library (Araya-Salas and Smith-Vidaurre 2017). We deleted axis descriptions, increased contrast, and resized all spectrograms using the ImageMagick library in Linux. We then selected all fragments that included at least one godwit call using gallery view with 120 × 90 px thumbnails in FastStone Image Viewer 6.4.
3. Using a collection of 14 329 spectrograms from the first nest, we divided all calls into five call types and labelled each (Fig. 2a). For each call type, we obtained at least 770 spectrograms. We then used these spectrograms to train a machine-learning model to help categorise calls from all nests. Specifically, we used a convoluted neural network (CNN) based on the Xception network with the weights pre-trained on the ImageNet dataset (Deng et al. 2009). The validation dataset contained 20% of randomly selected spectrograms excluded from the dataset of the first nest before training the model. We achieved 76% accuracy in the validation dataset after six epochs. The model could be modified to reach higher accuracy; however, we considered this result satisfactory and applied the model to the remaining nests.
4. To ensure the quality of call separation by the model, we manually checked the categorisation of all spectrograms and reclassified the calls where needed. Although we checked all detections manually, using the model – which resulted in a correct pre-assignment of approximately 70% of calls across all nests – still considerably sped up the categorisation process.

We detected 77 325 3-s fragments that contained calls at eight nests during 183 fully recorded days. To better represent an individual's decision to call, we used 'acoustic events', whereby all calls of the same type that are uttered with pauses of maximally 30 s are considered one event. In the case of the short call type, which often occurred randomly with longer gaps between calls, we considered a 90-s interval. In total, we detected 15 078 acoustic events. The microphone positioned near the nest allowed us to unequivocally detect any sudden departures of the incubating bird, identified by the sound of wing beats. This detection was done manually for a sample of randomly selected calls, as detailed in the results section.

Daily variation in use of calls

To study daily variation in vocal activity during different periods of the day, we defined three periods based on the light conditions for a given latitude using the package 'suncalc' (Thieurmel and Elmarhraoui 2019): night (defined as the sun being ≤ 18° below the horizon), twilight (sun is between 0° and 18° below the horizon), and day. To compare the number of calls birds used in periods of different lengths, we defined another variable, 'corrected acoustic events'. In practice, we multiplied events used during the twilight by 2.8 and events used during the night by 3.8, reflecting the ratio between recorded seconds during the day period and shorter periods, respectively. We used the package 'moonlit' to extract moon illumination for the given location and dates (Śmielak 2023).

Statistical analyses

To compare the relative amplitude of each call type, we measured the average power density using Raven Pro for an average of 119 calls per call type (range 59–150, minimum seven calls for each call type per nest). We used Dunn's post hoc test to compare differences between call type amplitudes. To illustrate the daily and seasonal variation in vocal activity at nests and across months of the breeding period, we used generalised additive models (gam) using the formula y ~ s(x, bs = 'cc'), family = Poisson and method = 'GCV' (Pérez-Granados and Schuchmann 2021). We checked the assumptions for all models and found the optimal number of knots, so the model has a k-index > 1 and a high R^2. We performed all statistical analyses with R 4.0.2 (www.r-project.org) using the package 'mgcv' for gams (Wood 2017).

Results

Characteristics of the different call types

Birds at all nests used calls that could be assigned into five major categories based on structural differences – rhythmic calls, staccato calls, long calls, short calls, and harsh calls (Fig. 2a). Among the long calls, we further distinguished between calls repeated in long sequences (long repetitive calls) and calls uttered separately with longer intra-call intervals

