

Nocturnal vocalizations in diurnal birds: a systematic review of current knowledge, research gaps and future directions

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CONFLICT OF INTEREST

The authors declare no conflict of interest

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Abstract

Nocturnal vocalisations by diurnal birds have been increasingly documented in recent decades, yet the functions and mechanisms underlying this behaviour remain poorly understood. Here, we conducted a systematic review to synthesize the current knowledge regarding nocturnal vocalisations in diurnal birds. The study is structured around 12 non-exclusive hypotheses proposed to explain why diurnal birds vocalise at night. We identified 39 peer-reviewed studies, comprising 92 case studies. The studies were geographically biased towards Europe and North America, with no studies conducted in Africa, Central America, or Antarctica. Most studies focused on passerines (67% of the case studies), males (73% among those reporting sex), songs (69%), and examined a single species (85%). We also found substantial variation among studies regarding what was considered nighttime, which may hinder future comparisons. We found uneven research and support among the 12 considered hypotheses. The hypotheses related to Elevated Light Levels, Mate Attraction, and Predator Avoidance received the strongest empirical support, with more than 80% of assessments supporting these mechanisms. In contrast, hypotheses such as Enhanced Sound Transmission, Reproductive Stimulation, Mate Guarding, and Territory Defence received mixed support. We did not find studies testing two of the proposed hypotheses (Nocturnal Roosting Groups and Pair Bonding). We found evidence that nocturnal vocalisations by diurnal birds are driven by multiple, non-exclusive mechanisms operating under different ecological and social contexts. Our review found that current knowledge regarding nocturnal vocalisations by diurnal birds presents major geographic, taxonomic, and methodological gaps, as well as a lack of standardized definitions. Overall, our review emphasizes a need for further research in this topic, which should prioritize comparative, experimental, and multispecies approaches for improving our understanding regarding the evolutionary and ecological drivers of nocturnal vocal behaviour in diurnal birds.

Keywords:

Acoustic communication, mate attraction, light level, song, vocal behaviour.

Birds use acoustic signals as primary communication systems for mate attraction and territorial defence, although these signals also serve other purposes, such as maintaining group contact and signalling the presence of food or danger (Farnsworth 2005, Catchpole and Slater 2008, Gil and Llusia 2020). Nevertheless, the reasons behind birds' vocal behaviour are still under study (Catchpole and Slater 2008), especially the daily and seasonal variations in bird vocalisations. For example, the vocal behaviour of most diurnal birds exhibits a peak of activity around sunrise ("dawn chorus", Gil and Llusia 2020). However, over the last decade, numerous studies have documented the presence of nocturnal vocalisations in several diurnal birds (Kułaga and Budka 2020, Budka et al. 2021, Alonso et al. 2021, Dickerson et al. 2023, Buda et al. 2025). Indeed, nocturnal vocalisations by diurnal birds is a phylogenetically widespread phenomenon (La 2012), occurring in lineages ranging from ratites (e.g., Pérez-Granados and Schuchmann 2021a, 2021b) to passerines (Foote et al. 2017, Dickerson et al. 2023). For instance, in North America, nocturnal vocalisations were reported in 106 of the 329 diurnal passerines analysed (32.2%, La 2012, and a study in central Europe revealed that approximately 25% of diurnal birds also vocalise at night (Kułaga and Budka 2020). However, a study from the Afrotropical highlands in Cameroon, found that unlike their counterparts in temperate regions, diurnal birds in the region remained silent at night (Budka et al. 2021).

These contrasting patterns across biogeographic regions suggest that nocturnal vocalisations in diurnal birds may be shaped by complex ecological or evolutionary factors, underscoring the need for broader comparative studies. In fact, La (2012) proposed 12 different hypotheses (see Box 1) regarding the possible functions of nocturnal vocalisations of diurnal birds, which are non-exclusive with each other (i.e., a single diurnal species may vocalise at night for multiple reasons, Budka et al. 2021). These 12 hypotheses were originally divided into two groups (La 2012): six in which vocalizing at night provides an advantage over vocalizing during the day (i.e., vocalisations function best at night, hypotheses 1-6 in Box 1), and six in which vocalizing both at night and during day provides an advantage by extending the period of vocal activity (hypotheses 7-12 in Box 1). Despite the growing number of studies published regarding this topic over the last decade, our understanding of why diurnal species vocalise at night remains remarkably limited and fragmented, with evidence scattered across taxa, geographical regions, and methodological

approaches. As a consequence, there is still no comprehensive assessment that synthesizes current knowledge, evaluates the empirical support for the different hypotheses, or determines whether new hypotheses or ideas have emerged owing to the increasing interest in this topic. Here, we aim to synthesize the available information on the reasons behind nocturnal vocalisations of diurnal birds, identify which functional hypotheses are best supported by current evidence, and highlight knowledge gaps and potential new avenues to explain this widespread yet poorly understood behaviour in birds.

Methods

Literature review

We conducted a systematic review of peer-reviewed articles following the PRISMA EcoEvo checklist (O’Dea et al., 2021; See Supplementary Online Material Table S2) and the guidelines of Pullin & Knight (2009). We first searched both Scopus and Web of Science using the following search string: ((night OR nocturnal) AND (call OR song OR vocal* OR acoustic OR sing*)) AND (bird OR ornith* OR avifauna OR passerine OR non-passerine OR avian) AND (diurnal OR day OR daily) NOT migration. We did not consider studies focused on nocturnal vocalisations of diurnal birds during migration, as migratory nocturnal vocalisations represent a distinct behaviour, which has been extensively reviewed previously (see Farnsworth 2005, Osterhaus et al. 2025). We searched the title, abstract and keywords and the search included scientific papers published until the end of November 2025. We considered peer-reviewed publications in all languages. The search yielded 129 articles (excluding duplicates in the Web of Science and Scopus databases).

Then, we screened articles in two stages, first by reading their title and abstract, and then, reading the full text for articles not excluded at the first stage. We included only papers that met our five eligibility criteria, selecting articles that (1) focused on nocturnal vocalisations of diurnal avian species, (2) were not about nocturnal flight calls, (3) included empirical data, (4) were not only anecdotal comments and (5) were not review papers. We identified 93 articles as eligible for full-text screening after examining the title and abstract and 39 articles, all written in English, were finally included in the review. When a single article proposed different functions for nocturnal vocalisations or assessed their function on multiple species, each was treated as a separate case study. An exception was made for two articles that,

although considered multiple species, carried out the analyses at the community level. Therefore, for these two articles, we were unable to gather information at species level to consider separate case studies. Overall, our dataset comprised 92 case studies. Hereinafter, to facilitate reading, we use the term article(s) when referring to information collected at the article level, and case study/studies when referring to the individual analyses or sub-results extracted from each article.

