



Review

A review of the literature on female birdsong function

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Growing research on the function of female birdsong now allows for identification of large-scale patterns emerging in the published literature. We conducted a review that analysed female birdsong function studies to characterize the literature and research approaches in this field. We examined when, where and how researchers study female birdsong function and then quantified which functions for female song were most often supported by authors. Our data set included studies published between 1900 and 2022 that concentrated on singing female birds and either investigated or addressed functions of solo female song directly. The number of female song studies published per year has increased rapidly in recent decades, with the majority of the work focused on North/Central American species, followed by Australian and South American species. Most research studies used natural observation techniques, about half used playback and only 21% used other manipulations. In 67% of the studies analysed, female song was reported to be used in defence of a territory, 43% of studies reported intrasexual competition/aggression and 45% reported intrapair communication. Mate attraction and parent–offspring communication were the song functions least often supported and least often tested by authors. Most authors identified multiple contexts in which female song functioned in each study species. Outcomes match the demonstrated multifunctionality of male birdsong. In contrast, females apparently use song for mate attraction much less than male birds do. Surprisingly, less than 10% of papers directly linked female song behaviour to reproductive success, a connection providing critical support for ultimate explanations of function. It is evident that scientific interest in female birdsong function is on the rise. Our review identified a need for future research to include African and Asian avian species and studies that comprehensively test the fitness correlates of female birdsong function.

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Documentation of female birdsong first appeared in scientific journals almost a century ago (Laskey, 1944; Miller, 1931; Nice, 1937; Sargent, 1940). There are even earlier mentions of female singing in the literature going back to Aristotle, who described how in some species, such as the nightingale, *Luscinia megarhynchos*, both sexes produce song (Aristotle, 1910/350 BCE). Despite this understanding, a male-centric view of birdsong behaviour has dominated research on avian vocal communication for most of recent history (Langmore, 2023; Riebel et al., 2005). Some ornithologists have justified this view by labelling reports of female singing as ‘aberrant’ or ‘abnormal’ occurrences caused by physiological anomalies, dismissing the potential for female song to have functional significance (Cunningham & Baker, 1983; Kriner & Schwabl, 1991). Other ornithologists categorized all female vocalizations as calls before the widespread acceptance of the occurrence

of female song (Rose et al., 2022), and despite how long ago birdsong research began, ornithologists have yet to reach a consensus on what criteria should be used to distinguish songs from calls (Barrington, 1773; Howard, 1920; Smith, 1991; Spector, 1994; Wittchell, 1896). Only in the last few decades has female birdsong become a widely studied phenomenon, with research on female song form and function rapidly growing (Riebel et al., 2019). Recent work suggests that female song is the ancestral state among songbirds (Odom et al., 2014; Perkes et al., 2019; Price et al., 2009). Currently, ornithologists estimate that female song occurs in approximately 64% of all songbird species (Webb et al., 2016), illustrating that it is a widely expressed trait across many lineages. Furthermore, ornithologists are discovering many overlooked female songs in familiar species and report that female song prevalence estimates (Odom et al., 2014; Webb et al., 2016) are minimums based on the available information.

Current research on multiple avian taxa demonstrates both similarities and differences in the song forms of males and females of the same species (Austin et al., 2021; Cain & Langmore, 2015;

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Odom et al., 2021; Rose et al., 2020; Wilkins et al., 2020). In some species, female songs differ from male songs in almost every aspect: song rate (Dutour & Ridley, 2020; Patchett et al., 2021), frequency (Kasumovic et al., 2003), song length (Sierro et al., 2022), song type (Byers & King, 2000; Searcy & Yasukawa, 2014), song 'complexity' (Ligon et al., 2018; Pavlova et al., 2005) and many other features (Hathcock & Benedict, 2018; Mennill & Vehrencamp, 2005). In other species, male and female songs are statistically indistinguishable (Campbell et al., 2016; Keen et al., 2016; Rose et al., 2019). The evidence collected to date on female song suggests wide variation in structure and usage across species; thus, it is possible that female song can also differ in functional context from male song. In rufous-and-white wrens, *Thryophilus rufalbus*, for example, there appears to be no significant difference in the rate at which females respond to song playbacks of conspecific song from either sex (Mennill, 2006). In contrast, males of this species respond far more aggressively to male conspecific song, showing functional song behaviours that differ from females (Mennill & Vehrencamp, 2005; Topp & Mennill, 2008). Function cannot be assumed ubiquitous for both sexes in a species where males and females sing (Kroodsmas & Byers, 1991; Searcy & Andersson, 1986).

Male birdsong is generally understood to function most often in contexts of sexual selection (Kroodsmas & Byers, 1991; Searcy & Andersson, 1986) and in defence of a territory (Beecher et al., 1994; Catchpole & Slater, 2003). Mating benefits of male birdsong include attracting a breeding partner (King et al., 1981; Marler & Slabbekoorn, 2004), ensuring fidelity by preventing extrapair copulations (Morse, 1970; Møller, 1991), synchronization of breeding events between mates (Merritt, 1985), coordination of brood care (Halkin, 1997), recruiting a mate to aid in defence of a joint territory (Read & Weary, 1992; Wheeldon et al., 2021) or settling same-sex conflicts (Searcy & Andersson, 1986; Westcott, 1992). Song is frequently used by male birds to protect against territory or resource usurpation, which can have the inherent benefit of securing frequent access to essential resources or areas being defended (ten Cate et al., 2002; Tobias et al., 2011).

Over the past few decades, researchers have begun to investigate whether female birdsong functions similarly to male song, with many reports concluding that it does (Austin et al., 2021; Cain & Langmore, 2015; Riebel et al., 2019). Female birds have been observed to use song in mate attraction, and many studies have demonstrated the use of female song in territory defence and intrasexual competition, although different authors discuss these ideas in different ways (Austin et al., 2021; Langmore, 1998; Riebel et al., 2019; Rose et al., 2022). Additionally, a considerable number of studies have observed that females sing when entering or leaving their nest (Leonard, 2008), suggesting a possible function for song in parent–offspring communication (Eens et al., 1993; Halkin, 1991, 1997; Kleindorfer et al., 2016; Stracey et al., 2023). Excellent reviews of multiple aspects of female song exist (Austin et al., 2021; Riebel et al., 2019; Rose et al., 2022), especially those that focus on female duets (Hall, 2004; Langmore, 1998). But despite a recent expansion of the literature, there has not yet been a detailed quantitative analysis or overview of the findings across many species to identify widescale patterns in solo female birdsong function. Such an analysis is critical in expanding our understanding of the evolution of female song and identifying sexually dimorphic behaviours in acoustic communication.