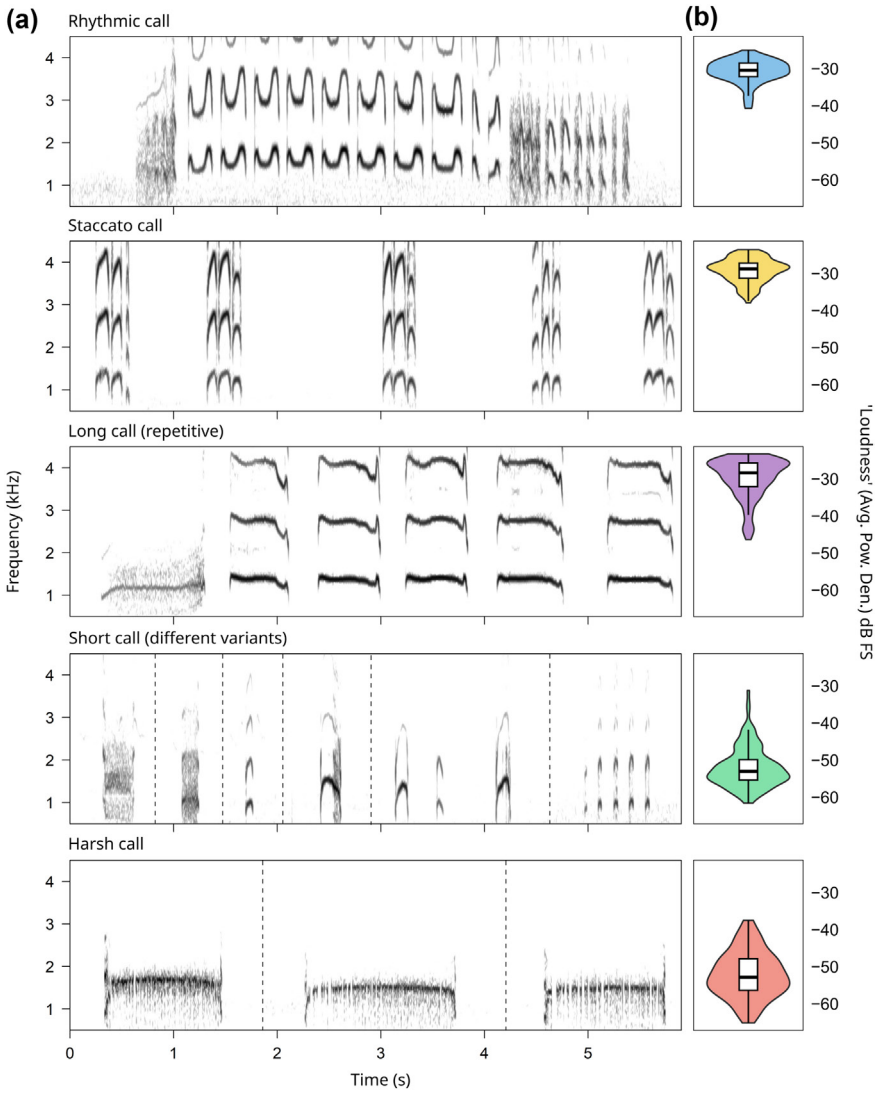

Figure 2. (a) Spectrograms of the five main call types of black-tailed godwits while at their nest during incubation. (b) The loudness of call types is expressed as average power density.

(long single calls). In 63% (140/224) of randomly selected long repetitive cases, the calls were initiated by harsh calls. Long single calls showed high structural variation, with some calls starting or ending with harsh quality or big frequency modulations (Fig. 3). Short calls also showed structural variation, but we did not further categorise them, except for long bouts of short calls that were very distinctive (Fig. 3). Furthermore, we detected grutto call type, which is typically part of the ceremonial flight and functions in pair and territory establishment (Lind 1961). At five nests, grutto calls also occurred in combination with long repetitive calls and rhythmic calls (Fig. 3). Comparison of the relative loudness of calls expressed as average power density showed no differences between short and harsh calls ($p = 0.979$, $n = 107–129$), but significant differences compared to louder calls (the rhythmic, staccato, long, and grutto calls; all comparisons: $p < 0.001$, $n = 59–150$; Fig. 2b).

Variation in the use of calls between nests

On average, each nest had 82 acoustic events per day (range: 8–244, $n = 183$ nest days; Supporting information). The most abundant call was the short call (mean: 54% of all acoustic events per nest; range: 40–74%, $n = 8$ nests), and the least common was the long call (mean: 4.5% of all acoustic events per nest; range: 0.4–16%). The number of acoustic events corrected for variable recording effort varied considerably between nests for all call types (Fig. 4).

Seasonal and daily variation in the use of calls

The frequency of rhythmic, staccato, and harsh calls did not show seasonal changes, while long and short calls increased towards the end of the incubation period when chicks were hatching (Fig. 5a).

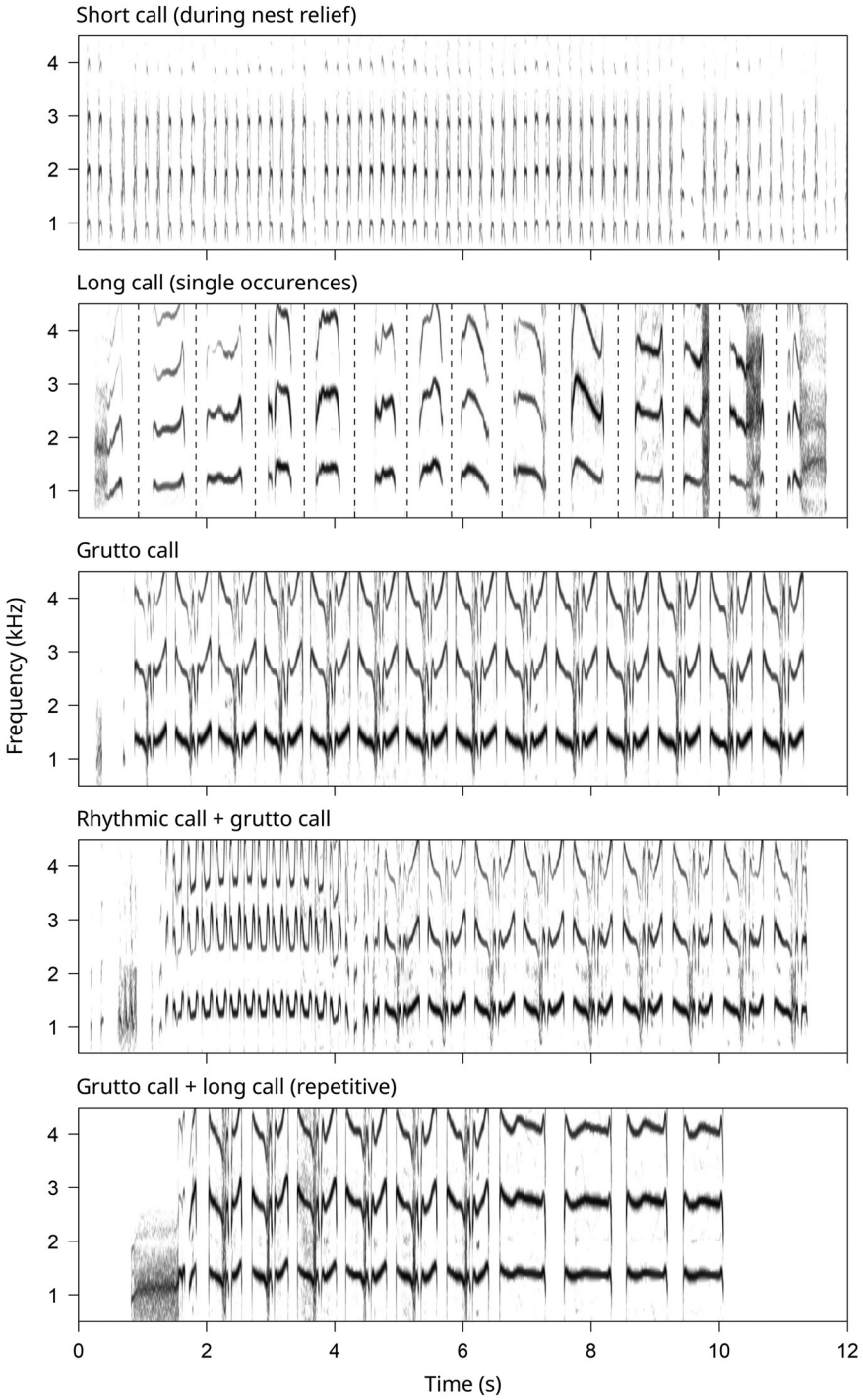

Figure 3. Spectrograms of other, less common call types (and their combinations) uttered by black-tailed godwits at their nest during the incubation period.

