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Avian vocalisations: the female perspective

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ABSTRACT

Research on avian vocalisations has traditionally focused on male song produced by oscine passerines. However, accumulating evidence indicates that complex vocalisations can readily evolve outside the traditional contexts of mate attraction and territory defence by male birds, and yet the previous bias towards male song has shaped – and continues to shape – our understanding of avian communication as a whole. Accordingly, in this review we seek to address this imbalance by synthesising studies on female vocalisations from across signalling contexts throughout the Aves, and discuss the implications of recent empirical advances for our understanding of vocalisations in both sexes. This review reveals great structural and functional diversity among female vocalisations and highlights the important roles that vocalisations can play in mediating female-specific behaviours. However, fundamental gaps remain. While there are now several case studies that identify the function of female vocalisations, few quantify the associated fitness benefits. Additionally, very little is known about the role of vocal learning in the development of female vocalisations. Thus, there remains a pressing need to examine the function and development of all forms of vocalisations in female birds. In the light of what we now know about the functions and mechanisms of female vocalisations, we suggest that conventional male-biased definitions of songs and calls are inadequate for furthering our understanding of avian vocal communication more generally. Therefore, we propose two simple alternatives, both emancipated from the sex of the singer. The first distinguishes song from calls functionally as a sexually selected vocal signal, whilst the second distinguishes them mechanistically in terms of their underlying neurological processes. It is clear that more investigations are needed into the ultimate and proximate causes of female vocalisations; however, these are essential if we are to develop a holistic epistemology of avian vocal communication in both sexes, across ecological contexts and taxonomic divides.

Key words: female vocalisations, birdsong, calls, function, oscines, non-oscines

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I. INTRODUCTION

Until recently, research on avian vocalisations in songbirds (oscine passerines) has been dominated by what we now know to be a false dichotomy: males produce complex, learned vocalisations or 'song' while females only produce simple, innate 'calls'. However, it is now clear that song in female oscine passerines is in fact widespread and ancestral, occurring in an estimated 60–70% of oscine passerines (Garamszegi *et al.*, 2007; Odom *et al.*, 2014; Webb *et al.*, 2016). This paradigm shift has two main consequences for our understanding of bird vocalisations. First, it is now realised that female song is not the rare, abnormal, or aberrant behaviour it was once thought to be, and instead must be considered a central feature of avian communication (Riebel, Hall & Langmore, 2005; Odom *et al.*, 2014; Odom & Benedict, 2018). Second, it is now accepted that bird song can evolve outside the traditional contexts of mate attraction and territory defence by males. However, despite recent advances in the field of female song (e.g. Odom *et al.*, 2014; Webb *et al.*, 2016), traditional, male-biased notions about the structure, function and development of oscine vocalisations continue to inform, and thus impede, progress in the field of vocalisations in birds more generally. Given these issues, and the recent spate of interest in female vocalisations more broadly (e.g. Hall & Langmore, 2017; Amy, Salvin & Leboucher, 2018; Odom & Benedict, 2018; Riebel *et al.*, 2019), we suggest that it is now time for a comprehensive, systematic appraisal of the functions and mechanisms of vocalisations in female birds.

Here we take a unique, holistic approach by synthesising studies on female bird vocalisations from across signalling contexts throughout the Aves, including across traditional song *versus* call divides. This approach is necessary given the many ways in which the new knowledge regarding female vocalisations challenges our existing understanding of the functions and mechanisms of avian vocalisations, across signalling contexts and taxonomic affiliations. Incidentally, this approach helps expose the entrenched male-bias in birdsong research, and highlights the need for a revision of existing male-centric definitions of songs *versus* calls. We begin by providing a short overview of current understandings of the similarities and differences between male and female vocalisations. This comparison serves to highlight that as with males, there exists rich diversity in female vocalisation behaviours and demonstrates that approaches to research should not be fundamentally different between the sexes. We then examine in detail the evidence for intraspecific and interspecific functions of female vocalisations. This approach reveals previously overlooked structural and functional diversity among female vocalisations in oscines and non-oscines alike. Further, the importance of vocalisations in mediating female-specific and female-biased behaviours (such as egg laying, incubation and rearing of offspring in some species) is emphasised. Next, we review the current understanding of the role of learning in the development of female vocalisations. Importantly, we present compelling evidence to suggest that our traditional notions about the structure, function and development of vocalisations in male *versus* female birds have led to erroneous conclusions about avian communication, thus necessitating a revision of the conventional, male-centric definitions of vocalisations to stimulate progress in the broader field. Accordingly, in light of what we have learnt about the functions and mechanisms of female vocalisations, we propose two tentative solutions to the issues surrounding current definitions of songs and calls, both independent of the sex of the singer. The first defines vocalisations strictly functionally as either a sexually selected vocal signal (song), or a non-sexually selected vocal signal (call). The second defines song mechanistically in terms of its underlying neurological processes. Both our functional and mechanistic alternatives remove the current ambiguity associated with existing definitions, and so provide a more inclusive epistemology for understanding avian vocalisations as exhibited by males *and* females.

II. FEMALE *VERSUS* MALE VOCALISATIONS

Like males, female birds exhibit an astonishing diversity of vocalisations (Langmore, 1998; Hall, 2009; Dalziell & Welbergen, 2016; Amy *et al.*, 2018). Yet the drivers of avian vocal diversity have not been as thoroughly considered in females as they have been in males. This has likely led to assumptions about the evolution and ontogeny of avian vocal signals in both sexes.

(1) Differences in vocalisations between females and males

Females and males may differ in the acoustic structure of their songs (e.g. eastern whipbird *Psophodes olivaceus*; Rogers, 2005) or calls [e.g. chaffinches *Fringilla coelebs* (Marler, 2004*a*) and zebra finches *Poephila guttata* (Vicario, Naqvi & Raksin, 2001)]. Sex differences in call and song structure may be subtle. For example, playback experiments have revealed that females and males can distinguish one

Table 1. Studies that have quantified and compared female and male vocalisations in (a) oscines and suboscines and (b) non-oscines. The tables include studies in which comparisons between male and female bird vocalisations have been quantified. The table is ordered by family in accordance with *Clements Checklist* (Clements *et al.*, 2019). Searches were conducted in *Google Scholar* using the key words “female”, “bird”, “avian”, “song”, “call”, “vocalisation” “song rate”, “song comparison”, “duet” and “dimorphism”. Many comparisons of male and female song are embedded in the literature and are not made apparent by paper titles, abstracts and key words alone. Thus, while this table is comprehensive, it is not exhaustive. Fields left blank indicate no data was available. Unless otherwise stated, vocalisation rate is based on natural rates, not rates that have been induced experimentally. Duetting species reported in this table focus on natural vocalisation rates outside of duets. Studies describing only one female were not included. Studies on seabirds and waterfowl have not been included because comparisons between males and females have been made extensively elsewhere [e.g. see James (1984), James & Robertson (1985) and Taoka & Okumura (1990)]. For a comprehensive summary of sexual comparisons between monomorphic species see Volodin *et al.* (2015). For a comprehensive summary of female New World blackbird song see Price (2009). For a comprehensive summary of song in wrens see Graves *et al.* (2009)