For each reviewed article, we extracted a set of variables of interest that were related to the spatial, temporal and taxonomic distribution of the studies, the way that “nocturnal vocalisation” was defined and the function of the nocturnal vocalisation. The spatial, temporal and taxonomic distribution of the studies was measured by identifying, for each study 1) the country/countries and continent(s) where the fieldwork was done, 2) publishing year, 3) species studied, 4) order, and 5) sex of the sampled individuals. We also identified 6) if the species is a song-learner or not, and 7) if the study focused on calls, songs or both. We further extracted (8) how nighttime was defined, including the criteria used to determine its onset and end, whether definitions were based on fixed clock times or solar position, and, where available, the exact temporal boundaries or offsets relative to sunset and sunrise. Finally, to describe the possible functions of nocturnal vocalisations we identified 9) which ones of the 12 hypotheses identified by La (2012) were tested in the study and 10) whether the data supported the hypothesis or not and 11) a description of the effect found. See full list of variables considered in Supplementary Online Material Table S3.

Results

Spatial, temporal and taxonomic patterns

Spatial coverage

The nocturnal vocalisations of diurnal birds have been studied across 17 countries (Figure 1A), mostly in a single country (37 out of 39 articles, 94.9%, Database S1). Europe was the region with the highest number of articles (48.7%, N=19), followed by North America (20.5%, N=8), Oceania (17.9%, N=7), South America (7.7%, N=3), and Asia (5.1%, N=2). No studies were conducted in Africa, Antarctica or Central America. The four most represented countries accounted for 51.3% of all articles (N=20): Australia (17.9%, N=7),

the United States of America (10.3%, N=4), the United Kingdom (12.8%, N=5), and Canada (10.3%, N=4).

Temporal coverage

There was an increasing trend in the number of published articles over time (Figure 1B). Three distinct periods were identified: (i) from 1977 to 1999, an initial period characterized by sporadic publication activity, during which only five articles (out of 39) were published (average rate of 0.2 articles per year); (ii) from 2000 to 2019, a period marked by a sustained increase in research output, during which 16 articles were published (average rate of 0.80 article per year); and (iii) from 2020 to 2025, a period characterized by the highest publication rate, during which 18 articles were published (average rate of 3 articles per year).

Taxonomic group, sex and species coverage

Species coverage was generally narrow, with 33 of the 39 articles (84.6%) focusing on one species, three articles included two species (7.7%), whereas the remaining studies considered nine (N=1), 21 (N=1), and 36 species (N=1) (Figure 1C). The studies covered 74 different species, 34 (45.9%) of which are non-vocal learners. A total of eight avian orders were represented in the dataset. Passeriformes were by far the most frequently represented order (67.4%, N=63 of 92 case studies). Among the remaining orders, Cuculiformes (5.4%, N=5), Otidiformes (5.4%, N=5), and Tinamiformes (5.4%, N=5) were the only orders represented by more than four case studies (see Supplementary Online Material Table S1 for the complete taxonomic breakdown). The sex of the study individuals was not reported in more than one quarter of all case studies (27.1%, N = 25 of 92). Among the 67 case studies that specified sex, research was strongly biased towards males (49 case studies, 73.1%), compared with 17 case studies including both sexes (25.4%), and only one focused on females (1.5%). Most studies focused on songs (69.2%), while the remaining studies examined calls, with only one article addressing both songs and calls.

Night definition

Of the 39 studies reviewed, 13 (33.3%) did not provide an explicit definition of nighttime. The definition of the survey period in the remaining 26 studies can be grouped in two main

approaches. The first group of articles provided detailed clock times when the nocturnal survey was carried out (14 studies; 35.9%), with survey periods ranging from 2 to 9 h in duration (mean = 5.0 h). The second group of articles defined nighttime relative to solar position (12 studies; 30.7%). Nine of the 12 studies monitored birds' vocal activity during the entire night, although there were variable definitions of nighttime. In two studies (5.1%) nighttime was defined as astronomical night (the sun more than 18° below the horizon), in five studies (12.8%) was considered the nautical night (5 studies; the sun more than 12° below the horizon), in one study (2.5%) the civil night (the sun more than 6° below the horizon), and in another one (2.5%) nighttime was considered as the interval between sunset and sunrise. In the remaining three articles defining night regarding solar position, birds' vocal activity was monitored only during a certain period. In one article (2.5%), nighttime was defined as the period from 40 min after evening civil twilight to 40 min before morning civil twilight, whereas the two remaining studies (5.1%) considered night as the period from one to four hours after sunset or as the period beginning four hours after sunset.

Function of the nocturnal vocalisation

Group 1: Hypotheses in which vocalizing at night provide unique advantages.

Elevated Light Levels

Seventeen case studies (13 articles, six focused on passerines and three at the community level) addressed the hypothesis that birds may vocalise at night because elevated natural or artificial light can trigger neurological pathways associated with the onset of vocal activity (Figure 3). Overall, 13 of the 17 case studies reported evidence or stated that the patterns found were consistent with the hypothesis, whereas four did not. More specifically, 15 case studies statistically tested the hypothesis, among which 12 provided statistical support (80% of assessments, Figure 3). All case studies that supported the hypothesis found a positive and significant relationship between nocturnal vocal activity and moon illumination, except for a case study relating higher nocturnal singing in areas with higher artificial light pollution (Fuller et al. 2007). The three case studies that did not support the hypothesis, but explicitly tested it, found the opposite pattern; with the three monitored species singing less frequently on nights with higher moon illumination (Foote et al. 2017, Broad et al. 2024).

Reduced Acoustic Competition

Six case studies (five articles), including five focused on passerines, addressed the hypothesis that diurnal birds may vocalise at night to take advantage of the reduced masking effect owing to anthropogenic and heterospecific sounds (Figure 3). In four case studies, the authors proposed reduced acoustic competition at night as a potential driver of nocturnal vocal activity without testing it. Among the two studies that tested the hypothesis, only one provided statistical support (50% of assessments, Figure 3). Broad et al. (2024) found that jackdaws (*Corvus monedula*) vocalised more at night at locations where overnight background noise levels were higher, although this pattern may likely reflect increased vocal activity following human disturbance at such locations. Fuller et al. (2007) found that European robins (*Erithacus rubecula*) sang more at night at those locations with significantly higher diurnal noise levels, supporting the hypothesis that nocturnal vocalisations may be a response to avoid acoustic masking from daytime noise.