Rhythmic, staccato, and short calls showed similar daily variation, with higher call rates in the morning and evening, a slight decrease around midday, and a clear drop during the night (Fig. 5b, Supporting information). Long calls and harsh calls showed a peak around midday. When considering the corrected number of acoustic events, taking into account different lengths of day, twilight, and night, birds would use most of the calls during the day (69%), followed by twilight (21%) and night (10%; Fig. 5c). Proportionally, the most used calls during the twilight period were rhythmic calls (30% of all corrected rhythmic calls), short calls (22%), and long calls (17%). Only rhythmic and short calls were frequently used at night (14 and 11%), particularly on nights with high moon illumination (average number of rhythmic

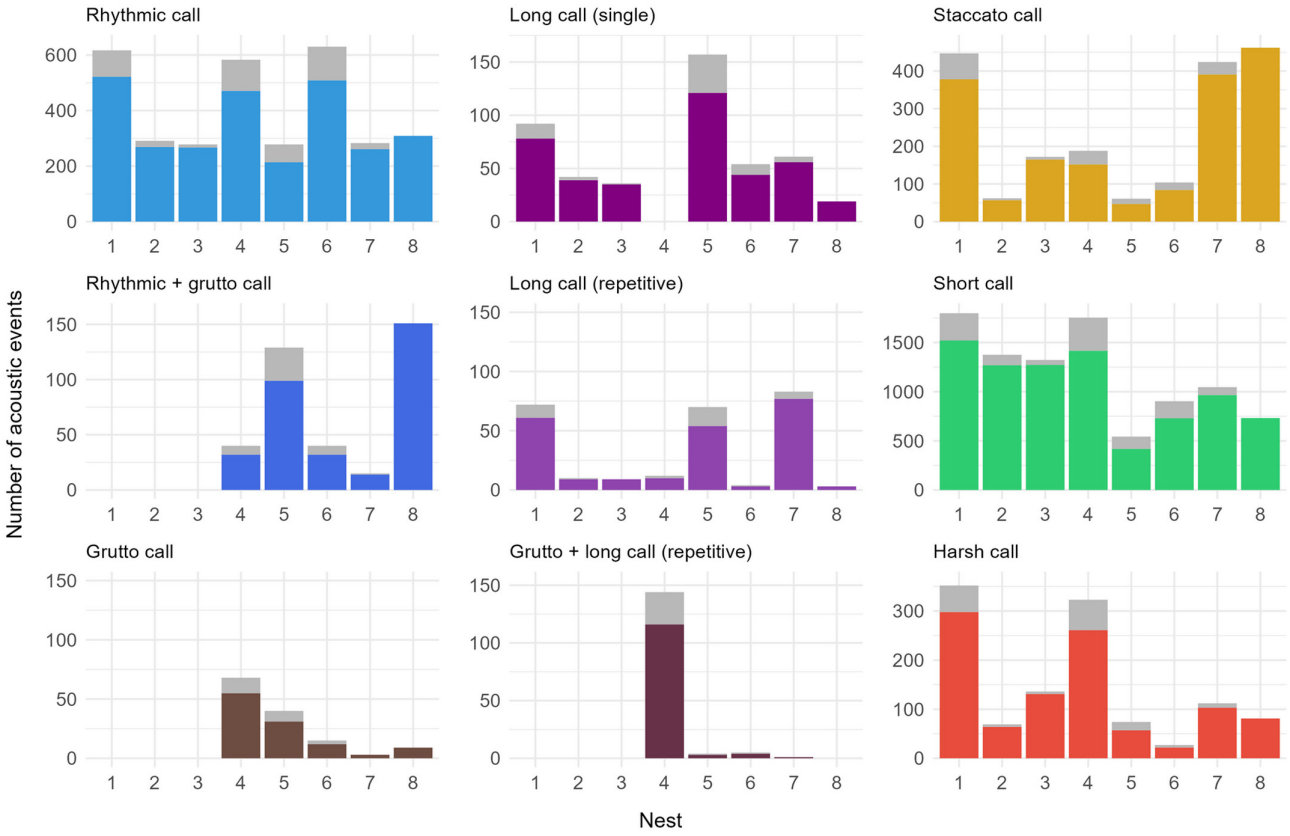

Figure 4. Total number of recorded acoustic events for each call type and nest with correction (grey) for variable recording effort across nests. The correction was done by calculating the average daily number of calls for a given call type multiplied by the difference between the maximum of 26 recorded days and the total number of days recorded at the given nest.

and short calls per night across nests in relation to moon illumination – Pearson's r = 0.71, p < 0.001, CI = 0.50–0.84, n = 36 nights). Staccato and harsh calls were rare during twilight (8 and 5%) and practically absent at night, along with long calls (0, 0.4, and 0.6%).

Video and direct observations

Video recordings provided examples of the context in which godwits used specific calls. Rhythmic calls were observed twice when another godwit passed nearby and twice when a godwit turned its head, seemingly following another passing godwit; in three cases, the bird on the nest did not show any apparent behaviour different from normal behaviour at the nest (Supporting information). The incubating bird suddenly left the nest in two out of 200 randomly selected rhythmic acoustic events.