Family	Species	Common name	Breeding stage (pre-breeding, breeding, non-breeding)	Vocalisation rate compared to males (same, lower, higher)	Dimorphic or monomorphic/ equivalent vocalisations	Vocalisation length compared to males (same, shorter, longer)	Repertoire compared to males (same, different, smaller, larger)	Vocalisation type (shared, distinct from males)	Reference
(a) Oscine and suboscine passerines									
Thamnophilidae	*Hypocnemis cantator*	Warbling antbird		Higher	Dimorphic			Distinct	Seddon & Tobias (2006) Isler *et al.* (2007)
Thamnophilidae	*Hypocnemis peruviana*	Peruvian warbling antbird	Breeding Non-breeding	Lower	Dimorphic	Shorter	Different (fewer notes, less raspy notes)	Distinct	Tobias & Seddon (2009) Tobias *et al.* (2011)
Thamnophilidae	*Hypocnemis subflava*	Yellow-breasted warbling antbird	Breeding Non-breeding	Lower	Dimorphic	Shorter	Different (fewer notes, less raspy notes)	Distinct	Tobias & Seddon (2009) Tobias *et al.* (2011)
Thamnophilidae	*Myrmeciza longipes*	White-bellied antbird	Breeding Non-breeding	Lower (per hour)					Fedy & Stutchbury (2005)
Tyrannidae	*Nesotriccus ridgwayi*	Cocos flycatcher		Higher (playback used)	Dimorphic	Longer	Smaller (1 song type)	Distinct (song type III)	Kroodsma *et al.* (1987)
Maluridae	*Malurus coronatus*	Purple-crowned fairy-wren	Breeding	Lower				Distinct	Hall & Peters (2008)
Maluridae	*Malurus splendens*	Splendid fairy-wren	Breeding	Same (type I) Lower (type II) Higher (trill)	Monomorphic/ equivalent (type I song and trill)			Shared (type I song and various calls)	Greig & Pruett-Jones (2008)
Maluridae	*Malurus cyaneus*	Superb fairy-wren	Breeding	Lower	Monomorphic/ equivalent	Shorter	Smaller	Shared (type I songs) Distinct (female chatter songs)	Various authors including: Cain & Langmore (2015); Cooney & Cockburn (1995); Langmore & Mulder (1992); Kleindorfer *et al.* (2013); Evans & Kleindorfer (2016)
Maluridae	*Malurus melanocephalus*	Red-backed fairy-wren	Breeding Pre-breeding				Smaller		Dowling & Webster (2013)
Meliphagidae	*Anthornis melanura*	New Zealand bellbird	Breeding Non-breeding	Higher (breeding) lower (non-breeding)	Dimorphic	Shorter	Smaller (song and syllable)	Distinct	Brunton & Li (2006)
Meliphagidae	*Cardinalis cardinalis*	Northern cardinal		Lower	Dimorphic (louder second harmonics and syllables less stereotyped)			Shared	Yamaguchi (1998)
Meliphagidae	*Manorina melanocephala*	Noisy miner	Pre-breeding Breeding					Shared (multiple) Distinct (pew vocalisation)	Holt *et al.* (2017)
Meliphagidae	*Manorina melanophrys*	Bell miner	Breeding	Same (during feeding bouts)	Dimorphic (mew call)			Shared (mew call)	McDonald *et al.* (2007)
Meropidae	*Merops apiaster*	European bee-eater	Breeding		Monomorphic/ equivalent (provisioning call)			Shared (provisioning call)	Lessells *et al.* (1995)
Acanthizidae	*Acanthiza pusilla*	Brown thornbill		Same (song and mimicry when captured)				Shared (both sexes mimic)	Igic & Magrath, (2013)

(Continues)

Table 1. *(Cont.)*

Family	Species	Common name	Breeding stage (pre-breeding, breeding, non-breeding)	Vocalisation rate compared to males (same, lower, higher)	Dimorphic or monomorphic/equivalent vocalisations	Vocalisation length compared to males (same, shorter, longer)	Repertoire compared to males (same, different, smaller, larger)	Vocalisation type (shared, distinct from males)	Reference
Pomatostomidae	*Pomatostomus ruficeps*	Chestnut-crowned babbler	Pre-breeding Breeding					Shared (numerous) Distinct (maternal contact call, rising chirrup)	Crane *et al.* (2016)
Psophodidae	*Psophodes cristatus*	Chirruping wedgebill	Breeding	Lower	Dimorphic	Shorter	Smaller	Distinct	Austin *et al.* (2019*a*)
Psophodidae	*Psophodes olivaceus*	Eastern whipbird	Breeding	Lower	Dimorphic (song type II and duet song)	Shorter (song type II)	Larger (song type II – more introductory elements)	Shared (song type II) Distinct (duet song)	Rogers (2005)
Artamidae	*Gymnorhina tibicen*	Australian magpie	Breeding	Higher	Dimorphic Monomorphic/equivalent		Larger (carol syllables – may vary with sub-species)	Distinct (4 carols) Shared (2 carols, warble song)	Farabaugh & Brown (1991) Baker (2009) Dutour & Ridley (2020)
Malaconotidae	*Laniarius atroflavus*	Yellow-breasted boubou	Breeding	Lower (rates vary for vocalisation types)	Dimorphic	Shorter (vocalisation dependent)	Different (songs and calls) Larger (5 types of vocalisation)	Distinct (3 song types, 2 call types)	Wheeldon *et al.* (2020)
Malaconotidae	*Laniarius funebris*	Slate-coloured boubou	Pre-breeding Breeding	Lower	Dimorphic Monomorphic/equivalent	Same (element length)	Different (song repertoires) *described as similar (song types and elements)	Shared (various calls) Distinct (duet song)	Sonnenschein & Reyer (1983) Gahr *et al.* (1998)
Corcoracidae	*Struthidea cinerea*	Apostlebird	Breeding					Shared (multiple vocalisations)	Warrington *et al.* (2014)
Monarchidae	*Grallina cyanoleuca*	Australian magpie lark	Breeding Non-breeding	Lower (solo songs)			Same (3–6 motif types)	Shared (9 different motifs)	Tingay (1974) Hall (2006)
Corvidae	*Pyrrhocorax pyrrhocorax*	Red-billed chough	Breeding		Monomorphic/equivalent Dimorphic (common call)			Shared	Laiolo *et al.* (2000)
Paridae	*Poecile atricapillus*	Black-capped chickadee			Dimorphic Monomorphic/equivalent (vocalisation dependent and note dependent)		Same	Shared (fee-bee song, tseet calls, chick-a-dee call)	Hahn *et al.* (2013) Campbell *et al.* (2016*a*,*b*) Guillette *et al.* (2010)
Paridae	*Poecile carolinensis*	Carolina chickadee			Dimorphic Monomorphic/equivalent (note dependent, site dependent)		Same	Shared (chick-a-dee call)	Freeburg *et al.* (2003)
Paridae	*Poecile gambeli*	Mountain chickadee			Dimorphic		Same	Shared (tseet call)	Guillette *et al.* (2010)
Paridae	*Parus major*	Great tit	Breeding	Lower	Dimorphic (quiet call)			Distinct (quiet call)	Gorissen & Eens (2004)
Hirundinidae	*Tachycineta bicolor*	Tree swallow	Breeding	Lower (song)	Monomorphic/equivalent (calls)		Same	Shared (5 call types and 1 song)	Sharman *et al.* (1994)
Hirundinidae	*Hirundo rustica erythrogaster*	Barn swallow	Breeding	Lower	Dimorphic	Shorter (songs) Longer (element duration)	Smaller (lower element diversity)	Distinct	Wilkins *et al.* (2020)
Troglodytidae	*Thryothorus*	Various							Graves *et al.* (2009) – see Table 5
Troglodytidae	*Thryothorus rufalbus*	Rufous-and-white wren		Lower	Dimorphic	Same	Smaller (whole song repertoires) Same (syllable types)	Distinct and shared	Brenowitz & Arnold (1986) Mennill & Vehrencamp (2005)