Enhanced Sound Transmission

Seven case studies (five articles), including three focused on passerines, addressed the hypothesis that birds may vocalise at night because atmospheric conditions at night, such as stable and cooler atmospheres and low turbulence, may enhance sound transmission and therefore improve signal propagation (Figure 3). We found three case studies in which the authors proposed improved sound transmission as a potential driver of nocturnal vocal activity in diurnal birds, without any statistical assessment supporting these assumptions. However, among the remaining four case studies that explicitly tested the hypothesis none provided support for it (Figure 3). In fact, two case studies found significant relationships, but in the opposite direction to that expected. For example, Broad et al. (2024) found that jackdaws vocalised more during colder nights, when birds were closer together, and under windier nights, when birds slept for less time, potentially reflecting increased nocturnal vocal activity under more disruptive conditions.

Predator Avoidance

Seven case studies (six articles), four focused on passerines, one on a galliform, and two at the community level, addressed the hypothesis that diurnal birds may vocalise at night

because reduced visibility during this period could decrease the likelihood of revealing their location and, consequently, reduce predation risk (Figure 3). All case studies provided support for the hypothesis, including six that explicitly tested it (100% of assessments, Figure 3). Two articles found that nocturnal singing by diurnal birds was more frequent in open habitats than in forests. More species sang at night at sites where diurnal predators were present, whereas the presence of night-active predators was associated with reduced nocturnal singing. (Kulaga and Budka 2020, Buda et al. 2025). Notably, this hypothesis has also been tested experimentally on four occasions using diurnal and nocturnal playbacks. For example, Buda et al. (2024) found that, in contrast to the diurnal experiment, neither the Yellowhammers (*Emberiza citrinella*) nor Common chaffinches (*Fringilla coelebs*) responded vocally to nocturnal playback. The authors proposed that this differential response might be related to the increased risk of predation at night, as nocturnal playbacks of either species' songs caused predators to approach, whereas this was not observed during the day. Similarly, in an experimental study with Indian peafowl (*Pavo cristatus*), Yorzinski and Platt (2012) found that, as a response towards a potential predator, individuals emitted loud antipredator calls during the day but soft hissing calls at night. Hissing calls are very soft but may allow Indian peafowls to communicate with nearby conspecifics while minimizing the risk of advertising their location to distant predators. Moreover, the authors also suggested that hissing calls may mimic the hissing of a snake, potentially deterring predators.

Nocturnal Roosting Groups

No case studies were found addressing the hypothesis that paired individuals may vocalise at night to strengthen social bonds when other activities are not possible.

Group 2: Vocal functions enhanced by extending vocal activity into night

Territory Defence

Sixteen case studies (14 articles), 12 focused on passerines, addressed the hypothesis that territorial species may vocalise during the night to defend valuable breeding sites by deterring nocturnal intruders or prospecting migrants, when visual cues are ineffective (Figure 3). Among them, ten case studies reported evidence or stated that the patterns found were consistent with the hypothesis, whereas six did not. Nine case studies explicitly tested the

hypothesis, among which five found relationships consistent with the territory defence hypothesis (56% of assessments, Figure 3), including three experimental studies using nocturnal playback experiments that elicited nocturnal responses to simulated territorial intrusions (Schmidt et al. 2007, Dickerson et al. 2023). Other evidence included Thrush nightingales (*Luscinia luscinia*) uttering territorial calls, but not courtship songs, during the night (Sorjonen 1977). The remaining four case studies that explicitly tested the hypothesis found no relationship, although these assessments were mainly based on comparing seasonal patterns of nocturnal vocal activity rather than experimental approaches.

Mate Attraction

Twenty-six case studies (from 24 articles), including 22 focused on passerines, addressed the hypothesis that birds may vocalise at night to increase opportunities to attract mates, particularly for individuals moving at night (Figure 3). Twenty-three case studies reported evidence or stated that the patterns found were consistent with the hypothesis, whereas three did not. Among the 21 case studies that explicitly tested the hypothesis, all but one provided some form of support (95% of assessments, Figure 3). Support came from two main patterns: a) studies showing that nocturnal vocal activity was associated with periods of mate acquisition or female mate-searching, finding males singing more during the night after spring arrival and reducing nocturnal singing activity during incubation but resuming it after breeding failure or hatching, while unmated males maintained high levels of nocturnal vocal activity throughout the breeding season (Amrhein et al. 2002, Roth et al. 2009), b) studies describing seasonal changes in nocturnal song patterns consistent with the hypothesis, finding diurnal birds vocalizing more at night during the first phase of the breeding season, suggesting that nocturnal singing was more closely associated with mate attraction than with territory defence (Foote et al. 2017, Pérez-Granados et al. 2021a). The only study that tested the hypothesis and did not support it found that the peak of nocturnal singing of Ovenbirds (*Seiurus aurocapilla*) was displaced towards the middle of the breeding season (Foote et al. 2017).

Pair Bonding

No case studies were found addressing the hypothesis that paired individuals may vocalise at night to strengthen social bonds when other activities are not possible.

Reproductive Stimulation

Five case studies (four articles, focused on passerines) addressed the hypothesis that diurnal birds may vocalise at night to stimulate physiological investment in mates, potentially influencing hormone levels, egg size, or clutch mass (Figure 3). Three articles did not report evidence in agreement with the hypothesis. In fact, among the four case studies that explicitly tested this hypothesis, only two provided support for it (50% of assessments, Figure 3). For example, Dickerson et al. (2023) found that Willie wagtail (*Rhipidura leucophrys*) males showed increased song nocturnal behaviour during fertile periods of resident females. Similarly, Foote et al. (2017) reported significant increased nocturnal singing during the first phase of the breeding season for White-throated sparrows (*Zonotrichia albicollis*) but not for Ovenbirds.

Mate Guarding

Four case studies, from three articles all focused on passerines, addressed the hypothesis that males may vocalise at night during the female's fertile period to deter rivals, reducing the risk of extra-pair copulations under low-light conditions (Figure 3). Two case studies reported that nocturnal singing may be related to mate guarding, but among the three case studies that explicitly tested this hypothesis, only one provided statistical support for it (33% of assessments, Figure 3).

Song Learning by offspring

Two case studies (both corresponding to a single article focused on passerines) addressed the hypothesis that parents may vocalise at night because their fledglings may benefit from increased exposure to species-typical vocalisations during sensitive learning periods later in the breeding season (Figure 3). Both case studies explicitly tested this hypothesis with Ovenbirds and White-throated sparrows, but none of them provided statistical support for it (Figure 3), since no peaks of nocturnal vocal activity were found after the end of the breeding period (Foote et al. 2017).

Continued Effort

Within this group of hypotheses related to extending vocal activity into night, two articles proposed a new hypothesis, not considered by La (2012), suggesting that nocturnal vocalisations may represent a continuation of diurnal vocal activity efforts, regardless of the specific function of these vocalisations (Figure 3). The Continued Effort hypothesis was tested in two case studies with non-passerines. Alonso et al. (2021) found a positive and significant relationship between diurnal and nocturnal booming of male African houbara bustards (*Chlamydotis undulata fuertaventurae*) on the same day (Figure 3), whereas Pérez-Granados and Schuchmann (2021a) found no significant relationship between the two times of the day in the Undulated Tinamou (*Crypturellus undulatus*).