We observed restless and alert behaviour when birds used staccato calls (Supporting information). In one case, a marsh harrier was observed flying nearby after the bird used staccato calls. Birds left the nest in 27% of randomly selected staccato events (n = 54/200). When other godwits nearby uttered staccato calls, and the godwits used mobbing calls, the incubating focal bird left the nest on 79% of occasions (n = 37/47; Fig. 6c–d). Once, we recorded a godwit suddenly leaving the nest, seemingly distressed, without using any sound. We found a quadratic relationship between the number of staccato calls and the likelihood that the focal bird left the nest, with the highest probability of leaving (46%) with three calls (Fig. 6a). We found no relationship between the average number of notes in staccato calls and the likelihood of a godwit leaving the nest (Fig. 6b).

Long calls varied in length, and birds never left the nest (0/109) but actively observed the surroundings (Supporting information). The Supporting information shows how a godwit quickly switched between a staccato call and a long call (and back) in the presence of an aerial predator. In 37% of 109 randomly selected long-call acoustic events (10–15 events chosen per nest), another godwit uttered the long call in the background. Similarly, in 34% of 116 randomly selected acoustic harsh events and in 10% of 120 randomly selected rhythmic events, another godwit uttered a long repetitive call in the background (Supporting information).

Short calls were used unexpectedly throughout the incubation or with hatched chicks (Supporting information). We recorded 283 acoustic events with long bouts of short calls at all nests (mean = 35.4, range: 13–76). In 127 of these events (45%), we detected a second bird calling in the recording (range = 30–75% per nest). We detected two nest reliefs of incubating birds at the nest on camera: both the incubating

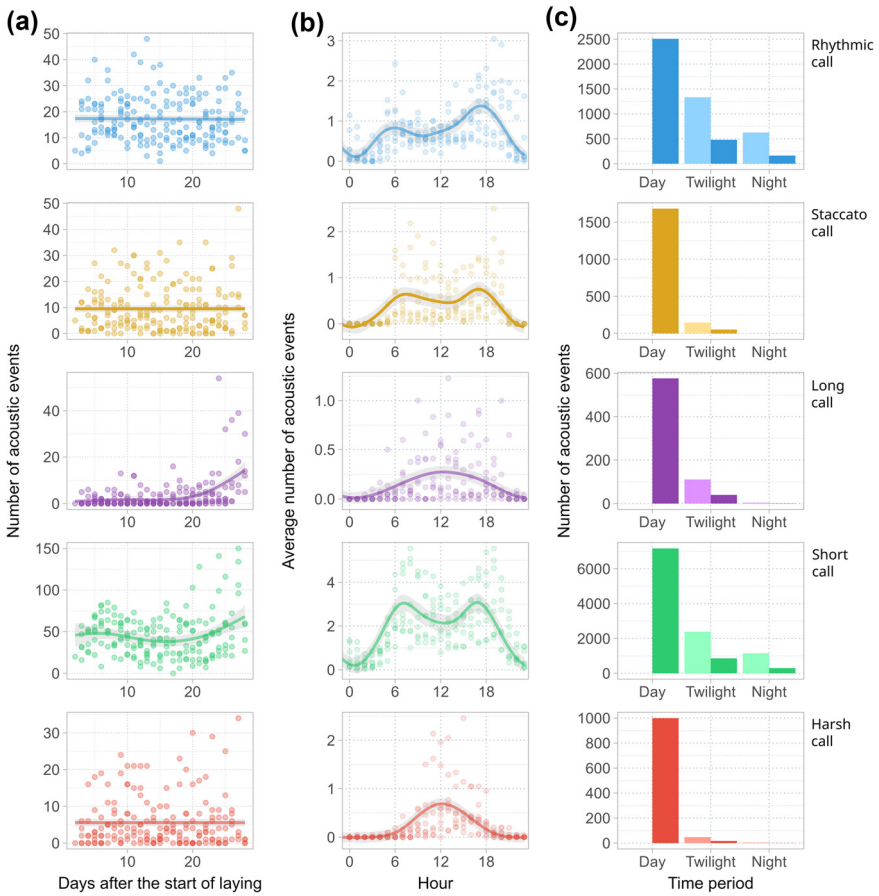

Figure 5. (a) The seasonal activity of five main nest call types during the incubation period. (b) The daily activity of five main nest call types during the incubation period. The average number of acoustic events for a given hour is presented separately for each nest. (c) Summary of different metrics representing the vocal activity of five call types compared between periods. The first column in (c) represents 'corrected acoustic events' (the number of acoustic events multiplied by the coefficient 2.8 for twilight and 3.9 for night), and the second column represents recorded acoustic events. Note that the total recording time for the day was 2710 h, for twilight 975 h, and for night 707 h.

and the returning birds briefly uttered short calls without long call sequences (Supporting information).

Discussion

We found high call activity throughout the incubation period at all nests of black-tailed godwits, with a considerable increase during the hatching period. We distinguished five main call types based on their structure, which differed in loudness and daily and seasonal use. The number of calls of each type varied between nests, including the call type used in anti-predation behaviour (staccato call).

Loud calls – rhythmic, staccato, and long calls

Rhythmic, staccato, and long calls had high amplitude levels, suggesting they are used for longer-distance communication. As shown in other species, calls at the nest might attract predators, and we expected godwits to be silent at night to avoid the risk of being detected by a predator (Haff and Magrath 2011, Ibáñez-Álamo et al. 2015). However, godwits sometimes used loud rhythmic, as well as quiet short calls, at night. This was especially the case on moonlit nights (around a full moon), suggesting that godwit-calling activity increased with increased visibility at night (see Dickerson et al. 2023 for a review of the effects of moonlight on vocal activity).