Table 1. *(Cont.)*

Family	Species	Common name	Breeding stage (pre-breeding, breeding, non-breeding)	Vocalisation rate compared to males (same, lower, higher)	Dimorphic or monomorphic/ equivalent vocalisations	Vocalisation length compared to males (same, shorter, longer)	Repertoire compared to males (same, different, smaller, larger)	Vocalisation type (shared, distinct from males)	Reference
Troglodytidae	*Thryothorus fasciatoventris*	Black-bellied wren		Same	Dimorphic	Shorter	Smaller	Distinct (also have sex-specific bell calls)	Logue & Gammon (2004) Rendall *et al.* (2007)
Troglodytidae	*Thryothorus nigricapillus*	Bay wren	Breeding		Dimorphic			Distinct	Brenowitz & Arnold (1985) Brenowitz & Arnold (1986) Levin (1996)
Troglodytidae	*Troglodytes aedon*	House wren	Breeding	Lower					Krieg & Getty (2016)
Troglodytidae	*Campylorhynchus rufinucha*	Rufous-naped wren	Breeding		Dimorphic		Same (sampling incomplete)	Shared	Bradley & Mennill (2009)
Cinclidae	*Cinclus cinclus*	White-throated dipper	Pre-breeding	Lower (see Fig. 2)	Monomorphic/ equivalent (pre-breeding males and females)			Shared	Magoolagan *et al.* (2019)
Sturnidae	*Onychognathus morio*	African red-winged starling	Breeding	Lower	Monomorphic/ equivalent (unitary whistles and some shared composite whistles) Dimorphic (9 distinct composite whistles)	Same (frequency and duration unitary whistles)	Same (unitary whistles) smaller (composite whistles)	Shared (unitary whistles and composite whistles) Distinct (9 composite whistles)	Houdelier *et al.* (2012)
Sturnidae	*Sturnus vulgaris*	European starling	Non-breeding		Dimorphic	Shorter	Smaller	Shared	Henry & Hausberger (2001) Pavlova *et al.* (2005)
Sturnidae	*Lamprotornis superbus*	superb starling	Breeding		Monomorphic/ equivalent (pitch)		Same	Shared	Pilowsky &Rubenstein (2013)
Turdidae	*Sialia sialis*	eastern bluebird	Breeding		Monomorphic/ equivalent	Shorter	Same	Shared	Rose *et al.* (2018) Sikora *et al.* (2021)
Muscicapidae	*Erithacus rubecula*	European robin			Dimorphic	Shorter	Smaller		Hoelzel (1986)
Ptiliogonatidae	*Phainopepla nitens*	Phainopepla	Breeding	Same (mimicry)				Shared (mimicry)	Chu (2001)
Ploceidae	*Ploceus bicolor*	Forest weaver	Breeding		Monomorphic/ equivalent		Same	Shared	Gahr *et al.* (2008) Wickler & Seibt (1980)
Estrildidae	*Uraeginthus bengalus*	Red-cheeked cordon-bleu	Breeding	Lower	Dimorphic	Shorter			Gahr & Guttingery (1986)
Estrildidae	*Uraeginthus cyanocephalus*	Blue-capped cordon-bleu		Lower	Dimorphic	Shorter	Smaller (syllables) same (song type)	Shared	Geberzahn & Gahr (2011)
Estrildidae	*Taeniopygia guttata*	Zebra finch			Dimorphic			Shared (long call)	Vicario *et al.* (2001)
Prunellidae	*Prunelli collaris*	Alpine accentor	Breeding			Shorter	Different (more repeated syllables)	Shared (trill)	Langmore *et al.* (1996)
Fringillidae	*Fringilla coelebs*	Common chaffinch	Non-breeding Breeding		Dimorphic		Smaller (in breeding season)	Shared (various including: tupe chink, zzzz, flight and alarm) Distinct (some sexual calls)	Marler (1956) Bergmann (1993) Marler (2004*a*)
Fringillidae	*Serinus canaria domestica*	Canary	Non-breeding	Lower	Dimorphic	Shorter (songs and syllable length)	Different (less stereotyped)	Distinct (see Fig. 4)	Ko *et al.* (2020)
Passerrelidae	*Aimophila R. ruficauda*	Stripe-headed sparrow	Pre-breeding Breeding	Higher	Dimorphic	Longer	Larger different (no chatter note types are shared)	Shared (chatter) and ticking calls)	Illes & Yunes-Jimenez (2009) Illes (2015)
Passerrelidae	*Junco hyemalis*	Dark-eyed junco	Breeding	Same (trill rate)	Dimorphic (lower minimum and peak frequencies)	Same	Smaller (1 song type)	Shared (quiet song, trill similar to male).	Reichard *et al.* (2018)
Passerellidae	*Melospiza melodia*	Song sparrow	Pre-breeding Breeding	Lower	Monomorphic/ equivalent	Shorter	Smaller (fewer note types)	Shared	Arcese *et al.* (1988)

(Continues)

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Passerellidae	*Pipilo crissalis*	California towhee	Breeding	Same (call rate)	Monomorphic/ equivalent (squeal vocalisation)		Same (squeal vocalisation)	Shared (squeal vocalisation)	Benedict & McEntee (2009)
Passerellidae	*Zonotrichia leucophrys nutallia*	White-crowned sparrow	Pre-breeding	Lower	Dimorphic	Shorter		Shared	Baptista *et al.* (1993)
Passerellidae	*Zonotrichia leucophrys oriantha*	White-crowned sparrow	Pre-breeding	Lower	Monomorphic/ equivalent			Shared	Baptista *et al.* (1993)
Icteridae	various								see Price (2009) for descriptions in various species
Icteridae	*Agelaius phoeniceus assimilis*	Red-winged blackbird	Breeding		Dimorphic (location dependent)	Longer		Distinct (song type I and song type II)	Whittingham *et al.* (1992) Beletsky & Corral (1983) Beletsky & Orians (1985)
Icteridae	*Icterus icterus*	Venezuelan troupial	Breeding Non-breeding	Higher (year round solo songs)	Dimorphic	Shorter	Same (syllables)	Shared	Odom *et al.* (2016)
Icteridae	*Icterus pustulatus*	Streaked-back oriole	Breeding Post-breeding	Higher	Monomorphic/ equivalent	Same	Same (syllables)	Shared	Price *et al.* (2008)
Parulidae	*Basileuterus rufifrons*	Rufous-capped warbler	Breeding Non-breeding		Dimorphic	Shorter	Smaller (syllable number and diversity)	Shared	Demko & Mennill (2018)
Parulidae	*Setophaga ruticilla*	American redstart			Dimorphic	Shorter	Same	Shared (flight call)	Griffiths *et al.* (2016)
(b) Non-oscines									
Apterygidae	*Apteryx mantelli*	North Island brown kiwi			Dimorphic	Same	Same (syllables per call)	Shared	Corfield *et al.* (2008)
Apterygidae	*Apteryx haasti*	Great spotted kiwi	Breeding		Dimorphic	Longer	Same (number of syllables)	Shared	Dent & Molles (2015)
Apterygidae	*Apteryx oweni*	Little spotted kiwi	Breeding Non-breeding	Lower	Dimorphic	Same	Same (number of syllables and type of syllables except 'hook' in males)	Shared	Digby *et al.* (2014) Digby *et al.* (2013)
Cracidae	*Crax rubra*	Great curassow						distinct (bark call)	Baldo & Mennill (2011)
Columbidae	*Streptopelia decaocto*	Collared dove	Breeding	Lower	Dimorphic		Same	Shared (perch coo)	Ballintijn & Cate (1997)
Mesitornithidae	*Monias benschi*	Subdesert mesite	Breeding	Higher (female solo)	Dimorphic	Longer (female solo)	Different	Shared (Nak alarm call and Large chorus) Distinct (Purr and solo Tu-Tu+)	Seddon (2002)
Cuculidae	*Centropus coucal grillii*	African black coucal	Breeding	Higher				Shared	Goymann *et al.* (2004)
Cuculidae	*Centropus phasianinus*	Pheasant coucal	Breeding		Dimorphic	Same	Same	Shared	Maurer *et al.* (2008)
Cuculidae	*Cuculus canorus*	Common cuckoo	Breeding	Lower	Dimorphic	Shorter	Smaller (number of syllables)	Distinct	Deng *et al.* (2019)
Podargidae	*Podargus ocellatus*	Marbled frogmouth			Dimorphic	Shorter	Smaller (fewer elements)	Shared	Smith & Jones (1997)
Trochilidae	*Lampornis clemenciae*	Blue-throated hummingbird			Dimorphic			Distinct (type 2 song)	Sigler Ficken *et al.* (2000)
Trochilidae	*Calypte costae*	Costa's hummingbird	Pre-breeding	Lower	Dimorphic			Distinct	Clark *et al.* (2018)
Rallidae	*Munia Lonchura phaethontoptila*	White-rumped munia			Dimorphic	Longer	Different	Distinct	Mizuta *et al.* (2003)
Tytonidae	*Tyto novaehollandiae castanops*	Tasmanian masked owl	Breeding		Dimorphic	Same	Same (shared calls) larger (more elements to chatter call)	Shared (chatter call)	Todd *et al.* (2018)
Strigidae	*Otus asio*	Eastern screech-owl			Dimorphic	Longer	Same	Shared (bounce call)	Cavanagh & Ritchison (1987)

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Strigidae	*Otus kenicottii*	Western screech-owl	Breeding		Dimorphic (frequencies)	Same	Same	Shared (bounce call and double trill)	Herting *et al.* (2001)
Strigidae	*Strix varia*	Barred owl	Breeding		Dimorphic		Same	Shared (12 calls) distinct (female begging call)	Odom & Mennill (2010)
Meropidae	*Merops apiaster*	European bee eater	Breeding		Monomorphic/ equivalent (provisioning call)			Shared (provisioning call	Lessells *et al.* (1995)
Strigopidae	*Nestor notabilis*	Kea		Lower (chatter calls)	Dimorphic	Shorter (chatter, mew, screech and warble)	Same	Shared	Schwing *et al.* (2012)
Cacatuidae	*Probosciger aterrimus*	Palm cockatoo	Breeding	Higher (solo calls)				Shared (various)	Zdenek *et al.* (2015)
Psittacidae	*Poicephalus rufiventris*	African orange-bellied parrot	Breeding		Dimorphic			Shared	Venuto *et al.* (2000)
Psittacidae	*Aratinga canicularis*	Orange-fronted conure		Higher				Shared (chee contact call)	Balsby & Scarl (2008)

another's calls (Kipper *et al.*, 2015) and songs (Mulder *et al.*, 2003), even in cases in which structural differences were not apparent to researchers. Human hearing and perception of bird songs and calls can be very different from those of the birds themselves (Dooling & Prior, 2017), and so examining the structure of vocalisations in fine detail, and using experiments to 'ask' study species themselves about sex differences in vocalisations, can be essential in furthering our understanding of the function of female vocalisations.