DISCUSSION

What has been studied?

Spatial and temporal coverage

Here, we provide the first review synthesizing current scientific knowledge on the nocturnal vocalisations of diurnal birds at a global scale. Our review reveals that interest in this topic has increased in recent years, particularly since 2020, mirroring the increase in the number of scientific papers published annually. This increase may partly reflect growing availability of low-cost sound recorders, which were used in a large proportion of studies published since 2020. We also found a clear spatial bias in the distribution of the studies covering this topic, with research focused in only 17 countries, mostly in Europe and North America (70% of studies). In contrast, very few studies were conducted in other regions, with the complete absence of research from Africa, Antarctica and Central America. This global geographical bias is consistent with patterns identified in previous reviews of ecoacoustics, which likely reflects the geographical distribution of the main research groups (Alcocer *et al.*, 2022, Sebastián-González and Pérez-Granados 2025). Further support for this interpretation comes from Australia, the country with the largest number of studies (N=7, 17.9% of the total), which also has a strong and long-standing research tradition in ecoacoustics (e.g., Vella *et al.*, 2022).

Taxonomic group, sex and species coverage

Most research on nocturnal vocalisations of diurnal birds has used passerines as study models (>68% of case studies), although eight avian orders were represented in the dataset. This result is consistent with previous reviews addressing different ecoacoustic topics, in which passerines are commonly overrepresented compared with other avian orders (Engel et al. 2024). The predominance of passerines might be partly explained because they represent a highly diverse and very vocally active avian lineage. Nevertheless, our review also included several studies conducted on early-diverging avian lineages, such as tinamous and rheas (Pérez-Granados and Schuchmann 2021a, 2021b), providing evidence that nocturnal vocalisations may have originated early in the evolutionary history of birds.

Research was strongly biased towards males (73.1%), with only one focusing exclusively on females (Yorzinski and Platt 2012). This bias is likely explained by the predominance of studies conducted in Europe and North America, where female song is generally less studied and less conspicuous than male song in comparison to tropical areas (Slater & Mann, 2004; but see Garamszegi et al., 2007). A striking result is that almost a quarter of the case studies did not report the sex of the monitored individuals, which may hinder comparisons among studies, our understanding regarding the functions of nocturnal vocalisations and limit the possibility of conducting meaningful meta-analyses in the near term.

Finally, we also found that 85% of the articles focused on a single species. There were only two articles (5% of the total) considering more than ten species, although in both articles the analyses testing the potential function of nocturnal vocalisations were carried out at the community level (Kułaga and Budka 2020, Buda et al. 2025). It would be particularly valuable that further research involving a large number of species aim for comparative approaches, among species and testing multiple hypotheses, which could help identify why some species vocalise at night whereas others do not. Such studies could also contribute to determining whether nocturnal vocal activity is related to phylogeny (but see La 2012) or associated with specific life-history traits and ecological characteristics.

What is night?

A notable finding of our review is the lack of a consistent definition of nighttime. One-third of the reviewed articles did not explicitly define nighttime, while more than half of those that provided a definition relied on fixed local clock times. Such definitions are difficult to compare across latitudes, seasons and dates because the same clock time may correspond to different ambient light levels and solar elevations. Definitions based on solar position are more reproducible, although the reviewed studies applied variable different twilight thresholds, ranging from the period between sunset and sunrise, which includes the dusk and dawn choruses, to astronomical night, when the sun is more than 18° below the horizon. This methodological heterogeneity may affect estimates of nocturnal vocal activity and limit comparisons among studies. For example, applying astronomical rather than civil night as the threshold may substantially reduce the number of diurnal species classified as vocalizing at night (e.g. Budka et al. 2021). We therefore recommend defining nighttime using explicitly stated solar-elevation thresholds and reporting the geographical coordinates and sampling dates. Such standardization would facilitate comparisons across regions and seasons and support future quantitative syntheses.

Why do diurnal birds vocalise at night?

Functions

Our review provides the first comprehensive synthesis of the functions and mechanisms proposed to explain nocturnal vocalisations in diurnal birds. It is important to highlight that we focused on the mechanisms rather than identifying which species vocalise at night or how prevalent nocturnal vocalisations are in diurnal birds. We found substantial variation in the extent to which the hypotheses proposed by La (2012) have been considered across the literature. Eight hypotheses have been cited in seven or fewer case studies, and some of them, such as the Pair Bonding and Nocturnal Roosting Groups hypotheses, have never been evaluated. In contrast, the other three hypotheses, Elevated Levels, Mate Attraction, and Territory Defence have each been examined in > 16 case studies. Two case studies assessed whether nocturnal vocal activity was related to vocal activity during the preceding day, as a potential explanation for the “Continued effort” hypothesis, a mechanism not explicitly stated

by La (2012). This imbalance limits our ability to draw robust conclusions about the relative importance of most hypotheses, making it difficult to advance our understanding of the mechanisms underlying nocturnal vocalisations.

The uneven and limited research on this topic becomes even more evident when considering that more than one quarter of the case studies included in our review (24, 26% of the total) did not explicitly test any hypothesis, but instead discussed potential mechanisms based on observations and interpreted patterns. Thus, for some hypotheses, a substantial proportion of the evidence was inferred rather than evaluated. This limitation is particularly pronounced because seven of the 11 hypotheses proposed by La (2012) have been examined in four or fewer case studies, whereas only two, Mate Attraction and Elevated Light Levels, have been tested in more than 10.

Overall, we found that the evidence does not support a single universal mechanism underlying nocturnal vocalisations in diurnal birds. Multiple hypotheses have received empirical support, sometimes even within the same case study (e.g., Fuller et al. 2007, Pérez-Granados and Schuchmann 2021a), consistent with the non-exclusive nature of the mechanisms proposed by La (2012). The strength of the evidence, considering only those case studies with scientific tests, differed markedly among hypotheses. The Elevated Light Levels, Predator Avoidance, and Mate Attraction hypotheses showed the strongest empirical support (>80% of case studies provided supporting evidence in favour of the hypotheses), whereas the other six hypotheses were supported by less than 50% of the case studies considered. Considering only case studies that explicitly tested the proposed mechanisms, the same three hypotheses received the strongest support (>80% of tests), whereas the remaining hypotheses received support in fewer than 50% of the tests. Nonetheless, the variable evidence support for some mechanisms should be interpreted cautiously, particularly since it is based on a small number of explicit tests.