Rhythmic calls had the most complex structure, with several phrases of different notes. Based on video recordings and field observations, we found that birds often used this call when another godwit was close to the incubating bird. Thus, we suggest that these calls might play a role in communication with neighbours or with other passing godwits, and possibly be a response to an intruder. The rhythmic call was also used at twilight and at night, perhaps with increased movement of predators in the evening, resulting in higher bird movement, thus causing more interactions with territory intruders. Structurally, it resembles the milder version of the 'attack call' used by excited birds or in aggressive situations

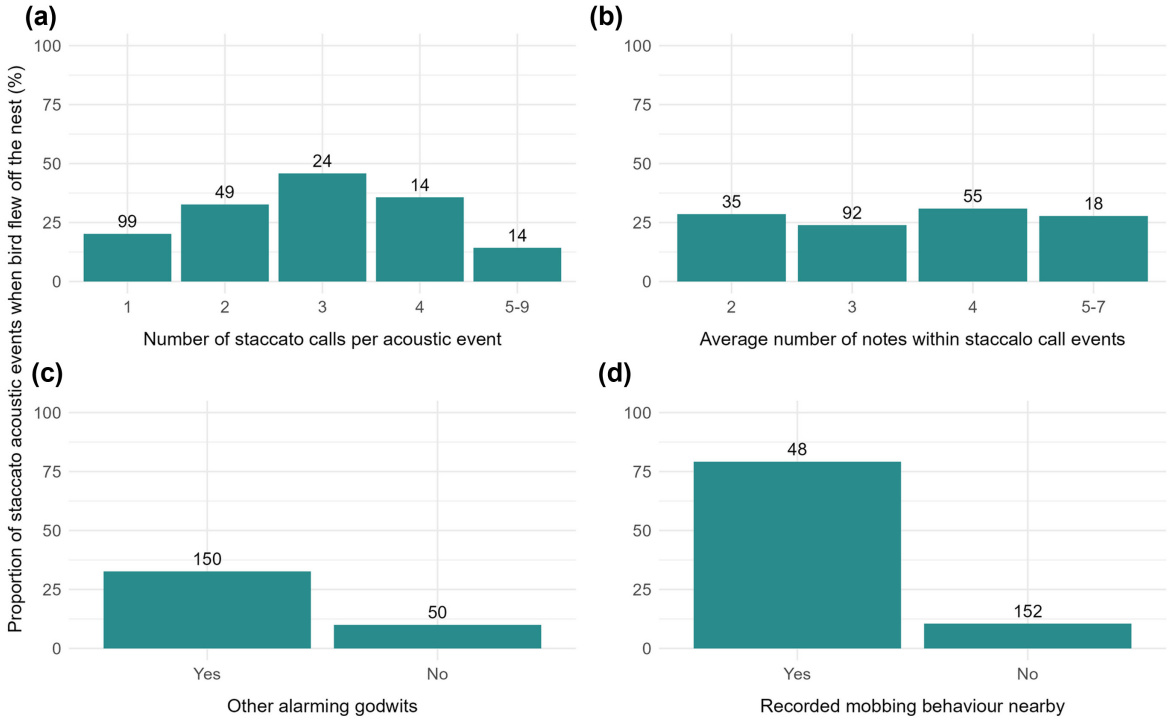

Figure 6. Probability of a godwit flying off the nest in relation to (a)–(b) characteristics of staccato calls. (a) Number of calls per acoustic event, (b) the average number of notes within a staccato call, and (c)–(d) the presence of other alarming or mobbing godwits nearby. (c) Presence of other alarming godwits in the background, (d) mobbing behaviour recorded nearby. The values above bars represent the total number of cases for the given situation.

away from the nest (Lind 1961, Cramp and Simmons 1983). Nevertheless, it remains unclear what the benefits of using the rhythmic call for the incubating bird might be.

Staccato calls were used as a response to the presence of a potential predator with a clear function as a warning, followed by sudden leaving of the nest, possibly because the predator was nearby. Godwits rarely used the staccato call during twilight and never at night; hence, godwits may use staccato calls during the day to warn against aerial predators because they can spot them from a distance and safely leave the nest. We did not record any other structurally distinct call that could be potentially used in relation to night-time predators. Staccato calls were often quickly repeated, and the number of repetitions and the number of notes differed (Fig. 6). Godwits suddenly flew off the nest regardless of the specific number of call notes; instead, the cues based on the presence of birds mobbing the predator were more informative. More work is needed to confirm if the number of notes or repetitions informs about the level of incoming danger as shown in other species (Shah et al. 2015).

The long call typically consisted of multiple repeated notes, often followed by another bird calling in the distance using the same long call type. The call could function in long-distance communication, possibly between pair members or other godwits in the same context. Long calls were more common towards the end of the incubation period around hatching, suggesting either higher demand for these calls or higher motivation to use them. Similar to staccato calls, long calls occurred typically during daylight while the birds seemed to be actively looking around the nest, with no calls at night. Therefore, we suggest that the occurrence of long calls relates to visual or acoustic triggers during the day. Long repetitive calls were used at all nests, but they were among the least common calls; thus, their function might be very specific and not directly related to nesting behaviour. Godwits often use variations of long calls in the open field motivated by escape drive (Lind 1961). Long single calls show the greatest structural variation compared to other call types. The underlying factors behind this variation and, hence, its potential role in godwit communication remain unknown.

Overall, birds at five nests used the grutto call, typically uttered during advertisement flights early in the season. Birds used the call alone but more often combined with rhythmic calls (five nests) or long repetitive calls (three nests, regularly only at one nest). The fact that birds at three nests did not use the grutto call at all suggests that the call does not have an essential role in nesting behaviour.