Sex differences in the delivery of vocalisations can also vary across species, a fact that may partially account for the former prevailing notion that females do not sing (see Table 1a and b). Females may sing less often than males [e.g. banded wrens *Thryophilus pleurostictus* (Hall, Rittenbach & Vehrencamp, 2015); yellow warblers *Dendroica petechia* (Hobson & Sealy, 1990)], more often than males (e.g. streak-backed orioles *Icterus pustulatus*; Price *et al.*, 2008) or in different but specific social contexts [e.g. song sparrows *Melospiza melodia* (Arcese, Stoddard & Hiebert, 1988; Langmore, 2002)]. However, even in species where song rates in females are lower than in males (e.g. Houdelier, Housberger & Craig, 2012; Magoolagan *et al.*, 2019), lower rates may not necessarily correlate with lower ecological importance.

(2) Similarities between female and male vocalisations

While vocal structures and vocal behaviours are seldom compared between sexes (see Table 1a and b for a comprehensive list of studies that have compared vocalisations between the sexes), there are good theoretical reasons for why some vocalisations are likely to be similar between males and females. The need to communicate location to family members or other allies, indicate the presence of food, or warn conspecifics of danger, may be similarly important for females and males, and this may account for why some vocalisations used in these contexts tend to be sexually monomorphic. Provisioning calls in European bee-eaters *Merops apiaster* (Lessells, Rowe & McGregor, 1995), alarm calls in European herring gulls *Larus argentatus* (Hardouin *et al.*, 2014), and distress calls in some parrots (Venuto *et al.*, 2001) show little or no distinguishable differences between males and females (see also Volodin *et al.*, 2015). Lack of sexual dimorphism between male and female vocalisations can also be found in complex vocalisations such as the songs of eastern bluebirds *Sialis sialis* (Rose *et al.*, 2018) and superb starlings *Lamprotornis superbus* (Pilowsky & Rubenstein, 2013). In addition to vocalisation structures, the presence of vocalisations and the rate at which they are produced can be the same for females and males (Rose *et al.*, 2018). Moreover, vocalisation rates can vary in a similar manner within both sexes according to age (e.g. Langmore *et al.*, 1996), breeding status (e.g. Portelli *et al.*, 2009; Crane, Savage & Russell, 2016), or levels of intrasexual competition in the population (e.g. Baptista *et al.*, 1993). Yet, even where such similarities exist, there are reasonable theoretical grounds for expecting that most if not all species may have at least some vocalisations that function differently between females and males, so perhaps similarities in vocal structures have been overstated. Monogamy and ongoing resource competition have been argued to select for convergence of signalling behaviour between females and males in some species (e.g. see Tobias *et al.*, 2011). However, intersexual conflicts over allocation of resources and paternity of offspring are thought to be ubiquitous among bird species, even among those with biparental care [e.g. see Eens & Pinxten (1995) and Korpimaki, Salo & Valkama (2011)]. Females invest in offspring for which they are certain of parentage, whereas male paternity is not assured (LeBas, 2006). Therefore, we must be careful not to generalise about the function of vocalisations for males and females, especially in species in which only a small subset of the vocal repertoire has been examined (see Table 1a and b).

(3) Foundations for future work

Our review reveals that not only are comparisons of male and female vocalisations relatively rare, but they are often hidden in the literature or are not considered as comprehensively as other results (see Table 1a and b). Further, there are many cases where male and female vocalisation structure and behaviour are described as 'different' between the sexes, yet these differences have never been tested. There are also studies in which female vocalisation structure and behaviour are described based on only one or two females [e.g. see Kasumovic, Ratcliffe & Boag, (2003), Taff, Littrell & Freeman-Gallant (2012), Campbell *et al.* (2016*a,b*) and MacDonald, Delancey & Islam (2019)]. These studies are of course important for identifying females that sing and should be documented (see Odom & Benedict, 2018), and small sample sizes probably reflect the lower vocalisation rates of females of some species. Yet, the question of why some individual females may vocalise and others may not is fascinating to consider, and further in-depth studies in these species would prove useful in identifying the ecological drivers of female vocalisations. Important exceptions to these statements can be found in literature on pelagic and waterbird species where formal comparisons between male and female vocalisations have been made extensively. In such species, vocalisations are often shared between the sexes. However, when the acoustic properties of such vocalisations are measured, sexual dimorphism often becomes apparent [e.g. see James (1984), James & Robertson (1985) and Taoka & Okumuru (1990)]. These differences are likely important for individual recognition in group living (Jouventin & Aubin, 2002), and may also play integral roles in inter- and intrasexual interactions (e.g. see Speirs & Davis, 1991). The literature on pelagic and waterbird species serves as an example of why detailed comparisons between the sexes of even seemingly identical vocalisations can be revealing. The literature on species that duet is also relatively comprehensive [see Hall (2004, 2009), Logue & Hall (2014) and Tobias *et al.* (2016)] and has added tremendously to our understanding of female birdsong. Further, the ability to compare male and female responses to playback in duetting species continues to provide valuable insights into the function of female vocalisations. While experimental studies play a vital role in establishing the function of vocalisations, sometimes lacking are systematic observations of natural singing behaviours in the wild, accompanied by quantitative descriptions of male and female vocal structure. Both approaches are essential to reaching a comprehensive understanding of all kinds of vocal behaviour (Catchpole & Slater, 2008). Observational studies of females that quantify natural vocalisation rates independently and in relation to males and at different stages of the reproductive cycle (during the breeding season and outside of it) will be particularly valuable in inferring potential functions of vocalisations. Our understanding of avian vocalisations would also benefit from a more unified approach to comparative studies. Descriptions of female vocalisations and intersexual comparisons of vocalisation structure, repertoire sizes and how and when each type is used will provide a firm foundation for increased understanding of female *and* male vocalisations across the Aves.

III. FUNCTIONS OF FEMALE VOCALISATIONS

Similarities and differences in vocalisations between the sexes may be accounted for, in part, by the context in which they are used. For example, if females and males share the same ecological pressures, vocalisations may be used similarly between the sexes. However, where ecological roles diverge, differences in vocalisations can arise. Unfortunately, experimental evidence indicating direct benefits to the singer is relatively rare and more such studies are urgently needed (Riebel *et al.*, 2019). Nonetheless, regardless of the nature of their evidence, the examples we cite here provide a foundation for which exciting future experimental research on female vocalisation function can be based.

(1) Mates

In birds, males usually have a greater variance in reproductive success than females, so that males compete for access to females and females are choosy (Trivers, 1972). Consequently, perhaps due to their often-overt singing behaviours, intersexual selection for vocal extravagance was conventionally thought to be generally stronger in males than in females [e.g. see Janicke *et al.* (2016) and Catchpole & Slater (2008)]. Therefore, it is possible that complex song in males may provide information about the male singer's ability to deliver direct or indirect benefits to the female. However, where females do compete for males, such as in some polygynous or in sex-role-reversed species, intersexual selection can operate strongly on females and their vocalisations as well (Langmore, 1998; Hare & Simmons, 2018). For example, experiments show that polygynous and polyandrous female dunnocks *Prunella modularis* use trill calls to attract established resident mates (Langmore & Davies, 1997). Similarly, in the polygynandrous alpine accentor *Prunella collaris*, females must compete with one another for copulations with males to ensure male assistance with parental care (Davies *et al.*, 1996), and they do so by singing to attract mates during their fertile period (Langmore *et al.*, 1996). In sex-role-reversed Eurasian dotterels *Charadrius morinellus*, females attract mates by performing display flights incorporating 'peep' vocalisations (Kålås & Byrkjedal, 1984). In cases where sexual selection is symmetrical between the sexes, both sexes can use song to advertise for mates (e.g. *Hypocnemis* antbirds; Tobias *et al.*, 2011). While clear examples of female vocalisations used to attract mates may be viewed as exceptions to the rule, this view is based on current information which is incomplete. It is also possible that further examples have simply been overlooked due to the often less-conspicuous behaviours of females relative to males (Eens & Pinxten, 1998).