Here, we aim to narrow this gap in knowledge by presenting a comprehensive review of the current literature on female birdsong function. We focus on solo songs of females, not including research conclusions about duets, which can evolve and function differently from solo song (Hall, 2004; Odom et al., 2015). In this review, we address research questions examining how female song has been studied, quantify the most commonly reported functions for female

birdsong and compare the degree of evidence for female song functions overall. To examine how female song function research has proceeded, we evaluated whether publication rates have increased through time, mapped the geographical distribution of study locations and determined which experimental methods were used most often. To summarize the results of female birdsong function research, we quantified which functions were most often supported or refuted by authors, and we assessed what evidence authors used in making those conclusions. We classified female song as functioning in mate attraction, intrapair communication, territory defence, intrasexual competition and parent–offspring communication (see Methods for definitions), as these were the functions most often discussed by authors in the existing literature.

METHODS

Literature Review

We compiled primary research articles that focused on or addressed female birdsong functionality published from 1900 to 2022. We searched three online resources for female birdsong function papers, including the University of Northern Colorado 'Summon' online library search, Google Scholar and Web of Science. We used a combination of search terms related to female song and birdsong function (Fig. 1). We also used the 'snowball' method and reviewed the cited references within many of the scientific articles to find additional papers to include in our review. The criteria used for inclusion/exclusion of studies for our sample are detailed in Fig. 1; in general, we included only primary peer-reviewed articles that examined natural female song function in one or two species. We used the authors' label or use of the term 'song' when describing female vocalizations to determine whether a study met our inclusion criteria. Studies of duetting species were included when they contained data on female solo song separate from duets. We restricted our analyses to solo female song because the literature already includes excellent reviews of avian duet function and because the evolutionary drivers of duetting differ from those of female song (Hall, 2004, 2009; Odom et al., 2015). Our literature search was conducted from September 2021 to February 2023 and resulted in 255 papers, of which 147 publications fit the inclusion criteria and focus explicitly on female song function (Supplementary Material 1). All future discussion of scored articles is thus focused on female song function rather than on other aspects of female song. Our sample included 88 studied species (Supplementary Material 2). We treated publications as our unit of measure because we wanted to investigate the typical research approach per study rather than the sum total of what is known about each species. Thus, the sample size for our analysis was 147 publications on female song in 88 avian species.

Scoring Procedures

Research approaches

Publication year was recorded for each study that we scored. To compare the growth of this field with the general growth of the scientific literature, we used data from Thelwall and Sud (2022) as reference data on scientific publication rates. We calculated an average number of publications per year in Web of Science and Scopus for each time period graphed in Fig. 2 using numbers provided in the Supplementary Material of Thelwall and Sud (2022). To conduct a geographical analysis, we noted the location where each female birdsong study was performed. Since not every study provided an exact location with GIS coordinates, we narrowed the location down to state/province and, when possible, the site location of where the study took place (i.e. a nature reserve or city

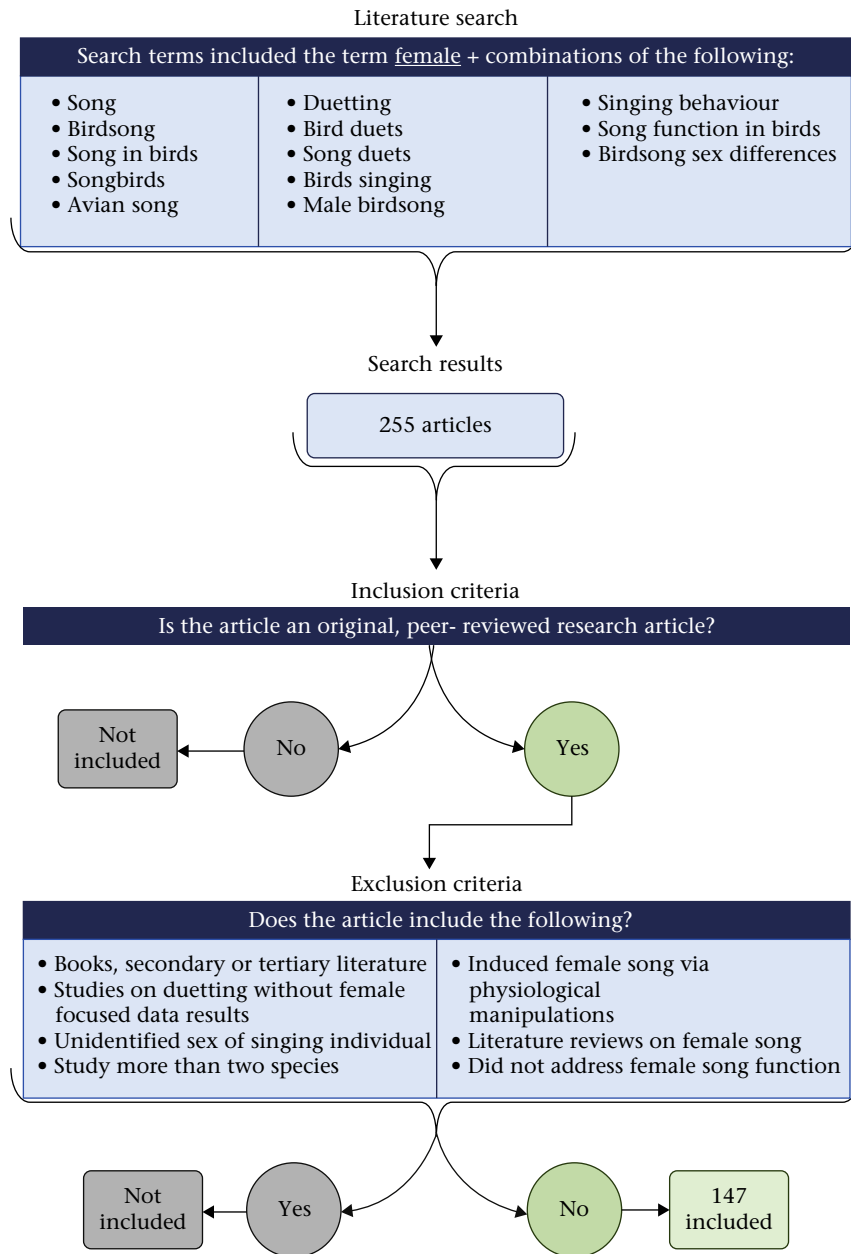


Figure 1. Flowchart demonstrating the literature review search and inclusion process.

park). A small number of studies performed research at multiple field sites that were substantially far apart from one another (i.e. in separate countries); in this case, we recorded a study location for each distinct region in which female song was surveyed.