The importance of explicitly testing hypotheses is further illustrated by the contrast between observational and empirical support for some of them. This importance is well illustrated for the Enhanced Sound Transmission hypothesis: three case studies inferred a positive relationship between calm nocturnal weather conditions and nocturnal singing, yet none of the four case studies that explicitly tested this hypothesis found supporting evidence. In fact, these four case studies found a significant relationship but in the opposite direction,

showing higher nocturnal vocal behaviour on nights with worse weather conditions. Broad et al. (2024) explained this pattern by increased disturbance during the sleeping period, and consequently higher nocturnal singing. This case represents a complete shift from apparent support when observational evidence is considered to no empirical support when the hypothesis is formally tested. Such discrepancies suggest that there is a need to increase the number of studies explicitly testing the different hypotheses, which will be essential to advance our understanding of the functions and mechanisms underlying nocturnal vocalisations in diurnal birds. Further research should especially aim to assess those hypotheses not yet tested, such as Pair Bonding and Nocturnal Roosting Groups. We acknowledge that some mechanisms, such as whether nocturnal vocalisations are related to Pair Bonding, Reproductive Stimulation, or Mate Guarding, are particularly difficult to disentangle using observational approaches alone and could require detailed experimental designs. Such designs may combine emerging approaches, such as devices able to record sound and video simultaneously (Guggenberger et al. 2024) or GPS data, to provide new opportunities to link nocturnal vocal activity with individual behaviour and social interactions, thereby helping to test these mechanisms more directly.

Conclusions and future research

Our review provides strong evidence that nocturnal vocalisations in diurnal birds can be explained by multiple mechanisms operating either simultaneously or under different ecological and social contexts. However, their relative importance and generality remain difficult to assess because research on this topic is still limited. Elevated Light Levels, Predator Avoidance, and Mate Attraction received the highest empirical support, but this pattern should not necessarily be interpreted as evidence that these mechanisms are universally more important, as alternative hypotheses remain poorly studied or entirely untested. Indeed, some hypotheses proposed more than a decade ago have received little or no empirical attention despite continued discussion in the literature, highlighting a significant mismatch between theoretical development and empirical evaluation. Technological advances, including sound recorders, camera traps, and GPS data, offer new opportunities to overcome many of the current limitations. Combined with experimental manipulations, behavioural observations, and environmental data, these approaches could allow mechanisms

that are currently difficult to distinguish, such as Pair Bonding, Mate Guarding, and Reproductive Stimulation, to be tested more directly.

A substantial proportion of the literature interpreted observed patterns as being consistent with particular hypotheses without explicitly testing alternative explanations. These interpretations sometimes differed from the conclusions of studies in which hypotheses were formally evaluated. Understanding the relative importance of the different mechanisms explaining why diurnal birds vocalise at night requires a shift from a collection of species-specific observations towards multispecies comparative approaches that evaluate competing hypotheses under comparable methodological frameworks. A key component of this transition will be the integration of experimental studies, including playback experiments (Dickerson et al. 2023, Buda et al. 2024) and manipulations of relevant environmental (e.g., light levels and background noise) or social conditions (e.g., presence or removal of breeding individuals), which will help to disentangle the relative contribution of the different mechanisms and facilitate comparisons among studies.

The field would also benefit from a broader taxonomic and geographic scope as well as greater attention to females, as current research is dominated by temperate regions, passerines and males. This limitation is particularly important, given that female participation in nocturnal vocal activity may be more pronounced in tropical species (Langmore 1998), and the current narrow scope restricts our ability to determine whether the patterns identified here represent general drivers of nocturnal vocal activity or lineage-specific patterns. Methodological standardization in further research is also essential to facilitate meaningful comparisons across studies and allow future meta-analyses. Researchers should clearly report the sex of vocalizing individuals and, where possible, present results separately by sex; define the type and timing of vocalisations, and provide a consistent definition of night. Likewise, reporting ambient light and background noise levels, as well as the breeding status of monitored individuals, would improve the comparability of studies and help disentangle the ecological and environmental factors shaping nocturnal vocal activity of diurnal birds.

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Box 1. Brief summary and grouping of the 12 hypotheses proposed by La (2012) regarding the functions of nocturnal vocalisations in diurnal birds. Hypotheses are grouped according to whether nighttime conditions provide unique advantages (Group 1) or whether extending daytime functions into nighttime increases their effectiveness (Group 2).

Group 1: Hypotheses in which vocalizing at night provide unique advantages

Elevated Light Levels: Birds may vocalise at night because elevated natural or artificial light (e.g., moonlight or urban light) can trigger neurological pathways associated with the onset of vocal activity, particularly in species with high retinal sensitivity or large eyes.

Reduced Acoustic Competition: Birds may vocalise during the quieter nighttime hours because, under these conditions, signal transmission is improved and avoids masking from anthropogenic or heterospecific sources.

Enhanced Sound Transmission: Stable nighttime atmospheres, temperature inversions, and low turbulence allow signals to travel farther. Birds may vocalise at night to take advantage of such conditions.

Nocturnal Calling in Migration: Diurnal species may vocalise while migrating at night, by producing flight or contact calls, to maintain group cohesion, coordinate movements, and locate suitable stopover sites.

Predator Avoidance: By vocalizing at night, birds may reduce the likelihood of revealing their location and therefore the risk of predation.

Nocturnal Roosting Groups: Diurnal birds may vocalise at night to coordinate group activities, maintain cohesion, or mediate social interactions within nocturnal roosts.

Group 2: Vocal functions enhanced by extending vocal activity into night

Territory Defence: Territorial species may vocalise at night to defend valuable breeding sites by deterring nocturnal intruders or prospecting migrants, when visual cues are ineffective.