A range of female vocalisations appear to play subtler roles in deriving indirect benefits from males. In some species, females produce specific songs or calls during their fertile period and these vocalisations could facilitate male–male competition by attracting extra-pair males (Montgomerie & Thornhill, 1989). For example, in the cooperatively breeding white-throated magpie-jay *Calocitta formosa*, loud begging-like calls made by breeding females prior to incubation may signal the female's fertility to extra-group males, thereby inducing male–male competition for extra-pair copulations (Ellis, Langen & Berg, 2009). Indeed, these calls are so loud they can be heard well beyond the female's territory boundary (Ellis *et al.*, 2009). Use of loud begging-like calls has also been noted in the brown jay *Cyanocorax morio* (Lawton & Lawton, 1985), a cooperatively breeding species where the female's social mate only sires 17% of offspring (Williams, 2004; Williams & Rabenold, 2005). These examples suggest that female sexual advertisement for indirect benefits is not always under selection for complexity, and indeed may have acoustic features similar (or identical) to those of begging calls.

Females also vocalise to advertise to males for direct benefits, such as food. In most species of bird, females incubate more than males and since incubation is energetically costly (Cresswell *et al.*, 2004), females may increase their present or future reproductive success by soliciting food from their mates or other breeding partners. Additionally, because of the shared interest between males and females during nesting (Moore & Rohwer, 2012), it is argued that signals produced at this time should represent an honest signal of need from females to their mates (Tobias & Seddon, 2002). Indeed, there is empirical evidence to support this hypothesis. For example, in an elegant experiment, female pied flycatchers *Ficedula hypoleuca* who had their primary flight feathers clipped begged more during incubation than control females, and the mates of clipped females increased the amount they fed their mates in response to the increased call rates (Cantarero *et al.*, 2014). The vocalisations of clipped females were longer than those of unclipped females and begging postures were also altered. Similarly, the begging calls of black-capped chickadees *Poecile atricapillus* produced during the female's fertile period are shown to be associated with hunger, with female call rates dropping when food supplies are supplemented (Otter, Atherton & van Oort, 2007). Female call rates may also reflect habitat quality with females from resource-poor young forests calling more than females from resource-rich older forests providing further evidence that these begging calls are honest signals of need (Otter *et al.*, 2007). However, females may also be able to exploit male provisioning behaviour. For example, begging calls of European robins *Erithacus rubecula* are suggested to incite allo-feeding by males but also attract extra-pair mates (Tobias & Seddon, 2002). Hence, paired males of this species may be forced to increase feeding rates to females in order to reduce female begging and the associated risk of cuckoldry that has been described as a type of 'blackmail' by females (Tobias & Seddon, 2002). As can be seen, female vocalisations during nesting can be a powerful form of acoustic communication that has the potential greatly to influence the physical and reproductive fitness of females and the fitness of their mates and suitors. Consequently, we believe these often-overlooked vocalisations will be valuable for increasing our understanding of female vocalisations and suggest they are worthy of increased attention.

Female vocalisations made during courtship may be important for signalling sexual receptivity to displaying males or in altering male display behaviour in subtle ways. For example, female whitethroats *Sylvia communis* jump and use two types of call to influence male courtship behaviour; however, each component of the display (jump and call type) elicits a different response from males (Balsby & Dablesteen, 2002). Similarly, female blackbirds *Turdus merula* utter quiet copulation trills that are thought to elicit mounting by males (Dabelsteen *et al.*, 1998). Playback experiments on canaries *Serinus canaria* have shown that females will use female-specific trills while performing copulation solicitation displays (Amy *et al.*, 2015). The use of these trills in conjunction with copulation displays occurred most frequently in response to male songs of high performance: i.e. songs of greater complexity sung at a higher rate. Vocalisations in the context of courtship may also be crucial for predicting reproductive output for females. In a recent study it was shown the number of chatter vocalisations produced by female brown-headed cowbirds *Molothrus ater* in response to male song displays predicted the number of eggs produced in this species (Kohn, 2018). Further it is also been suggested that in some birds, such as blue grouse *Dendragapus obscurus* (Bendell & Elliott, 1967) and scrub jays *Aphelocoma coerulescens* (Goodwin, 1976), copulation calls may incite male–male competition (Montgomerie & Thornhill, 1989). Clearly, such precopulatory calls by females are not uncommon across the Aves, and may provide benefits to females while also influencing male courtship. As a consequence, we suggest that pre-copulation calls by females represent an intriguing and important avenue for future research.

Vocalisations made by females may also function to signal when it is not a suitable time for fertilisation ('anti-copulation calls'). The post-oviposition cackle made by female domestic fowl *Gallus Gallus domesticus* is suggested to signal non-receptivity to mates (Pizzari & Birkhead, 2001). Males of this species are socially dominant and copulations with females can be forced (McBride, Parer & Foenander, 1969), in some cases resulting in lethal internal injuries to females (Pizzari & Birkhead, 2001). In addition, artificial insemination experiments suggest that time of day can affect the success of fertilisation, and also that fertilisation after oviposition is relatively infrequent (Christensen & Johnston, 1975). As such, it is thought that these vocalisations may prevent sexual harassment from males at a time that is less likely to result in successful fertilisation (Pizzari & Birkhead, 2001). However, an alternative explanation is that these 'distress calls' actually provide an example of copulation calls. If females derive indirect benefits from mating with a more dominant male, then the 'distress' calls can actually be considered a form of mate attraction. Indeed, cackle calls in female red junglefowl *Gallus gallus spadiceus* are shown to attract males, increasing agonistic interactions between males and often resulting in matings from dominant males (Thornhill, 1988). Evidently, both complex and simple female vocalisations play important roles in interactions with mates in both oscines and non-oscines alike.

(2) Rivals

Intrasexual competition is believed to be the main driving force behind the evolution of secondary sexual characteristics in females (West-Eberhard, 1984; Clutton-Brock, 2009), and given that competitive signals are associated with the defence of mates and resources such as territories (West-Eberhard, 1984), it should not seem surprising that female birds would use vocalisations to deter rivals. Indeed, although experimental evidence is lacking, several studies support the hypothesis that female birds use vocalisations to mediate intrasexual competition for territories or mates (Langmore, 1998; Cain, Cockburn & Langmore, 2015; Illes, 2015).

Competition for reproductive resources has been shown to be high across the animal kingdom (e.g. Robinson & Kruuk, 2007; Rosvall, 2008; Watson & Simmons, 2010) and so the ability to defend a territory can be particularly important for nesting success in female birds. If a resident bird is evicted from a territory during the breeding season, the likelihood of finding a new territory in time to breed is low (Fedy & Stutchbury, 2005). In addition, vocalisations may provide females with direct benefits (Cain & Langmore, 2015). In New Zealand bellbirds *Anthornis melanura* female song plays a crucial role in intrasexual competition, and both spontaneous song rates and song complexity in females (but not males) strongly predict the number of fledglings produced (Brunton, Roper & Harmer, 2016). In superb fairy-wrens *Malurus cyaneus*, females with higher response rates to simulated intruders are more likely to have successful nesting attempts, although rates of spontaneous singing do not relate to any known measure of fitness (Cain *et al.*, 2015). Variation among species in female singing behaviour may thus correlate with variation in female–female competition for nesting resources. For example, in some species, such as eastern whipbirds *Psophodes olivaceus* (Rogers, Langmore & Mulder, 2007), high female-to-male sex ratios at hatching have been recorded, and in such cases the pressure to keep same-sex rivals at bay is particularly high. This may explain why females in this species coordinate their songs with males as duets. In other species, such as superb fairy-wrens, females disperse from natal territories (Cockburn *et al.*, 2008) and must establish their own in order to survive (Cain *et al.*, 2015); consequently, rival females pose a significantly greater threat to resident females than do males.