Experimental approaches used to investigate female song function were extrapolated from the 'Methods' section of each article. We first looked for general patterns to identify the experimental designs used most often. Through our initial review of female song function studies, it was apparent that authors very frequently used 'natural observation' or 'acoustic playback' when collecting data on singing female birds. Occasionally, studies used experimental approaches other than playback, so we grouped all of those into a category of 'other manipulations'. Natural observation was scored when researchers conducted observation periods of females singing under natural conditions without enticement from

playback. Under our definition, a period of 'natural observation' must have been performed to collect data, such as spontaneous singing rates of females, and results must have been analysed quantitatively. Playback was scored when researchers exposed study subjects to acoustic playback recordings. Other manipulations included any experimental manipulation method used in a natural setting besides playback. For example, female song function experiments involving mate removal treatments would be scored as 'other manipulation' (Levin, 1996; McElroy & Ritchison, 1996). Research approaches involving the capturing of birds for the purpose of banding them to identify each study subject individually, perform body measurements or extract blood samples were not considered manipulation. Research methods were not scored as mutually exclusive, and many studies included more than one method.

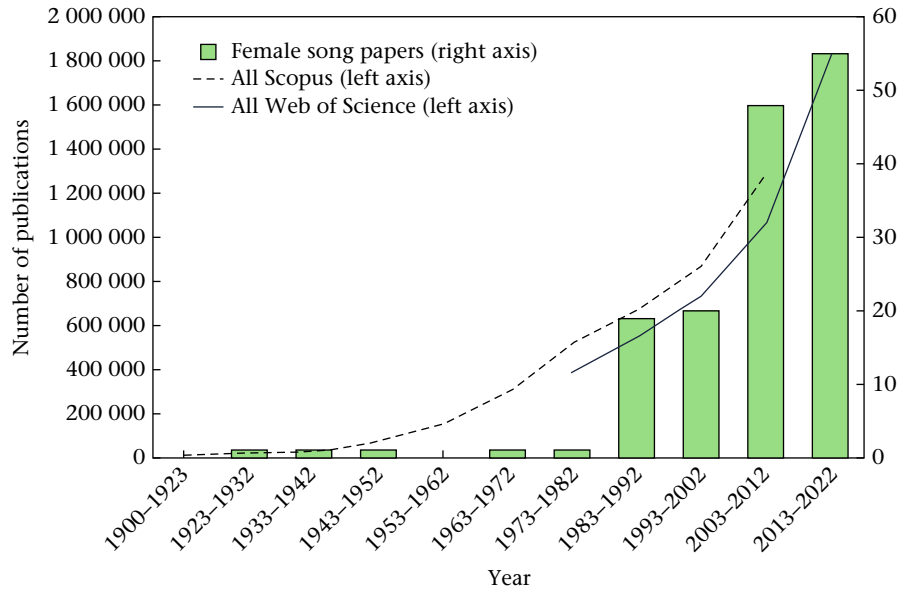


Figure 2. Number of research articles discussing the function of female birdsong published every 10 years between 1900 and 2022, in reference to the overall growth of the scientific literature indexed in Scopus (1900–2012) and Web of Science (1970–2022), as reported by [Thelwall and Sud \(2022\)](#).

Song functions

We first reviewed papers to look for common patterns in functions of female birdsong, then created functional categories based on that preliminary review, using functional categories and terminology that appeared most often. The five categories we selected to score were as follows: mate attraction, intrapair communication, territory defence, intrasexual competition (including mate guarding) and parent–offspring communication ([Table 1](#)). We scored each female song study for any functional categories out of the five that the authors explicitly drew conclusions about in their article. These categories were not mutually

exclusive; for example, if authors determined that female song functioned in coordinating joint territory defence with pair-bonded mates, we scored female song function as both territorial defence and intrapair communication. We based our scores solely on what the authors reported the functions to be. When the song functions addressed or reported by authors did not match our scored categories (i.e. species or sex identification, individual identity, etc.), we classified them as ‘other’. When scoring was completed, the number of articles that had addressed or tested for song function in the ‘other’ category was fewer than 10, and thus we did not analyse this song function category further.

Table 1
Definition of song function types

	Definition
Song function type	
Mate attraction	Songs directed at an individual of the opposite sex to acquire a breeding partner
Intrapair communication	Song used for communication between members of a breeding pair
Territory defence	Song used in defence of territory or other physical environmental resources
Intrasexual competition	Song used in aggressive contexts specifically with same-sex individuals competing for either physical resources or social resources
Parent–offspring communication	Song used by a parent, directed at young
Support level categories	
Hypothesized	An author's decision to confirm or refute a given female song function was formulated using logical/hypothetical reasoning based on data collected and reported in the study. Song function was not experimentally tested
Tested	An author's decision to confirm or refute a given female song function was formulated based on results from a behavioural experiment that directly tested for that female song function
Fitness tested	An author's decision to confirm or refute a given female song function was formulated in conjunction with the use of a fitness proxy. Song function was directly tested for and related to reproductive success

Support levels

To determine the relative strength of support for female song function assertions in each study, we first scored the article based on whether the functional hypothesis was either ‘confirmed’ or ‘refuted’ given the results of the study for each of the five song function categories we chose to consider in this review. We subsequently assigned a support level category based on how rigorous the support was in favour of (confirmed) or against (refuted) each song function. Our support levels were fitness testing (F), behavioural testing (T) and hypothesized (H). Fitness testing included any experiment conducted on female song in which a fitness proxy, such as fledging success, was correlated with female song function. Testing involved a behavioural manipulation such as the use of playbacks, mounts or mate removal experiments. The hypothesized support level was assigned to a function when authors in a study did not experimentally test for that function category but made a conclusion about it based on results from systematic observations or experiments conducted in that same study (see [Table 1](#) for definitions of these scoring categories). A fourth support level was initially included in our scoring process; we assigned support as conjectured (C) when authors postulated a plausible function for female song based only on previous literature and not on the data from the study being reviewed. For analysis, we removed all conjectured functions and included only support levels for which conclusions were based on data collected within the scored study. For a detailed example of our scoring procedure, see [Supplementary Material 3](#).