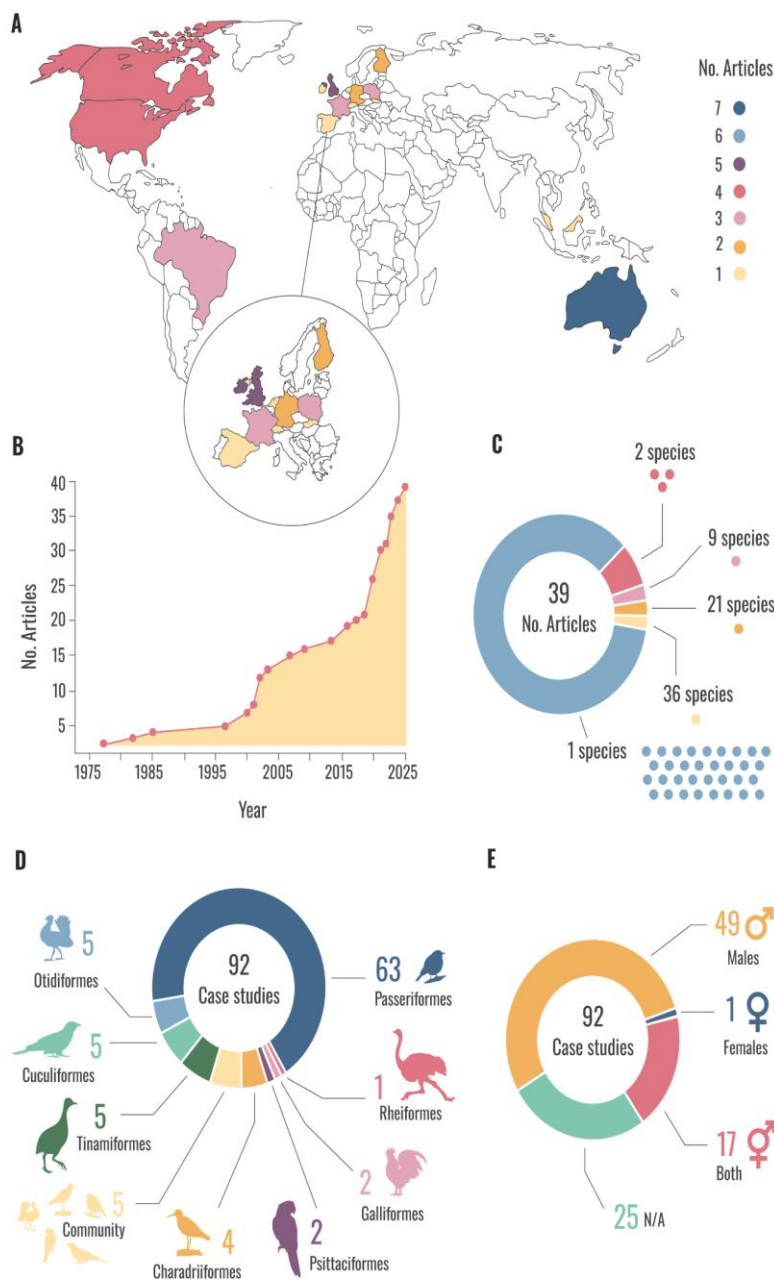
Mate Attraction: Vocalizing at night may increase opportunities to attract mates, particularly for those migrating or moving at night.

Pair Bonding: Paired individuals may vocalise at night to strengthen social bonds, when other activities (e.g., foraging) are not possible.

Reproductive Stimulation: Individuals may vocalise at night to stimulate physiological investment in mates, influencing hormone levels, egg size, or clutch mass.

Mate Guarding: Males may vocalise at night during the female's fertile period to deter rivals, reducing the risk of extra-pair copulations under low light conditions.

Song Learning by Offspring: Parents may vocalise at night because their fledglings may benefit from increased exposure to species-typical vocalisations during sensitive learning periods later in the breeding season.



650 Figure 1: Summary of the articles included in the review. (A) Geographic distribution of the
651 articles according to the country where data were collected, colours indicate the number of
652 published articles per country. (B) Accumulated number of published articles over time. (C)
653 Number of species monitored per article, number of circles indicates the number of articles.
654 (D) Number of case studies by Order. (E) Number of case studies according to the sex of the
655 monitored individuals.

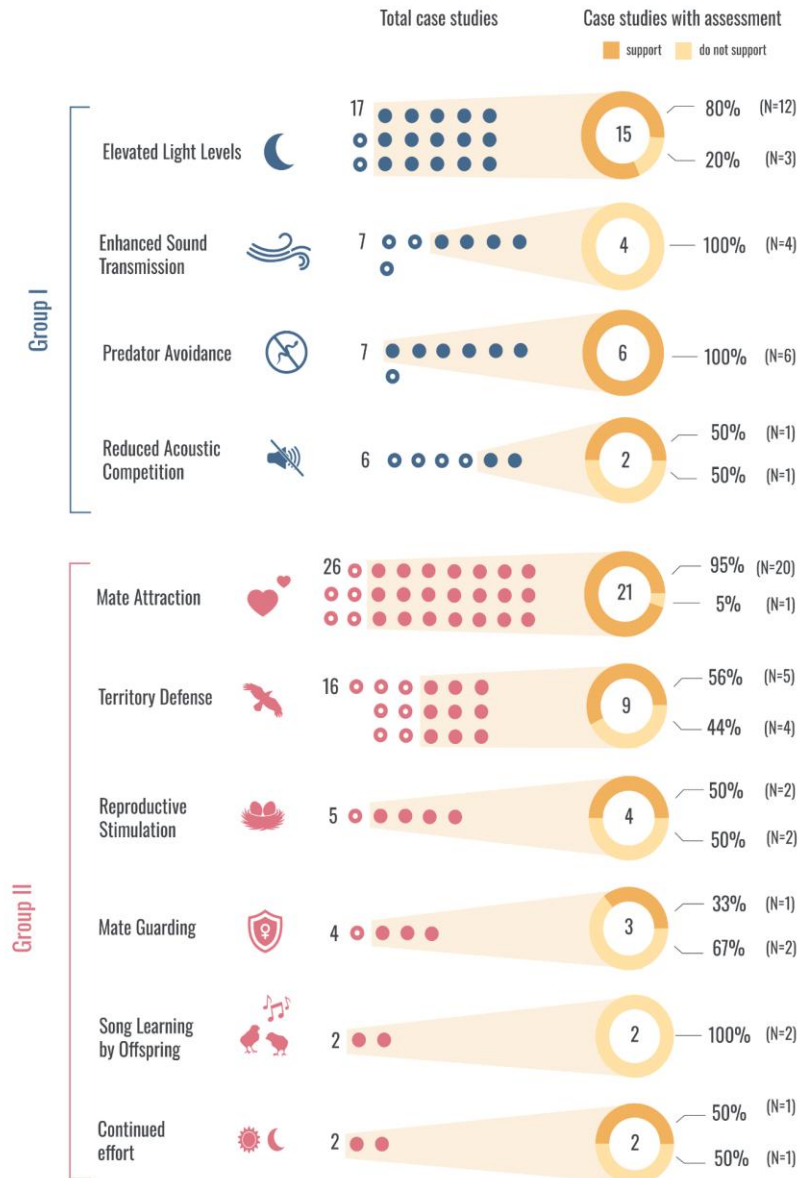


Figure 2: Summary of the evidence supporting the main hypotheses proposed to explain nocturnal vocalisations in diurnal birds, grouped according to the two functional categories defined by La (2012, see Box 1). For each hypothesis, the left panel indicates the total number of case studies documenting the hypothesis, whereas the right panel shows the subset of case studies that evaluated the hypothesis using a formal test. Dark orange segments represent the proportion of assessed case studies that supported the predicted relationship, whereas light orange segments refer to those case studies that did not support the hypothesis. Percentages and corresponding numbers of case studies (N) are provided alongside each hypothesis.