Quiet calls – harsh and short calls

Harsh and short calls showed low amplitude and were barely audible even close to the nest, indicating that birds used this call only for nearby receivers – eggs, chicks, or mates. Structurally, the harsh call has the longest note of all calls, with the highest entropy and the lowest frequency. Godwits

often used the harsh call before long, repetitive calls, or when another godwit in the background uttered a long call.

The harsh call was most frequently used around midday. Thus, this behaviour might correlate with the increased temperature towards noon when the nests are often exposed to direct sunlight. A similar nest call type related to temperature has been described in Australian zebra finches *Taeniopygia castanotis*. Under high temperatures, adults increased the number of incubation calls close to the hatching period, potentially to signal the environmental conditions to their embryos (Mariette and Buchanan 2016). However, McDiarmid et al. (2018) challenged this conclusion, showing that the birds uttered this call at times of high temperature during the breeding and the non-breeding period. Thus, the nest call seems related to temperature but may not function in communication with embryos. If the harsh call of the godwits is not just correlated but also caused by higher temperatures, we would expect to detect more such calls later in the season when temperatures are higher or on days without cloud cover. However, all birds at all nests used the calls, and we found no seasonal changes in frequency. To conclude, the function of harsh calls remains unclear. However, given the harsh call's distinct structure, it is unlikely to be only a 'byproduct' of a yawn or grunt. We hypothesise that the harsh calls could be the quiet equivalent of long calls. It also remains unclear why harsh calls often co-occur with long repetitive calls.

The short call was the most abundant. It is brief, with low frequency, and uttered most of the day and sometimes at night. This quiet call is undoubtedly related to the hatching period, given the strong seasonal increase and long bouts of these calls around hatching. The short call possibly functions to encourage the chicks to hatch and to guide chicks out of the nest. However, during the pre-hatching incubation period, its typical occurrence suggests other functions than communicating with chicks. Often, birds used this call alone without any obvious receiver or context; perhaps it did not have any communicative role.

Based on the sound recordings, we detected 283 long bouts of short calls, typically with clear vocal interactions between two birds and the sound of one bird flying off the nest as part of nest relief. Lengthy bouts of short calls recorded during nest relief resemble those uttered during copulation or scrape display (Cramp and Simmons 1983). However, both nest reliefs recorded on video were without the long bouts of short calls. Without a camera set up at nests, we could not identify nest relief events with certainty; therefore, we could not say what proportion of the nest reliefs were accompanied by long bouts. Variability in calling length during nest relief was also recorded in semipalmated sandpipers and in northern lapwings, where the vocalizations also differed between females and males (Sládeček et al. 2019, Bulla et al. 2022).

Between-nest variation in call frequency

The frequency of independent acoustic events differed between nests for all call types. The few studies comparing the number of calls between individuals (Guillette and Sturdy 2011, Bulla et al. 2016, Sládeček et al. 2019) suggest that such differences might be related to personality traits, sex, variable incubation lengths, or variation in the species' life histories.

Although the observed nests were close to each other and thus likely exposed to the same predator pressure, individuals at different nests considerably differed in the use of staccato calls, which seem related to warning of the presence of a predator (Supporting information). As shown in Fig. 6c–d, the number of actively warning godwits in the neighbourhood increases the likelihood that an incubating bird will leave its nest and join the mobbing behaviour, similar to what has been observed in redshanks (Cresswell et al. 2000). This, then, raises the question of who the intended receiver of the call is – the partner of the calling bird, conspecifics, or even individuals of other species – and what motivates the incubating bird to warn others? Godwits might benefit from warning more neighbours because they then could all join the mobbing of the predator (Igic et al. 2019, Carlson and Griesser 2022). On the other hand, too many warnings for predators that are not a direct risk followed by leaving the nest could lengthen the total incubation period or negatively affect hatching success. Note that the highest levels of staccato calls were at nests close to the small water pools, places which could attract predators and other bird species, thus triggering the warning behaviour of nesting godwits.

Are godwits vocally cryptic at the nest?

In contrast to the expected cryptic behaviour, incubating godwits often used three different types of loud calls and two quiet calls while near or at their nest. However, at night they used fewer calls of only one loud and one quiet type, with most calls occurring on bright nights with full moon. These results suggest that on nights without moonlight when visibility would be reduced, incubating godwits minimize acoustic cues. Do they do this to avoid detection by predators that are harder to spot from a distance?

Our observations come from a dense community of breeding godwits, which daytime aerial predators should easily be able to locate, even if all godwits remain silent. Thus, staying vocally cryptic may be ineffective against primarily visually oriented avian predators, but vocalizations may help communicate predator presence to other community members; together, individuals may successfully mob them off. It is hard to determine if the daily calls are frequent enough to be used as an acoustic cue for nest location by the occasional day-active mammalian predator like the stoat (Teunissen et al. 2008). The situation may well differ in areas with lower nest densities where individuals may be less effective at detecting and deterring predators and therefore might behave more cryptically.

Birds at nests appeared to be actively involved in predator warning during daylight, but the number of warning calls varied considerably between nests. This raises the question of how individual experience or the position of a nest relative

to other breeding birds influences participation in warning behaviour. The function and benefits of rhythmic, repetitive, and two types of quiet calls for incubating birds, especially during the pre-hatching period, remain unclear. To better understand the calling behaviour of godwits and other shorebirds at nests, it is essential to study the vocal behaviour of individuals in different contexts, using contrasts in nest density, habitat structure, and predator occurrence.

Acknowledgements – This work would not have been possible without Murk Nijdam, who provided us with accommodation at his farm during the whole research period and allowed us to go to his fields daily. Moreover, there would be no similar place with such high densities of godwits to study without his godwit-friendly (life) farming management. Searching for nests would not be as efficient without the help of volunteers Teade de Boer, Jelle Rienk Hibma, Atser Sybrandy, and Eddy de Boer.
Funding – This work was supported by research funds to TP at the University of Groningen and by the Max Planck Society to BK.