In some species, competition among females for breeding territories can be so extreme that females will even destroy the nesting attempts of rivals to facilitate the acquisition of further mates or to reduce competition for nesting resources. For example, video footage and anecdotal reports show that female superb lyrebirds *Menura novaehollandiae*, a species that displays female-only parental care, destroy the nests of rival females during the breeding season and it is suggested that this high intrasexual competition between females may account for the presence of elaborate and complex female song in this species (Dalziell & Welbergen, 2016; Austin *et al.*, 2019*b*). House wrens *Troglodytes aedon* are known to engage in ovicide in neighbouring nests, destroying any unattended clutches that are found (Belles-Isles & Picman, 1986; Krieg & Getty, 2016). Female house wrens that sing more at intruders lose significantly fewer eggs (Krieg & Getty, 2016). Thus, female vocalisations are likely to be essential not only in defending valuable foraging territory from rival females, but also in directly ensuring the survival of offspring in the face of competition for resources for reproduction. Consequently, the importance of female interactions at and around the nest, and the vocalisations made in this context, cannot be overstated. Studies that focus on female behaviours and vocalisations in the context of the nest will likely provide valuable advancement of our understanding of the evolutionary drivers that give rise to female vocalisations generally.

While the majority of studies on female territory defence have been conducted on oscine passerines, female territory defence is not limited to this group. In parrots, for example, selection to defend territories immediately around nest hollows is shared across species, and defence is mediated through vocalisations (Bradbury & Balsby, 2016). Mating pairs of peach-faced lovebirds *Agapornis roseicollis* (Mebes, 1978) and yellow-naped amazon parrots *Amazona auropalliata* (Wright & Dorin, 2001) are known to defend their nest sites using coordinated joint complex vocalisations that are referred to as 'song'. In the case of the latter species, duets are highly structured and as complex as many duets exhibited by oscine passerines (Wright & Dahlin, 2007). Palm cockatoos *Probosciger aterrimus* defend year-round territories and both sexes have a large vocal repertoire (Zdenek, Heinsohn & Langmore, 2015). While field-based observations suggest that males more frequently defend nesting territories than females, females also perform elaborate displays involving vocalisations and body movements (such as foot stamping and wing spreading) that are suggested to be used to defend their hollows (Murphy, Legge & Heinsohn, 2003).

The examples provided above suggest that the hypotheses that territorial interactions are a major driver of vocalisations in female birds is probably correct; however, conclusive experimental evidence is needed on the territorial function of female song (Riebel *et al.*, 2019). Moreover, evidence that female birds are competing for resources crucial to nesting is still lacking.

(3) Kin and other allies

Vocalisations play a pivotal role in the recognition of and communication with kin and other allies, and may be particularly important for female birds because of the relatively higher costs associated with reproduction for females. In certain ecological contexts, recognition by vocalisations alone may be favoured, such as in flock situations or group foraging (Bradbury & Balsby, 2016) as well as flight calls made during migration and movement (Marler, 2004*a*). The costs and benefits of kin and social group recognition can differ between the sexes because of sex differences in parental roles, certainty of paternity, or other ecological and social factors (Waldman, 1988). As a consequence, sexual differences in communication mechanisms for recognising kin are likely, and more so in cooperatively breeding species. Recent research suggests that vocal communication in cooperatively breeding species is both complex and diverse (Leighton, 2017). That female breeders are often the epicentre of these cooperative groups (Caffrey, 2000; Cockburn *et al.*, 2008; Crane *et al.*, 2016) suggests that a focus on female vocalisations may provide an efficient way to unravel complex vocal communication in cooperatively breeding species.

Differential selection on female and male vocalisations may occur early in development, particularly if there is competition among kin. For example, food begging calls of chipping sparrow *Spizella passerina* nestlings have been shown to become sexually dimorphic at approximately 11–14 days post hatching with female calls showing less diversity in structure than male calls (Liu, Wada & Nottebohm, 2009). While the authors suggest such differences occur because females do not sing as adults in this species (Liu *et al.*, 2009), it is also possible that female and male chipping sparrows experience different selective pressures within the nest itself, resulting in functionally distinct vocalisations. Indeed, sexual differences in non-vocal behaviours have been shown to occur in nestlings (Fresneau & Müller, 2016), suggesting that at least in some species, selection for sex-specific behaviours begins before fledging.

Sex differences in nestling vocalisations could also be affected by competition among kin. For example, parents may increase their inclusive fitness by feeding one sex more than the other (Frank, 1990; Mainwaring, Lucy & Hartley, 2011; Lees *et al.*, 2018), and parents could use sex differences in vocalisations to distinguish between female and male chicks. However, if sexual dimorphism of vocalisations facilitates parental discrimination of young, we would expect selection for mimicry of calls made by the preferred sex, while the preferred sex would be under selection for innovation. Hence, the lack of sexual dimorphism of vocalisations in some young birds and the delay in developing differences in others may in fact function to prevent parental discrimination. For example, barn swallow *Hirundo rustica* nestlings have been shown to have sexually dimorphic calls from 16 days old, but 12-day-old nestlings appear to be identical (Saino *et al.*, 2003). This begs the question: are there identifiable social or ecological factors that occur after 12 days of development that may favour the sexual divergence of vocalisations? Identifying these factors would help advance our understanding of the development of differences in female and male vocalisations. Moreover, the presence of these differences so early in development highlights the importance of examining sex-specific vocalisations from within the nest.

Vocalisations can also function to facilitate reciprocal relationships among species, and sex differences in such vocalisations would be expected where the sexes have different ecological roles. Some fascinating examples of such mutualistic vocalisations exist, such as used in interactions between dwarf mongoose *Helogale parvula* and two species of hornbill *Tockus deckeni* and *T. flavirostris* in Kenya (Anne & Rasa, 1983), as well as between human honey hunters and greater honeyguides *Indicator indicator* in Mozambique (Spottiswoode, Begg & Begg, 2016). At this stage, it is unclear whether sex differences in interspecific communication with mutualists exist, but this provides a promising area for future research.

(4) Predators and parasites

Predator and brood parasite avoidance and deterrence is a key component of survival for many adult birds and their young (Lima, 2009) and so sex differences in reproductive investment can be expected to result in sex differences in alarm call structure and production. In birds, alarm calls may signal danger (Griesser, 2009) or incite conspecifics to mob (Langmore *et al.*, 2012; Wheatcroft & Price, 2018). They can further be functionally referential (Gill & Sealy, 2004; Feeney *et al.*, 2013) or indicate the urgency of the threat (Leavesley & Magrath, 2005). Sexual dimorphism in alarm call structure and behaviour is not uncommon and these differences may be particularly apparent during times of breeding (Marler, 2004*a*). For example, when confronted with a mammalian nest predator, female yellow warblers *Dendroica petechia* respond more quickly and intensely than males, using 'chipping' alarm vocalisations in conjunction with distraction displays (Hobson, Bouchart & Sealy, 1988; Hobson & Sealy, 1990), while female hooded warblers *Wilsonia citrina* respond to brown-headed cowbirds *Molothrus ater*, a known brood parasite, with greater intensity and with more alarm calls than males (Mark & Stutchbury, 1994). Yet, to date, surprisingly little investigation has been conducted to quantify and account for sex differences in alarm calling.

Both female and male birds must trade off the benefits of vocalising at the nest with the risks of inadvertently attracting the attention of predators and brood parasites, but differential investment in nesting effort between the sexes may be expected to select for sex differences in vocal behaviour. There is good general evidence that alarm calling can be costly. For example, mobbing vocalisations have been shown to increase the risk of predation by specialised nest predators such as pine martins (Krams *et al.*, 2007), and can be associated with an increased risk of brood parasitism in some cuckoo hosts (e.g. Welbergen & Davies, 2009). Given these costs, we might expect differences between female and male alarm call structure and strategies around the nest; however, whether these differences exist is yet to be thoroughly investigated in most species. Singing can also be costly. For example, systematic observations of nesting superb fairy-wrens *Malurus cyaneus* revealed that females sing significantly closer to the nest and sing from within the nest more often than males. Female song rate while incubating and when chicks were present is also positively correlated with predation rate, potentially creating strong selection on females to modulate their singing behaviour in response to predation risk (Kleindorfer, Evans & Mahr, 2016). While little is known about the differences in trade-offs faced by each sex when vocalising at the nest, given that in many birds females are responsible for most of the incubating, these differences are likely to be stark.