We assessed inter-rater reliability of our scoring by conducting two agreement tests in which all authors scored 10 articles (7% of studies reviewed). When all three scored independently, we agreed on 82% of data fields. When two observers scored after seeing the primary scorer's data, we agreed on 89% of data fields. Disagreements among observers occurred mostly as discrepancies regarding scores for level of support (hypothesized, tested, fitness tested), not whether a certain function was supported/refuted or whether a certain experimental approach was used. The first author performed all subsequent scoring. We calculated summary statistics and report rates and trends for publications through time and space.

RESULTS

Research Approaches to Studying Female Birdsong Function

Studies of female birdsong function have grown in conjunction with the general scientific literature (Thelwall & Sud, 2022), but female birdsong function studies show a recent rise that differs from the more consistent growth of the overall literature (Fig. 2). There was a sharp increase in female song studies beginning in the 1980s and another uptick in female song studies at the turn of the century, beginning in the early 2000s. The number of female song studies published in 2003–2012 was more than double the number published in the previous decade, and that number continues to grow (Fig. 2).

Research on female birdsong has been conducted across the globe, with concentrations in some areas. The number of studies per state/province ranged from one study to 16 studies. Of the 147 papers we reviewed, the percentage focusing on species native to each region were as follows: 35% North America (U.S.A., Canada and

Mexico), 20% Central America, 10% South America, 16% Australia and New Zealand, 10% Europe, 8% Africa and 3% Asia (Fig. 3).

Our analysis revealed that 69% of studies of female birdsong function had a period of natural observation wherein researchers collected natural female song data (Fig. 4). About half of the studies performed playback experiments (51%), and only 21% of studies performed manipulations other than playback, such as mate removal experiments, manipulation of the females themselves or changes to some element of their environment (Fig. 4).

Results of Research Studying Female Birdsong Function

The evaluated functions of female song were supported much more often than they were refuted (Fig. 5). Among the 147 scored papers, territory defence had the highest rates of study and confirmed support scores for function of female song, followed by intrasexual competition and intrapair communication (Fig. 5). Most authors identified multiple contexts in which female song was used; it was rare for authors to identify just one function. In most cases, the papers that tested a hypothesis supported it, and most studies did not test more than one to three functions at one time. Less than 10% of the 147 studies analysed tested fitness correlates of song by using some measure of reproductive success (Fig. 5). These studies linked reproductive success to multiple functional hypotheses and varied in their support for or against those hypotheses.

Levels of Support for Mate Attraction

Our results indicated that 42 out of 147 articles addressed mate attraction in the study. Of those, 25 articles confirmed mate attraction as being a likely function for female song, with most of

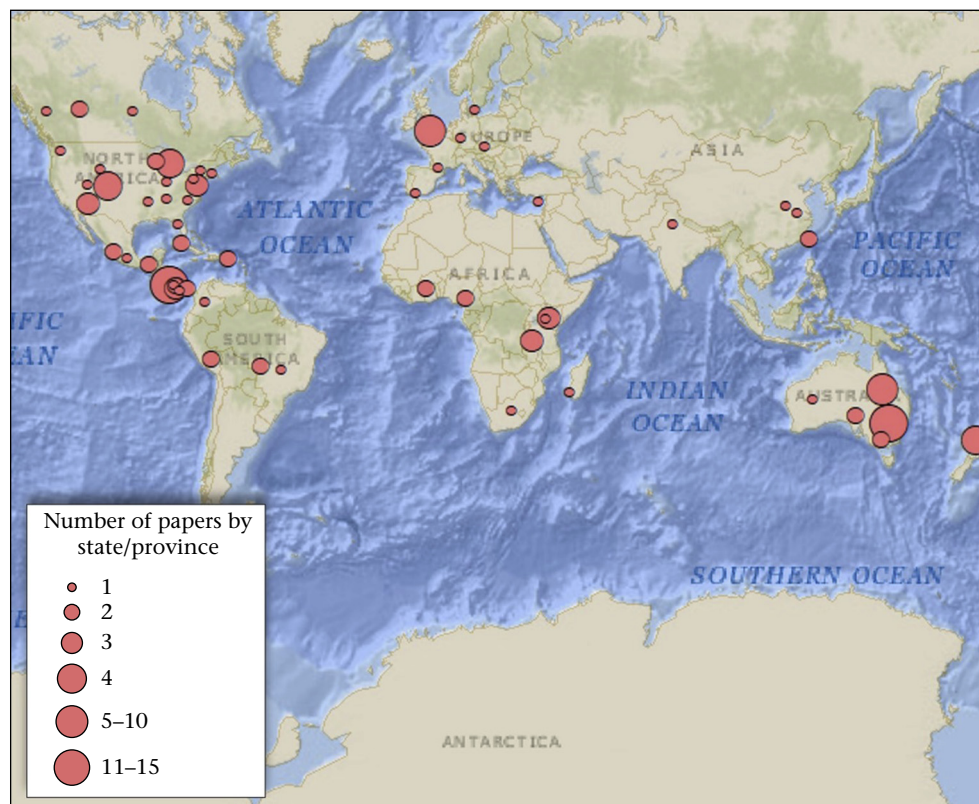


Figure 3. Geographical distribution of female song function studies.