Supplementary Online Material Table S1: Distribution of the 92 case studies across avian orders, ranked by frequency. The percentage of the total dataset represented by each order, and the cumulative percentage are also shown. *Studies carried out at the community level.

Order / category	Number of case studies	Percentage of case studies	Cumulative percentage
Passeriformes	63	68.5%	68.5%
Community level*	5	5.4%	73.9%
Cuculiformes	5	5.4%	79.3%
Otidiformes	5	5.4%	84.8%
Tinamiformes	5	5.4%	90.2%
Charadriiformes	4	4.3%	94.6%
Galliformes	2	2.2%	96.7%
Psittaciformes	2	2.2%	98.9%
Rheiformes	1	1.1%	100.0%
Total	92	100.0%	100.0%

Supplementary Online Material Table S2: PRISMA EcoEvo checklist (O'Dea *et al.*, 2021).

Checklist item	Sub-item number	Sub-item	Reported by authors?	Notes
Title and abstract	1.1	Identify the review as a systematic review, meta-analysis, or both.	Yes	
	1.2	Summarise the aims and scope of the review.	Yes	
	1.3	Describe the data set.	Yes	
	1.4	State the results of the primary outcome.	Yes	
	1.5	State conclusions.	Yes	
	1.6	State limitations.	Yes	
Aims and questions	2.1	Provide a rationale for the review.	Yes	
	2.2	Reference any previous reviews or meta-analyses on the topic.	NA	There are no previous reviews or meta-analyses on the topic.
	2.3	State the aims and scope of the review (including its generality).	Yes	
	2.4	State the primary questions the review addresses (e.g. which moderators were tested).	Yes	
	2.5	Describe whether effect sizes were derived from experimental and/or observational comparisons.	NA	The study does not calculate effect sizes
Review registration	3.1	Register review aims, hypotheses (if applicable), and methods in a time-stamped and publicly accessible archive and provide a link to the registration in the methods section of the manuscript. Ideally registration occurs before the	No	

		search, but it can be done at any stage before data analysis.		
	3.2	Describe deviations from the registered aims and methods.	NA	The paper was not previously registered.
	3.3	Justify deviations from the registered aims and methods.	NA	The paper was not previously registered.
Eligibility criteria	4.1	Report the specific criteria used for including or excluding studies when screening titles and/or abstracts, and full texts, according to the aims of the systematic review (e.g. study design, taxa, data availability).	Yes	
	4.2	Justify criteria, if necessary (i.e. not obvious from aims and scope).	NA	The criteria were obvious from the aims and scope.
Finding studies	5.1	Define the type of search (e.g. comprehensive search, representative sample).	Yes	
	5.2	State what sources of information were sought (e.g. published and unpublished studies, personal communications).	Yes	
	5.3	Include, for each database searched, the exact search strings used, with keyword combinations and Boolean operators.	Yes	
	5.4	Provide enough information to repeat the equivalent search (if possible), including the timespan covered (start and end dates).	Yes	

Study selection	6.1	Describe how studies were selected for inclusion at each stage of the screening process (e.g. use of decision trees, screening software).	Yes	
	6.2	Report the number of people involved and how they contributed (e.g. independent parallel screening).	Yes	
Data collection process	7.1	Describe where in the reports data were collected from (e.g. text or figures).	Yes	
	7.2	Describe how data were collected (e.g. software used to digitize figures, external data sources).	Yes	
	7.3	Describe moderator variables that were constructed from collected data (e.g. number of generations calculated from years and average generation time).	Yes	
	7.4	Report how missing or ambiguous information was dealt with during data collection (e.g. authors of original studies were contacted for missing descriptive statistics, and/or effect sizes were calculated from test statistics).	NA	There were no missing data.
	7.5	Report who collected data.	Yes	
	7.6	State the number of extractions that were checked for accuracy by co-authors.	NA	There was no double-check of the data.
Data items	8.1	Describe the key data sought from each study.	Yes	
	8.2	Describe items that do not appear in the main results, or which could not be extracted due to insufficient information.	NA	All items appear in the main results and

				could be extracted from the studies.
	8.3	Describe main assumptions or simplifications that were made (e.g. categorising both ‘length’ and ‘mass’ as ‘morphology’).	Yes	
	8.4	Describe the type of replication unit (e.g. individuals, broods, study sites).	Yes	
Assessment of individual study quality	9.1	Describe whether the quality of studies included in the systematic review or meta-analysis was assessed (e.g. blinded data collection, reporting quality, experimental <i>versus</i> observational).	Yes	
	9.2	Describe how information about study quality was incorporated into analyses (e.g. meta-regression and/or sensitivity analysis).	NA	This review does not include a meta-analysis.
Effect size measures	10.1	Describe effect size(s) used.	NA	This review does not include a meta-analysis.
	10.2	Provide a reference to the equation of each calculated effect size (e.g. standardised mean difference, log response ratio) and (if applicable) its sampling variance.	NA	This review does not include a meta-analysis.
	10.3	If no reference exists, derive the equations for each effect size and state the assumed sampling distribution(s).	NA	Effect sizes were not calculated.
Missing data	11.1	Describe any steps taken to deal with missing data during analysis (e.g. imputation, complete case, subset analysis).	NA	There were no missing data.

	11.2	Justify the decisions made to deal with missing data.	NA	There were no missing data.
Meta-analytic model description	12.1	Describe the models used for synthesis of effect sizes.	NA	No models were used.
	12.2	The most common approach in ecology and evolution will be a random-effects model, often with a hierarchical/multilevel structure. If other types of models are chosen (e.g. common/fixed effects model, unweighted model), provide justification for this choice.	NA	No models were used.
Software	13.1	Describe the statistical platform used for inference (e.g. <i>R</i>)	NA	No statistical platform was used.
	13.2	Describe the packages used to run models.	NA	No models were used.
	13.3	Describe the functions used to run models.	NA	No models were used.
	13.4	Describe any arguments that differed from the default settings.	NA	No models were used.
	13.5	Describe the version numbers of all software used.	NA	No software was used.
Non-independence	14.1	Describe the types of non-independence encountered (e.g. phylogenetic, spatial, multiple measurements over time).	NA	This review does not include a meta-analysis or modelling, so this does not apply.