Author contributions

Ondřej Belfín: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Bart Kempenaers**: Conceptualization (equal); Funding acquisition (equal); Writing – review and editing (equal). **Theunis Piersma**: Conceptualization (equal); Funding acquisition (equal); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.m37pvmdc2 (Belfín et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Araya-Salas, M. and Smith-Vidaurre, G. 2017. warbleR: an R package to streamline analysis of animal acoustic signals. – Methods Ecol. Evol. 8: 184–191.
Belfín, O., Kempenaers, B. and Piersma, T. 2024. Data from: Daily and seasonal use of vocalizations by nesting black-tailed godwits. – Dryad Digital Repository, https://doi.org/doi:10.5061/dryad.m37pvmdc2.
Bergmann, H.-H., Helb, H.-W. and Baumann, S. 2008. Die Stimmen der Vögel Europas 474 Vogelporträts mit: 914 Rufen und Gesängen auf 2200 Sonagrammen. – Aula-Verlag.
Bulla, M. et al. 2016. Unexpected diversity in socially synchronized rhythms of shorebirds. – Nature 540: 109–113.
Bulla, M., Muck, C., Tritscher, D. and Kempenaers, B. 2022. Nest reliefs in a cryptically incubating shorebird are quick, but vocal. – Ibis 164: 1013–1034.
Burger, J. and Olla, B. L. (eds). 1984. Shorebirds: breeding behavior and populations. – Springer.
Carlson, N. V. and Griesser, M. 2022. Mobbing in animals: a thorough review and proposed future directions. – In: Healy, S. and Podos, J. (eds), Advances in the study of behavior. – Academic Press, pp. 1–41.
Caro, T. 2005. Antipredator defenses in birds and mammals. – Univ. of Chicago Press.
Cramp, S. and Simmons, K. E. L. 1983. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western Palearctic. – Oxford Univ. Press.
Cresswell, W., Hilton, G. M. and Ruxton, G. D. 2000. Evidence for a rule governing the avoidance of superfluous escape flights. – Proc. R. Soc. B 267: 733–737.
De Felici, L., Piersma, T. and Howison, R. A. 2019. Abundance of arthropods as food for meadow bird chicks in response to short- and long-term soil wetting in Dutch dairy grasslands. – PeerJ 7: e7401.
Deng, J., Dong, W., Socher, R., Li, L.-J., Li, K. and Fei-Fei, L. 2009. ImageNet: a large-scale hierarchical image database. – 2009 IEEE Conference on computer vision and pattern recognition, pp. 248–255.
Dickerson, A. L., Hall, M. L. and Jones, T. M. 2023. Effects of variation in natural and artificial light at night on acoustic communication: a review and prospectus. – Anim. Behav. 198: 93–105.
Glutz von Blotzheim, U. N., Bauer, K. M. and Bezzel, E. (eds). 1977. Handbuch der Vögel Mitteleuropas, Band 7: Charadriiformes (2. Teil). – Akademische Verlagsgesellschaft.
Gochfeld, M. 1984. Antipredator behavior: aggressive and distraction displays of shorebirds. – In: Burger, J. and Olla, B. L. (eds), Shorebirds: breeding behavior and populations. Springer, pp. 289–377.
Guillette, L. M. and Sturdy, C. B. 2011. Individual differences and repeatability in vocal production: stress-induced calling exposes a songbird's personality. – Naturwissenschaften 98: 977.
Haff, T. M. and Magrath, R. D. 2011. Calling at a cost: elevated nestling calling attracts predators to active nests. – Biol. Lett. 7: 493–495.
Hancock, G. R. A., Grayshon, L., Burrell, R., Cuthill, I., Hoodless, A. and Troscianko, J. 2023. Habitat geometry rather than visual acuity limits the visibility of a ground-nesting bird's clutch to terrestrial predators. – Ecol. Evol. 13: e10471.
Hooijmeijer, J., Rakhimberdiev, E., Velde, E., Howison, R., Stessens, M., Kraamwinkel, C., Craft, T., Fokkema, R., Lagendijk, G., Ligtelijn, M., Onrust, J., Saarloos, A., Vansteelant, W., Belfín, O., Basting, S., Zijlstra, N., Verkuil, Y. and Piersma, T. 2024. Grutto Landschap Project Jaarverslag 2023: de staat van ons landschap: biomonitoring van duurzame landbouw innovaties. – Univ. of Groningen.
Humphreys, R. K. and Ruxton, G. D. 2020. Avian distraction displays: a review. – Ibis 162: 1125–1145.
Huxley, J. S. and Montague, F. A. 1926. Studies on the courtship and sexual life of birds. VI. The black-tailed godwit, *Limosa limosa* (L.). – Ibis 68: 1–25.
Ibáñez-Álamo, J. D., Magrath, R. D., Oteyza, J. C., Chalfoun, A. D., Haff, T. M., Schmidt, K. A., Thomson, R. L. and Martin, T. E. 2015. Nest predation research: recent findings and future perspectives. – J. Ornithol. 156: 247–262.
Igic, B., Ratnayake, C. P., Radford, A. N. and Magrath, R. D. 2019. Eavesdropping magpies respond to the number of heterospecifics giving alarm calls but not the number of species calling. – Anim. Behav. 148: 133–143.

Kentie, R., Both, C., Hooijmeijer, J. C. E. W. and Piersma, T. 2014. Age-dependent dispersal and habitat choice in black-tailed godwits (*Limosa limosa limosa*) across a mosaic of traditional and modern grassland habitats. – J. Avian Biol. 45: 396–405.

Kentie, R., Senner, N. R., Hooijmeijer, J. C. E. W., Márquez-Ferrando, R., Figuerola, J., Masero, J. A., Verhoeven, M. A. and Piersma, T. 2016. Estimating the size of the Dutch breeding population of continental black-tailed godwits from 2007–2015 using resighting data from spring staging sites. – Ardea 104: 213–225.