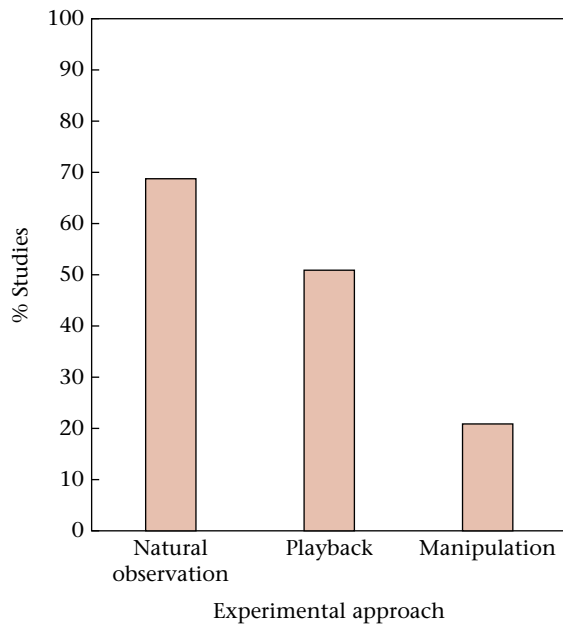


Figure 4. Percentage of studies using natural observation, playback and experimental manipulation in female song studies.

that support coming from authors via hypothesized conclusions. Mate attraction was refuted in 17 studies that addressed this function, and in most cases this conclusion stemmed from results of behavioural testing. Only one study performed a fitness test for this song function and did not find evidence in support of mate attraction (Hall & Magrath, 2000). Seventy-one per cent of reviewed studies ($N = 105$) did not experimentally address this function for female birdsong.

Levels of Support for Intrapair Communication

Seventy-nine papers drew conclusions about whether female song functions in intrapair communication. Of those, 67 confirmed it, with the majority drawing hypothesized conclusions. Twelve papers found evidence to refute this function. Across all papers in this category, only the authors of one study supported their conclusions with fitness data relating female song use to reproductive success; and they found support for an intrapair communication function of female song (Hall & Magrath, 2000). Forty-six per cent of studies ($N = 68$) did not address or test for this function for female birdsong.

Levels of Support for Territorial Defence

Territory defence was the female song function category most often addressed ($N = 106$) by authors. Ninety-eight of 106 articles confirmed this function for female song, with most of the support provided by authors that performed behavioural experiments, often playback. Only eight articles refuted territorial defence as a likely female song function, with most support stemming from behavioural experiments. Five articles examined this function with fitness testing, and of those, all but one supported it. Twenty-eight per cent of studies ($N = 41$) did not test or address this function.

Levels of Support for Intrasexual Competition

Intrasexual competition was confirmed as the second most frequently studied function of female song after territory defence. Eighty-five articles explored this function, 62 of which supported it. Twenty-three studies refuted this song function category for female song, mostly via behavioural experiments and playback studies. Four articles supported this function via fitness experiments and one refuted it. Overall, 42% of studies ($N = 62$) did not address this function for female birdsong.

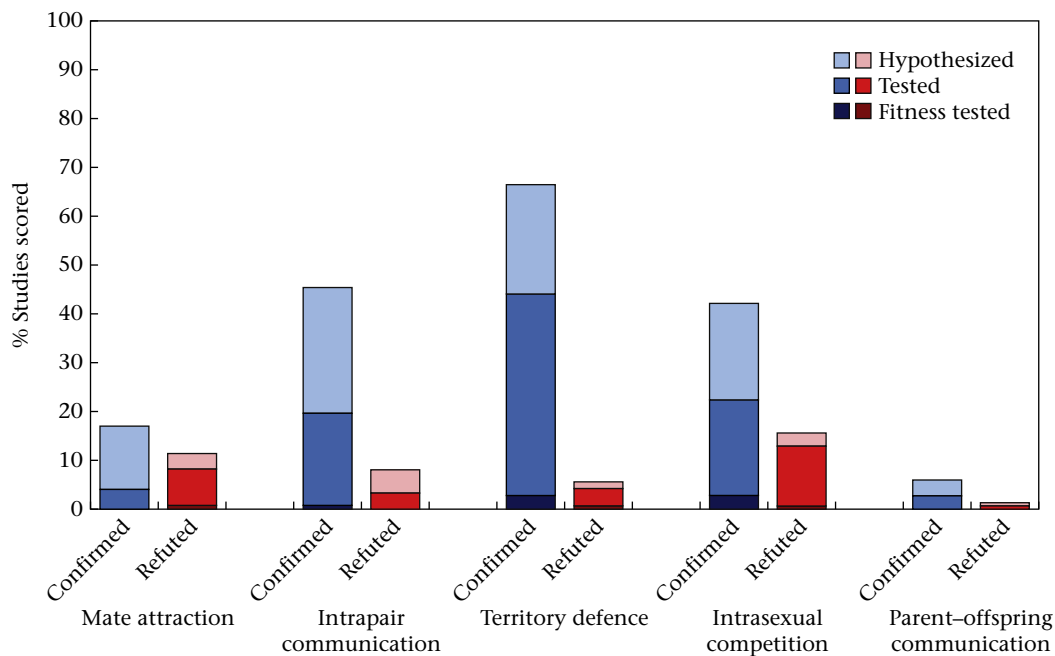


Figure 5. Song function scores with levels of support. Blue bars represent the studies in which authors confirmed female song function for their study species. Red bars represent the studies in which authors refuted female song function for their study species. Each support level is stacked, where bars with the darkest colour represent studies that confirmed or refuted a given function category based on fitness testing, those of medium colour represent behavioural testing and those with the lightest colour represent hypothesized conclusions about each song function category.

Levels of Support for Parent–Offspring Communication

Among the papers we reviewed, parent–offspring communication was the least supported and least addressed function of female song; 93% of studies ($N = 136$) did not address it. Nine studies confirmed this function for female birdsong, four of which came from behavioural testing. No studies performed fitness tests or measures that supported this function. A few articles found indirect evidence (H) that parent–offspring communication was not likely to be a function of female song (Gahr & Güttingery, 1986; Patchet et al., 2021), but no articles performed any direct behavioural testing or fitness assessment in order to conclude that parent–offspring communication was not a supported function for female song.