	14.2	Describe how non-independence has been handled.	NA	This review does not include a meta-analysis.
	14.3	Justify decisions made.	NA	This review does not include a meta-analysis.
Meta-regression and model selection	15.1	Provide a rationale for the inclusion of moderators (covariates) that were evaluated in meta-regression models.	NA	No meta-regressions were run.
	15.2	Justify the number of parameters estimated in models, in relation to the number of effect sizes and studies (e.g. interaction terms were not included due to insufficient sample sizes).	NA	No models were used.
	15.3	Describe any process of model selection.	NA	No models were used.
Publication bias and sensitivity analyses	16.1	Describe assessments of the risk of bias due to missing results (e.g. publication, time-lag, and taxonomic biases).	Yes	
	16.2	Describe any steps taken to investigate the effects of such biases (if present).	NA	No statistical analyses were used.
	16.3	Describe any other analyses of robustness of the results, e.g. due to effect size choice, weighting or analytical model assumptions, inclusion or exclusion of subsets of the data, or the inclusion of alternative moderator variables in meta-regressions.	NA	No statistical analyses were used.

Clarification of <i>post hoc</i> analyses	17.1	When hypotheses were formulated after data analysis, this should be acknowledged.	NA	There are no hypotheses that were formed after data collection.
Metadata, data, and code	18.1	Share metadata (i.e. data descriptions).	Yes	
	18.2	Share data required to reproduce the results presented in the manuscript.	Yes	
	18.3	Share additional data, including information that was not presented in the manuscript (e.g. raw data used to calculate effect sizes, descriptions of where data were located in papers).	Yes	
	18.4	Share analysis scripts (or, if a software package with graphical user interface (GUI) was used, then describe full model specification and fully specify choices).	NA	No statistical analyses were used.
Results of study selection process	19.1	Report the number of studies screened.	Yes	
	19.2	Report the number of studies excluded at each stage of screening.	Yes	
	19.3	Report brief reasons for exclusion from the full text stage.	Yes	
	19.4	Present a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA)-like flowchart (www.prisma-statement.org).	No	This information can be found in the text.
Sample sizes and study	20.1	Report the number of studies and effect sizes for data included in meta-analyses	NA	This review does not include a meta-analysis.

characteristics	20.2	Report the number of studies and effect sizes for subsets of data included in meta-regressions	NA	No meta-regressions were run.
	20.3	Provide a summary of key characteristics for reported outcomes (either in text or figures; e.g. one quarter of effect sizes reported for vertebrates and the rest invertebrates).	Yes	
	20.4	Provide a summary of limitations of included moderators (e.g. collinearity and overlap between moderators).	NA	No meta-regressions were run.
	20.5	Provide a summary of characteristics related to individual study quality (risk of bias).	NA	No meta-regressions were run.
Meta-analysis	21.1	Provide a quantitative synthesis of results across studies, including estimates for the mean effect size, with confidence/credible intervals.	NA	This review does not include a meta-analysis.
Heterogeneity	22.1	Report indicators of heterogeneity in the estimated effect (e.g. I^2 , τ^2 and other variance components).	NA	This review does not include a meta-analysis.
Meta-regression	23.1	Provide estimates of meta-regression slopes (i.e. regression coefficients) and confidence/credible intervals.	NA	No meta-regressions were run.
	23.2	Include estimates and confidence/credible intervals for all moderator variables that were assessed (i.e. complete reporting).	NA	No meta-regressions were run.
	23.3	Report interactions, if they were included.	NA	No interactions were included.
	23.4	Describe outcomes from model selection, if done (e.g. R^2 and AIC).	NA	No model selection was used.

Outcomes of publication bias and sensitivity analyses	24.1	Provide results for the assessments of the risks of bias (e.g. Egger's regression, funnel plots).	NA	This review does not include a meta-analysis.
	24.2	Provide results for the robustness of the review's results (e.g. subgroup analyses, meta-regression of study quality, results from alternative methods of analysis, and temporal trends).	NA	No statistical analyses were used.
Discussion	25.1	Summarise the main findings in terms of the magnitude of effect.	NA	This review does not include a meta-analysis.
	25.2	Summarise the main findings in terms of the precision of effects (e.g. size of confidence intervals, statistical significance).	NA	This review does not include a meta-analysis.
	25.3	Summarise the main findings in terms of their heterogeneity.	Yes	
	25.4	Summarise the main findings in terms of their biological/practical relevance.	Yes	
	25.5	Compare results with previous reviews on the topic, if available.	NA	There are no previous reviews or meta-analyses on the topic.
	25.6	Consider limitations and their influence on the generality of conclusions, such as gaps in the available evidence (e.g. taxonomic and geographical research biases).	Yes	
	26.1	Provide names, affiliations, and funding sources of all co-authors.	Yes	

Contributions and funding	26.2	List the contributions of each co-author.	Yes	
	26.3	Provide contact details for the corresponding author.	Yes	
	26.4	Disclose any conflicts of interest.	NA	There are no conflicts of interest.
References	27.1	Provide a reference list of all studies included in the systematic review or meta-analysis.	Yes	
	27.2	List included studies as referenced sources (e.g. rather than listing them in a table or supplement)	Yes	

Supplementary Online Material Table S3: PRISMA EcoEvo checklist (O’Dea *et al.*, 2021).

Name of variable	Description of category	Type of extracted data
META-INFORMATION		
Study ID	Study identification code.	Numerical
Author(s)	Article author names.	Nominal
Title	Article title.	Nominal
Journal	Journal in which the article was published.	Nominal
Year	Year when the article was published.	Numerical
TEMPORAL, GEOGRAPHICAL AND TAXONOMIC DISTRIBUTION		
Country	Country where the study was conducted.	Nominal
Continent	Continent where the study was conducted.	Nominal
Biome	It includes 13 categories: (1) tropical-subtropical forest, (2) temperate-boreal forests & woodlands, (3) shrublands & shrubby woodlands, (4) savannas and grasslands, (5) deserts and semi-deserts, (6) polar-alpine, (7) intensive land-use systems, (8) palustrine wetlands, (9) wetlands, (10) rivers, (11) shoreline systems, (12) supralittoral coastal systems, (13) anthropogenic shorelines. From IUCN Global Ecosystem Typology 2.0	List
Species	Species studied in the study	
Order	Order of the species	
Sex	Male, Female or Both	List
Song-learner	Yes/no	List
Vocalisation type	Song/call	List
NIGHT DEFINITION		
Was night defined?	Yes/no	List
Definition	Definition used in the study	

DRIVERS OF NOCTURNAL VOCALISATION		
Category according to La (2012)	Includes 8 options: (1) elevated light levels, (2) reduced acoustic competition, (3) enhanced sound transmission, (4) predator avoidance, (5) nocturnal roosting groups, (6) territory defence, (7) mate attraction, (8) pair bonding, (9) reproductive stimulation, (10) mate guarding, (11) song learning by offspring and (12) others (specify).	List
Data supports the hypothesis?	Yes/no	List
Statistically tested	Yes/no	List
How was the effect?	Description of the effect found	Nominal