Kostoglou, K. N., van Dongen, W. F. D. and Weston, M. A. 2020. Parental defence in shorebirds is mediated by embryonic calling, ambient temperature and predator latency. – J. Ornithol. 161: 1153–1165.

Lee, D.-Y., Lee, J.-H., Kim, W.-Y. and Sung, H.-C. 2023. Nest-relief behaviors and usage of call types in the Kentish plover (*Charadrius alexandrinus*). – J. Ethol. 41: 231–241.

Lind, H. 1961. Studies on the behaviour of the black-tailed godwit (*Limosa limosa*). – Munksgaard.

Lourenço, P. M., Kentie, R., Schroeder, J., Groen, N. M., Hooijmeijer, J. C. E. W. and Piersma, T. 2011. Repeatable timing of northward departure, arrival and breeding in black-tailed godwits *Limosa l. limosa*, but no domino effects. – J. Ornithol. 152: 1023–1032.

Magrath, R. D., Haff, T. M., Horn, A. G. and Leonard, M. L. 2010. Calling in the face of danger: predation risk and acoustic communication by parent birds and their offspring. – Adv. Stud. Behav. 41: 187–253.

Mariette, M. M. and Buchanan, K. L. 2016. Prenatal acoustic communication programs offspring for high posthatching temperatures in a songbird. – Science 353: 812–814.

Martin, G. R. 2012. Through birds' eyes: insights into avian sensory ecology. – J. Ornithol. 153: 23–48.

Martin, G. R. and Piersma, T. 2009. Vision and touch in relation to foraging and predator detection: insightful contrasts between a plover and a sandpiper. – Proc. Biol. Sci. 276: 437–445.

McDiarmid, C. S., Naguib, M. and Griffith, S. C. 2018. Calling in the heat: the zebra finch 'incubation call' depends on heat but not reproductive stage. – Behav. Ecol. 29: 1245–1254.

Miller, E. H. 1992. Acoustic signals of shorebirds: a survey and review of published information. – Royal British Columbia Museum.

Onrust, J. and Piersma, T. 2017. The hungry worm feeds the bird. – Ardea 105: 153–161.

Peeters, H. 2023. Gruttoland – erfgoed van Murk Nijdam. – Stichting Agrarisch Natuurfonds Fryslân.

Pelech, S. A., Smith, J. N. M. and Boutin, S. 2010. A predator's perspective of nest predation: predation by red squirrels is learned, not incidental. – Oikos 119: 841–851.

Pérez-Granados, C. and Schuchmann, K.-L. 2021. Passive acoustic monitoring of Chaco chachalaca (*Ortalis canicollis*) over a year: vocal activity pattern and monitoring recommendations. – Trop. Conserv. Sci. 14: 19400829211058295.

Piersma, T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. – J. Ornithol. 148 (Suppl. 1): S45–S59.

Reneerkens, J., Piersma, T. and Damsté, J. S. S. 2005. Switch to diester preen waxes may reduce avian nest predation by mammalian predators using olfactory cues. – J. Exp. Biol. 208: 4199–4202.

Richardson, R. A. and Bishop, W. F. 1968. The godwits of Cley. – Trans. Norfolk Norwich Nat. Soc. 25: 284–291.

Santisteban, L., Sieving, K. E. and Avery, M. L. 2002. Use of sensory cues by fish crows *Corvus ossifragus* preying on artificial bird nests. – J. Avian Biol. 33: 245–252.

Seymour, A. S., Harris, S., Ralston, C. and White, P. C. L. 2003. Factors influencing the nesting success of lapwings *Vanellus vanellus* and behaviour of red fox *Vulpes vulpes* in lapwing nesting sites. – Bird Study 50: 39–46.

Shah, S. S., Greig, E. I., MacLean, S. A. and Bonter, D. N. 2015. Risk-based alarm calling in a nonpasserine bird. – Anim. Behav. 106: 129–136.

Sládeček, M., Vozabulová, E., Brynychová, K. and Šálek, M. E. 2019. Parental incubation exchange in a territorial bird species involves sex-specific signalling. – Front. Zool. 16: 7.

Śmielak, M. K. 2023. Biologically meaningful moonlight measures and their application in ecological research. – Behav. Ecol. Sociobiol. 77: 21.

Sung, H.-C., Miller, E. H. and Flemming, S. P. 2005. Breeding vocalizations of the piping plover (*Charadrius melodus*): structure, diversity, and repertoire organization. – Can. J. Zool. 83: 579–595.

Teunissen, W., Schekkerman, H., Willems, F. and Majoor, F. 2008. Identifying predators of eggs and chicks of lapwing *Vanellus vanellus* and black-tailed godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. – Ibis 150: 74–85.

Thieurmel, B. and Elmarhraoui, A. 2019. suncalc: compute sun position, sunlight phases, moon position and lunar phase. R package version 0.5.0. – https://CRAN.R-project.org/package=suncal.

Verhoeven, M. A., Loonstra, A. H. J., McBride, A. D., Macias, P., Kaspersma, W., Hooijmeijer, J. C. E. W., van der Velde, E., Both, C., Senner, N. R. and Piersma, T. 2020. Geolocators lead to better measures of timing and renesting in black-tailed godwits and reveal the bias of traditional observational methods. – J. Avian Biol. 51: jav.02259.

Vickery, P. D., Hunter, M. L. and Wells, J. V. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. – Oikos 63: 281–288.

Wood, S. N. 2017. Generalized additive models: an introduction with R. – Chapman and Hall/CRC.

Yorzinski, J. L. and Platt, M. L. 2012. The difference between night and day: antipredator behavior in birds. – J. Ethol. 30: 211–218.