Overlap Between Function Categories

Our three most well-studied functions of female birdsong were often included in the same research studies. Many studies supported territory defence in conjunction with intrapair communication (generally during joint territory defence) and intrasexual competition (when females showed sex-specific territory defence). To evaluate the level of overlap between these hypotheses, we quantified the number of articles that supported and refuted the territory defence hypothesis plus each of the two hypotheses with which it frequently overlapped (Tables 2–3). Although authors often concluded support for territory defence in conjunction with intrapair communication, some studies did not support these functions together (Table 2). The same was true for territory defence and intrasexual competition; these hypotheses were variably included, supported and refuted by authors in the same studies (Table 3).

DISCUSSION

Research Approaches

We reviewed 147 articles on 88 species of birds where female song function has been studied to provide an overview of the function of female song research to date. We documented increasing female song publication rates, particularly in North America, Central America, Australia and Europe, and found that playback experiments coupled with natural observations are driving new discoveries in this field. We scored female song function according to five frequently discussed functional categories. Among the studies we reviewed, we found that authors concluded the highest support for territorial defence, followed by intrapair communication and intrasexual competition as functions of female song.

We first examined rates of publication on female song to determine whether interest in and research on female birdsong function has increased between the years 1900 and 2022. We found that the publication rates on female song have grown substantially each decade, with an impressive upswing in female song

Table 2
Overlap between territory defence and intrapair communication as functions of female song concluded by researchers

Intrapair communication	Territory defence		
	Yes	No	Not addressed
Yes	45	4	18
No	6	2	4
Not addressed	47	2	19

Table 3
Overlap between territory defence and intrasexual competition as functions of female song concluded by researchers

Intrasexual competition	Territory defence		
	Yes	No	Not addressed
Yes	49	2	11
No	17	3	3
Not addressed	32	3	27

publications after the 1980s that has continued to rise. This likely reflects the growth of the scientific literature in general, coupled with an increased focus on females. There are several possible explanations for the sudden increase beginning in the 1980s. The first could be technological advances in audio recording equipment, such as the advent of portable audio recorders along with the development of sound analysis software that together enabled researchers to manipulate sounds to be used in field playback experiments in novel ways (Douglas & Mennill, 2010; Falls, 1992; McGregor, 2013). Second, studies have shown that women are more likely to be first authors on female birdsong research in recent decades and that research topics change as more women join the field (Haines et al., 2020). Finally, advances in genetic sequencing technologies, beginning in the 1990s, may have allowed blood sample extractions taken from bird specimens to be analysed for the purpose of identifying a singer's sex, which is particularly valuable in species with monomorphic plumage (Griffiths et al., 1997; Odom & Benedict, 2018; Price, 2015; Price et al., 2009). The increasing amount of research conducted on female song suggests that additional studies on this topic are likely to appear in the published literature in coming years, and ornithologists will continue to learn more about how female song functions, both in coordination with and separate from male song.

Locality data collected from the articles reviewed suggest an under-representation of female song function studies from Asian, African and South American countries (excluding Central America). Given that females with the most elaborate and conspicuous traits are often found in the tropics (Dale et al., 2015; Slater & Mann, 2004), as well as increasing evidence of female song in these areas (Price, 2015; Price et al., 2009; Stutchbury & Morton, 2022; Webb et al., 2016), we expected to find female song studies clustered around the tropics. However, our review demonstrates that researchers are not targeting tropical locations to study female song. Rather, we found an over-representation of female song studies in the United States, Europe and Australia (Fig. 3). Our data reflect general geographical biases identified in the literature on birdsong (Christie et al., 2021; Ducatez & Lefebvre, 2014; Winker, 1998). This is likely an artefact of the Eurocentric history of academic publication in ornithology and reflects the exclusion of scientists from the Global South (MacGregor-Fors et al., 2020; Soares et al., 2023). We note, however, that we excluded many studies of avian vocal duet function that were conducted in tropical locales. Inclusion of those studies might have reduced our geographical bias.

In the studies we examined, authors were most likely to employ natural observation methods to investigate female birdsong function. Thus, much of the data were collected from spontaneously singing females under natural conditions. Such basic natural history observations and quantifications of behaviour are fundamental to our understanding of how female song functions. In particular, natural observation was common in the earliest studies of female song (Laskey, 1944; Sargent, 1940), but continues to be important in recent work (Campbell et al., 2016; Clark et al., 2018). It is apparent that descriptive data provide an underpinning for experimental

studies of birdsong function. Additionally, we found that 51% of studies conducted playback experiments, which is lower than our initial impression that an overwhelming majority of female song research would use this approach. Playback as an experimental method is widespread across female song function studies, but not ubiquitous. With the increase in the number of studies on female song, researchers are diversifying the ways in which female birdsong function is investigated. Future research should prioritize including experimental manipulations other than playback to increase our range of understanding on this topic. Robust comprehensive approaches include intensive nest monitoring (Stracey et al., 2023), mate removal experiments (McElroy & Ritchison, 1996), speaker replacement studies similar to those that have been performed on male song (Catchpole & Slater, 2003; Nowicki et al., 1998) or interactive playback experiments (Douglas & Mennill, 2010). Technologies including acoustic cameras, autonomous recording units and individual tracking devices offer exciting opportunities for future research associating female song with functional context.

Functions of Female Song

Mate attraction

In many songbird species, males use song to attract female mates (Bradbury & Vehrencamp, 2011; Johnson & Searcy, 1996; Krebs et al., 1981) and female birds evaluate male song performance to assess the 'quality' of a potential mate (Nowicki & Searcy, 2004; Podos & Sung, 2020). While it is true that, in many bird species, females are the 'chooser' sex during courtship (Alcock, 2009), there are bird species in which females also sing to attract mates (Langmore et al., 1996; Morton et al., 2000). We expected that mate attraction would be an extensively supported song function in our analyses, as it is for males (Logan & Hyatt, 2024; Slagsvold et al., 1994; Wasserman, 1977). Surprisingly, however, our analyses showed that less than one third of all studies we scored addressed, let alone tested for, mate attraction as a possible function of female song (71% of studies ignored this function). Of the studies that did address mate attraction, just over half (25 out of 42 studies) found evidence to confirm this function, generally via hypothetical reasoning (H) extrapolated from findings within the study. In contrast, most studies that used direct behavioural experiments to test whether mate attraction was a likely function of female birdsong found evidence to refute it. Perhaps even more remarkable is the fact that the only scored study that tested this hypothesis and used a measure of reproductive success concluded that female song did not function in mate attraction (although it is worth noting that females were already paired during the period when song was quantified) (Hall & Magrath, 2000). Our results therefore suggest that in many bird species surveyed thus far, mate attraction is unlikely to be a vital function of female birdsong, delineating a clear difference in song use between the sexes (Langmore & Davies, 1997; Levin, 1996; McElroy & Ritchison, 1996). Given the low number of studies of this function and the conflicting results, the use of female songs in mate attraction deserves more study.