Female birds may also use mimetic vocalisations to defend their young from predators. For example, observations of nesting female thick-billed euphonia *Euphonia laniirostris* revealed that females would imitate calls of other birds nearby and would only use the alarm calls of birds nesting concurrently (Morton, 1976). However, not all species that nested concurrently were mimicked by female euphonias, indicating that their vocal mimicry is selective (Morton, 1976). As a further example, female great tits *Parus major* produce hissing calls during incubation and these are reported to sound similar to a snake and are thought to represent a type of vocal mimicry (Krams *et al.*, 2014). Experiments show that these calls can startle predators, providing opportunity for escape, or deter them completely (Krams *et al.*, 2014). Further, females that employ these vocalisations escaped capture significantly more often than those that remained silent (Krams *et al.*, 2014) and it has also been shown that these hiss calls can reduce the amount of time that an intruder spends at the nest (Zub *et al.*, 2017). In addition to nest defence, female-specific vocal mimicry may help female brood parasites lay their eggs in host nests. The female common cuckoo *Cuculus canoris* emits a 'chuckle call' that sounds similar to the calls of *Accipiter* hawks, which are known avian predators (York & Davies, 2017). Experiments show that reed warblers *Acrocephalus scirpaceus*, a common host of the cuckoo, become vigilant and distracted by the female cuckoo's chuckle call in a manner that is similar to the warblers' responses to calls of hawks. Hosts reject foreign (cuckoo) eggs less often when this call is used by the cuckoo female compared to when the 'chuckle call' is not used (York & Davies, 2017). While limited, the available evidence suggests that vocal mimicry could play an important ecological role for female oscines and non-oscines alike and yet, studies of vocal mimicry by females are rare. Overall, reports of vocal mimicry production during nest disturbance – by either sex – remain mostly anecdotal (Dalziell *et al.*, 2015) and constitute an intriguing area for future empirical research.

IV. VOCAL LEARNING IN FEMALES

How females learn vocalisations, and from whom, is critical for our overall understanding of the evolution of complex vocalisations in females (Riebel, 2003) as it may provide insights into the different selective pressures faced by each sex (Riebel, 2016). However, currently little is understood about the mechanism for vocal learning in female oscines and even less is known about female vocal learning in birds outside of this group (Marler, 2004*b*; Odom *et al.*, 2014; Riebel, 2016). However, available evidence suggests that the pathways that facilitate female song learning are complex, and may be the same as in males in some respects but different in others. For example, in northern Cardinals *Cardinalis cardinalis* it has been shown that females learn the same number of songs as males and in less time; however, unlike males, females require auditory experience to learn song (Yamaguchi, 2001). One recent study on New Zealand bellbird *Anthornis melanura* (an oscine passerine) demonstrated that each motor phase of song learning occurs at the same age for juvenile females and males, with song components being similar at the commencement of learning, but diverging into distinct sex-specific repertoires by adulthood (Roper, Harmer & Brunton, 2018).

In addition to oscines, vocal learning is known to occur in hummingbirds (Araya-Salas & Wright, 2013), parrots (Bradbury & Balsby, 2016), and at least one family of suboscine (Cotingidae; Saranathan *et al.*, 2007). Previously, vocal learning in oscine passerines was hypothesised to have evolved in response to sexual selection on males, with males learning their songs from male 'tutors' (Nowicki & Searcy, 2014). However, the fact that female song is an ancestral character in oscine passerines (Odom *et al.*, 2014) requires a hypothesis that accounts for both sexes. While the vocal tutor hypothesis may still remain valid for males, we must now also assess the mode of acquisition of female vocalisations (Riebel *et al.*, 2005; Riebel, 2016), and importantly, determine whether female vocalisations affect song learning in males as well. Furthermore, while the mechanism of production may differ between oscines and non-oscine passerines, the ecological and social selective pressures faced by female birds may not. Therefore, we stand to gain valuable knowledge about the acquisition of complex vocalisations by examining mechanisms for vocal learning in female non-oscine passerines as well.

Few studies have examined the influence of female tutors on offspring. It seems reasonable to suspect that at least some female vocalisations influence learning and acquisition of vocalisations in young birds of both sexes. For example, juvenile female blue-capped cordon-bleus *Uraeginthus cyanocephalus* were shown to learn song from adults of the same and opposite sex; however, they were less accurate in their imitation of adult tutors than were males (Geberzahn & Gahr, 2013). Similarly, recent evidence shows that young red-backed fairy-wrens *Malurus melanocephalus* incorporate maternal elements into their songs (Dowling, Colombelli-Négrel & Webster, 2016) and that young superb fairy-wrens *Malurus cyaneus* acquire vocal elements from both male *and* female tutors (Evans & Kleindorfer, 2016). Moreover, experiments on hand-reared slate-coloured boubous *Laniarius funebris* show that females learn exclusively from female tutors when raised with conspecifics of both sexes (Wickler & Edith, 1989). Like much of our current understanding of song learning in females (Riebel, 2016), whether females benefit from tutoring young is unclear. However, emerging research in male song sparrows *Melospiza melodia morphna* suggests that tutoring and song learning may be mutually beneficial for tutor and tutee (Beecher, Akay & Campbell, 2020), and raises questions as to whether fitness benefits exist for female tutors as well. Given the potential for females to interact frequently with offspring of both sexes, it is clear that this remains an underexplored but important aspect of female bird vocalisations.

Vocal learning has been a fundamental component of the definition of song, with learning enabling the complexity and variation for which bird song is renowned [e.g. see Bolhuis & Gahr (2006) and Catchpole & Slater (2008)]. Vocalisations classified as songs use higher vocal centre (HVC)-associated brain nuclei and the anterior forebrain pathway (Reiner *et al.*, 2004). By comparison, these same pathways are not used by innate, simple vocalisations, termed 'calls', and these separate neurological pathways would seem to support the notion that songs and calls are physiologically distinct. Yet, as has been shown, there are many exceptions to this with some calls being learned – in songbirds and other taxa (e.g. see Mammen & Nowicki, 1981) – and complex vocalisations termed as song being present in non-oscine species (see Section V). Further, with the realisation that many female birds 'sing' in the traditional sense of the word, there again may be too many exceptions to the rules to continue confidently to rely on these distinctions.

V. IMPLICATIONS FOR THE TRADITIONAL DEFINITIONS OF AVIAN VOCALISATIONS

This review shows that female birds are clearly capable of producing structurally complex and learned vocalisations (see also Langmore, 1998; Hall, 2009). In addition, we know that song in female oscine passerines is in fact widespread, occurring in over two-thirds of species across 32 songbird families, and moreover, is likely to be ancestral (Odom *et al.*, 2014). Yet, conventionally, avian vocalisations have been broken down into two categories: 'songs' and 'calls' and these categories remain male-centric. In general, songs have been defined as structurally complex and learned, and by some definitions were the exclusive hallmark of sexual selection for extravagance acting on oscine passerine *males* (Catchpole & Slater, 1995). Calls, on the other hand, have been defined as structurally simple and innate (Marler, 2004*a*), and were thought to result from other selection pressures acting on both sexes throughout the Aves (Marler, 2004*b*). However, the now-overwhelming evidence for female song indicates that song can readily evolve outside the traditional contexts of male mate attraction and territory defence, which draws into question the conventional (and male-biased) semantic, structural, and functional distinctions between songs and calls.

In response, the definitions of song and calls have recently begun to shift. Derived from a largely European natural history perspective whereby song was viewed as a perfect example of a sexually selected trait (Darwin, 1872), song in oscine passerines traditionally has been described as "long, complex vocalisations produced by males in the breeding season" (Catchpole & Slater, 1995 p. 10). By contrast, female song was considered both rare (Thorpe, 1958) and functionless (Catchpole & Slater, 1995), and was largely absent from early song research. There is now a large body of evidence indicating not only the widespread presence of female song but the functionality of song as well (e.g. Cooney & Cockburn, 1995; Hall & Magrath, 2000; Langmore, 2002; Riebel, 2003; Logue & Gammon, 2004; Slater & Mann, 2004). In response to these new findings Catchpole and Slater revised their definition of song (Catchpole & Slater, 2008). While still maintaining that song was a complex vocalisation by males during the breeding season, they acknowledged that there were "innumerable exceptions…" to this definition "especially in the tropics" where "it is common for females to sing as well as males" (Catchpole & Slater, 2008, p. 8).