Intrapair communication

Pair-bonded birds often cooperate to collectively defend a territory and/or coordinate brood care activities such as nest building, incubation of eggs, provisioning to chicks and protection of chicks from predators (Beletsky & Orrians, 2010; Benedict, 2010; Cézilly et al., 2000; Halkin, 1991). In pair-bonded avian species, communication between members of the pair is essential, and song can be an efficient modality to facilitate the coordination of behaviours by allowing the transmission of complex signals (Amy et al., 2018; Marshall-Ball et al., 2006; Thorpe, 1973). Intrapair communication was the third highest supported function for female song in our

quantitative analysis, with more than 53% of studies addressing this function. Evidence of females using song to facilitate intrapair communication was often found in studies involving duetting species, but also in a number of studies focused on nonduetting species (Logue, 2007; Mays et al., 2006; van den Heuvel et al., 2014). Many more studies confirmed intrapair signalling as a song function than refuted it, with most arriving at this conclusion via hypothetical reasoning (38 studies) or via behavioural testing (28 studies). We did observe a considerable variety of ways that authors defined intrapair communication in each study, with some labelling it 'pair bond maintenance' and others discussing 'joint territory defence'. We note that in many studies, this result could not be explicitly separated from other song function categories, especially territory defence (Table 2) and intrasexual competition, highlighting the potential for simultaneous multifunctionality of female song. To further test this function, future studies may require more long-term data collection, because both members of a bonded pair must be reliably identified and surveyed over extended time spans to document repeated patterns and contexts of intrapair song communication.

Territory defence

Birdsong in males has been well documented to function in territory defence (Catchpole & Slater, 2003; Hinde, 1956; Lovette & Fitzpatrick, 2016). Females in some bird species also use song as a form of territorial defence (Arcese et al., 1988; Miller, 1931), either individually (Illes & Yunes-Jimenez, 2009; Kriner & Schwabl, 1991) or in conjunction with their mate to defend a joint territory ('joint territory defence': Logue & Gammon, 2004; Read & Weary, 1992; Wheeldon et al., 2021). Joint territory defence might benefit a breeding pair in species where one individual is not enough to prevent territorial evictions by conspecifics (Leitão et al., 2022; Tobias et al., 2011). Territorial defence via song can have other benefits as well; engaging in territorial singing may help to advertise your willingness to fight should a trespasser intrude on your territory (Falls, 1988; Morse, 1970; Yasukawa, 1981) and aid in maintaining control over that territory (Kroodsma, 2004; McDonald & Greenberg, 1991) or, perhaps more importantly, ensure your own survival by securing resources in times of low abundance (Cain & Langmore, 2015; Morton et al., 2000). Our review of the literature shows that the most frequently tested and highly supported female song function was that of territory defence (only 28% of studies did not test for it).

Our review indicates that at every level of support assessed, territory defence had the highest confirmation rates, and that this song function has been robustly explored, including in the ways that it co-occurs with other functions (Tables 2–3). Importantly, territory defence had the highest ratio of behaviourally tested (T) to hypothesized (H) confirmation scores of the song functions examined (Fig. 5). In fact, in all other functions scored, there were higher percentages of confirmations via hypothetical reasoning (H), compared to confirmation scores via behavioural testing (T). Territory defence also had the highest number of fitness tests performed, all except one of which resulted in confirmative evidence for female song being adaptive in territorial conflicts. Territory defence is a song function category that lends itself to simple testing methods, such as simulated intruder playback experiments (Cain et al., 2015). The ease of testing a given function category may be a major contributor to rates of support for that song function; nevertheless, substantial evidence exists that female birds of many species use song to defend environmental resources.

Intrasexual competition

Intrasexual competition is defined as any sex-specific aggression occurring between two or more individuals of the same sex,

including sex-specific resource defence and mate guarding (Harts et al., 2016; Møller & Birkhead, 1991; Sonnenschein & Reyer, 1983). Female–female intrasexual competition has been reported in a range of bird species in association with both sexual and social selection (Clutton-Brock & Huchard, 2013; Rosvall, 2011). Although the literature widely recognizes mate guarding as a function of female song in several species, many authors also report intrasexual aggression in territory defence and in unknown contexts, so we included multiple types of intrasexual aggression in this category.

Intrasexual competition was the second most highly supported function for female song in our review of female song function studies. The degree of support for female song use in intrasexual contexts approached that of the territory defence function category. The most notable difference was that the ratio of the number of studies confirming territory defence function via behavioural experiments (61 studies) was almost double the number of studies that confirmed it via hypothetical reasoning (H), and in intrasexual competition, the number of studies confirming this function was an even split between behavioural testing and hypothetical reasoning (29/29) (Fig. 5). A factor in high confirmation scores for intrasexual competition might be that it was often tested as part of an experiment also testing territorial defence via playback of separate male and female stimuli. Evaluating response rates to playback treatments can provide simultaneous insight as to whether females use song to defend their territories and for intrasexual competition.

It is clear that female birdsong is regularly used in intrasexual conflict (Krieg & Getty, 2016; Searcy & Yasukawa, 1990; Siervo et al., 2022). In superb fairy-wrens, *Malurus cyaneus*, for example, females are more likely to sing in response to playbacks from an unfamiliar conspecific than in response to playbacks from their mates (Cooney & Cockburn, 1995), and they respond even more strongly if that unfamiliar individual is a female intruder (Cain & Langmore, 2015). Female superb fairy-wrens may be using song in intrasexual aggressive contexts to prevent mates from engaging in extrapair mating with other females (and potentially abandoning parental care duties). In this scenario, however, it is also possible that females are competing to assert dominance or for other reasons. Overall, researchers regularly found that females responded more aggressively to female song than to male song, but they could not always determine whether that reflected sex-specific territory defence, mate guarding or another function; general intrasexual competition was therefore concluded by many authors and might sometimes reflect overlap with those other functions (Dahlin & Benedict, 2014).

Parent–offspring communication

Although it is not often tested for, a fifth female song function that was repeatedly reported by ornithologists was parent–offspring communication. Females can benefit from communicating with their chicks or fledglings to confirm their spatial location, to warn against impending dangers, to tutor them in what adult song should sound like, or in other contexts (Beecher & Stoddard, 1990; Magrath et al., 2010; Mann & Slater, 1995; Ritchison, 1983). Our data indicated that parent–offspring communication was one of the least tested female song functions at every support level. Reasons for this lack of testing could be due to a lack of detection as this behaviour may be inconspicuous, or the difficulty in verifying whether the female is directing songs at young (Chen et al., 2016) versus singing for other reasons while at the nest (Leonard, 2008).

Sound arguments can be made either way as to whether a female's singing directed at her offspring is beneficial, and this will remain unclear until more testing is done in additional species with female song at multiple levels of experimental rigour (Stracey et al.,

2023). Females that sing while at the nest could suffer a fitness cost if they inadvertently advertise the location of chicks to potential predators or brood parasites (Kleindorfer et al., 2016). On the other hand, female singing in the context of parent–offspring communication might be adaptive for kin recognition and vocal learning as illustrated in studies conducted on red-backed fairywrens, *Malurus melanocephalus*, and New Zealand bellbirds, *Anthornis melanura* (Brunton et al., 2016; Dowling et al., 2016). One of the few studies that did test the fitness value of female birds singing in this context found that high song rates in the nest reduced survival (Kleindorfer et al., 2016; Magrath et al., 2010). With few studies testing this hypothesis, it is difficult to make any definitive conclusions about whether female song is often used in parent–offspring communication across bird taxa. More research should be done to better evaluate this song function.

Conclusion

Existing research has concluded that female song in birds functions primarily in territorial defence, followed by intrasexual competition and intrapair communication, with functions overlapping in many situations. These three functions of female birdsong are also the most often investigated. Like their male counterparts, females use song to serve multiple functions (Eens et al., 1993; Gil & Gahr, 2002; Kroodsmas & Byers, 1991; Wilkins et al., 2020). Where the sexes seem to diverge in song function is in the context of mate attraction. While male birds frequently (if not predominantly) sing to attract mates (Ballentine, 2004; Eriksson & Wallin, 1986; Nowicki & Searcy, 2004), in female birds this is not the case. Many researchers claim that female mate choice provides an ultimate explanation for males producing more 'complex' songs than female conspecifics in some species (Catchpole, 1980; Mountjoy & Lemon, 1991), and why males may have larger repertoires or other exaggerated song features (Byers & Kroodsmas, 2009; Collins, 2004; Podos, 1997; Vallet & Kreutzer, 1995). Future studies could test these ideas by correlating sex differences in song form with sex differences in song function (Benedict et al., 2021).

In contrast to sex differences in mate attraction, we found robust support for female song being used similarly to male song in resource defence. Territories belonging to pair-bonded females may be especially valuable and therefore costly to lose. A female that has invested extensive energy into parental care activities such as nest building, incubating and feeding young (Lovette & Fitzpatrick, 2016) may suffer a higher fitness cost compared to her mate, should they lose their territory (Tobias et al., 2011). This selective pressure might maintain female song in species with strong territory defence needs, an idea that is supported by studies demonstrating that female song is likely to be ancestral in most bird lineages (Mitchell et al., 2019; Najar & Benedict, 2019; Odom et al., 2014; Riebel et al., 2019), secondarily lost among species that have adapted to a migratory lifestyle and prevalent in species with year-round territoriality (Irestedt et al., 2009; Najar & Benedict, 2015; Price et al., 2008; Slater & Mann, 2004). If female birdsong has been maintained evolutionarily mainly in the context of advertising territoriality, this trait should be most prominent in bird species that are year-round territory holders (Logue & Hall, 2014; Zink, 2002).

Territorial defence, intrapair communication and intrasexual competition functions for song do not always occur separately from each other. Often, authors reported a combination of these three song functions simultaneously (Benedict, 2010; Collins, 2004; Marshall-Ball et al., 2006). For example, in barred antshrikes, *Thamnophilus doliatus*, females and males engage in joint territory defence, which would be considered both intrapair communication and territory defence (Koloff & Mennill, 2013a, 2013b), as we have

defined these (Table 1). A similar phenomenon is often observed in duetting species (Grafe & Bitz, 2004; Marshall-Ball et al., 2006; Templeton et al., 2011; Whittingham et al., 1997). This, combined with our observations that all three functions can be tested for using relatively simple playback experiments (Douglas & Mennill, 2010; Falls, 1992), is certainly one explanation for the overwhelming evidence supporting territorial defence, intrapair communication and intrasexual competition as functions of female birdsong. Future studies should attempt to untangle these overlapping functions and to conduct tests using experimental approaches other than playback, coupled with measurement of fitness proxies.

In summary, our quantitative review of the female birdsong literature identified an encouraging upward trend in the publication rates of female song research and a diversity of song functions with levels of support that do not match those of male birds. Our knowledge about how and why female birds sing, as well as how it contributes to their individual fitness, can only increase in scope with future work. We documented multiple methods that researchers use to study female birdsong function, and we identified a surprisingly low number of research studies from tropical locations outside of the Americas. Future work can diversify research methods and locations to provide a clearer picture of female song across avian taxa. Finally, we encourage fitness-linked studies of the functions documented here.

Data Availability

Data are available as Supplementary material.

Declaration of Interest

The authors have no conflict of interest.

Author Contributions

Cristina M. Barros: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Lauryn Benedict:** Conceptualization, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – review & editing. **Karina Sanchez:** Resources, Validation, Visualization, Writing – review & editing.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2024.07.018>.

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