Despite this shift and recognition of female vocalisations in songbird research, arbitrary distinctions between songs and calls and their reliance on functional characteristics associated with males remain. Yet, the clear diversity in structure and function of female vocalisations across the Aves means that these prevailing male-centric definitions are increasingly problematic as a framework for understanding avian vocalisations in both sexes. Irrespective of sex of the singer, we have known for a long time that there are many exceptions that challenge the distinctions between songs and calls (e.g. see Marler, 2004*a*). Now, by learning about female vocalisations there appear to be too many 'exceptions' to these distinctions to ignore. As highlighted by Marler (2004*a*), in practice there are several reasons why it remains difficult to differentiate calls from song irrespective of the sex of the singer. First, "it is increasingly evident that the supposedly strict innateness of bird calls is a myth" (Marler, 2004*a*, p. 176). Evidence of call learning includes: imitation (e.g. European siskins *Spinus spinus*: Mundinger, 1970), plasticity in the begging calls of brood-parasitic nestlings (e.g. brown headed cowbird *Molothrus ater*; Liu, Rivers & White, 2016) and rapid, within-flock convergence (e.g. black-capped chickadee *Poecile atricapillus*; Mammen & Nowicki, 1981). When we also consider that we know very little about vocal learning in female birds in particular (see Riebel, 2016), to continue to view 'innateness' as a defining feature of a 'call' makes too many assumptions about vocal learning in females that are not truly understood. Second, in addition to learned calls, there are many instances whereby a song or call appears to overlap in either structure or function, even in females. For example, female alpine accentors *Prunella collaris* vocalise to attract males, with young females producing simple trills and older females combining trills with different syllables to produce more complex song (Langmore *et al*., 1996). There is also evidence that host-distracting calls of the female common cuckoo *Cuculus canorous* a non-oscine passerine (York & Davies, 2017), may have other functions more akin to territorial song witnessed in passerines, with peak call rates not associated with times of egg laying (see Deng *et al*., 2019). A strict adherence to the traditional song *versus* call dichotomy risks overlooking such 'trans-categorical' cases. Another problem is that the term 'call' tends to be used to encompass all vocalisations in avian species outside the oscine passerines making it difficult to identify homologous or analogous vocalisations. For example, 'calls' have been suggested to provide an opportunity to examine the evolution of vocalisations across the Aves (Benedict & Krakauer, 2013). However, the often highly sophisticated, learned vocalisations of parrots are also traditionally referred to as 'calls' (see Bradbury & Balsby, 2016), as are the learned song-like vocalisations of hummingbirds (Sigler Ficken *et al*., 2000; Ornelas *et al*., 2002), causing semantic confusion and highlighting the need for a more consistent nomenclature of vocalisations across the Aves more broadly.

The problematic dichotomy between calls and songs becomes further apparent when avian vocal mimicry is considered, particularly vocal mimicry produced by females. Far from being an exception to the rule, the imitation of heterospecific sounds is thought to occur in as many as 56 families (48.7%) of songbirds (Goller & Shizuka, 2018). Vocal mimicry is often viewed through the lens of sexual selection acting on males for complex song repertoires. Yet female birds also mimic and there is currently no evidence that female vocal mimics use mimetic repertoires to attract mates. Further, both sexes can use mimicry outside the context of attracting mates [e.g. Igic *et al*. (2015) and Flower (2011)]. Studies that examine mimicry irrespective of sex of the mimic are valuable, but failure to differentiate and identify the sex of the mimic may mask vital information about sex-specific mechanisms and functions of vocal mimicry. While sex differences in avian vocal mimicry have been rarely examined, there is now clear evidence that females are capable of elaborate mimicry of complex heterospecific vocalisations. Female birds can have mimetic repertoires that differ from those of males (e.g. superb lyrebirds; Dalziell & Welbergen, 2016) and/or that are used in different ecological contexts [e.g. see Krams *et al*. (2014) and York & Davies (2017)]. Such sex differences in vocal mimicry raise fundamental questions about the evolution of complex learned vocalisations and the functional significance of vocal learning (Dalziell & Welbergen, 2016). That female non-oscine passerines can also mimic (York & Davies, 2017) raises further questions about the functions and mechanisms of vocal learning in female non-oscines and about how widespread vocal mimicry is in clades other than songbirds. Any broad attempt to analyse the function of complex vocalisations in birds thus also needs to consider vocal mimicry as produced by both sexes (Dalziell *et al*., 2015). Dismissing female vocal mimicry as merely another exception to the rule risks overlooking a class of vocalisations that may have particular importance to the behavioural ecology of females across the Aves.

In sum, given the accumulating evidence that complex vocalisations can readily evolve outside the contexts of male mate attraction and territory defence, in oscines and non-oscines of both sexes, traditional definitions of songs and calls, that are inherently male-centric, are in urgent need of revision.

(1) A new definition of 'song'?

One potential solution to the current problems surrounding the distinctions between songs and calls would be to define 'song' in purely functional terms, that is without reference to sex, vocalisation structure, mode of acquisition, season of production, or taxonomic affiliation. As outlined above, more functional definitions of song traditionally contain sexual selection acting on males as a core defining criterion. However, while males in general are thought to compete more intensely for mates, and females are thought to compete more intensely for reproductive resources, ultimately the mechanisms resulting in the evolution of secondary sexual characteristics are similar for males and females (Clutton-Brock, 2009). Thus, 'songs' could be defined as *any vocalisations that are the product of inter- or intrasexual selection.* 'Calls' could then be defined as the logical complement, i.e. as *any vocalisations that are <u>not</u> the product of inter- or intrasexual selection.* This framework also distinguishes song from vocalisations that are socially selected (*sensu* Lyon & Montgomerie, 2012) outside the context of sexual competition (e.g. sibling competition in barn owls *Tyto alba*; Dreiss *et al*., 2016) and vocalisations that may function in cooperation (e.g. chestnut-crowned babblers *Pomatostomus ruficeps*; Crane *et al*., 2016), and hence avoids blending the selective processes underlying vocal signal design. For those cases where species appear to use the same vocalisations inside and outside of the breeding season (e.g. see Tobias *et al*., 2011), our definition forces us to consider carefully the underlying selective processes responsible for the maintenance of these vocalisations across both contexts.

Where reference to complexity of acoustic structure may be operationally important for distinguishing between song types, the adoption of further subcategories such as 'simple song' and 'complex song' may be required. Similar qualifiers could be applied to distinguish experience-dependent (learnt) from experience-independent (innate) vocalisations, or to denote taxonomic affiliation. Under this simplified functional framework, some vocalisations that traditionally have been considered song would now inevitably be considered calls, and *vice-versa*. For example, the pursuit-deterrent 'song' sung by flying skylarks *Alauda arvensis* in response to attacking merlins *Falco columbarius* (Cresswell, 1994) would become a 'call', and sexual advertisement calls of parrots (e.g. palm cockatoos *Probosciger aterrimus*; Zdenek *et al.*, 2015) would be classified as 'song'. Under this framework, the vast majority of male vocalisations would retain their traditional classifications, whilst the myriad female vocalisations can now simultaneously be accounted for within the same framework in a functionally coherent way.

An alternative solution could be to adopt a more mechanistic definition of song, based on the neurological processes involved in song production in oscines. Under this definition, song would no longer be defined by sex, function, or the season of production, but would encompass only those vocalisations that are controlled by the two closely connected brain pathways: the motor pathway that controls song production (HVC-associated brain nuclei), and the anterior forebrain pathway (which controls song learning) (Reiner *et al.*, 2004). These brain pathways are not involved in the production of simple, unlearned vocalisations (Simpson & Vicario, 1990). The vocalisations produced by these brain pathways are learned and relatively complex compared to calls (Mischler, 2017). They may be produced by both males and females and can occur throughout the year, although they are typically restricted to the breeding season in northern temperate oscines. This definition facilitates cross-taxonomic comparisons, because analogous brain pathways have evolved in the two other avian taxa that produce learned vocalisations: the parrots and the hummingbirds (Nottebohm, 2005). One advantage of this mechanistic approach is that the ambiguity associated with some behavioural contexts is eliminated. For example, provided the (analogous) brain pathways are involved, complex vocalisations produced outside of the breeding season would still be classified as song regardless of sex or function.

The functional and mechanistic solutions proposed above to the issues surrounding conventional definitions of songs and calls offer inclusive, coherent ways for classifying avian vocalisations and make explicit the empirical requirements of song and call definitions. As such, they provide parsimonious foundations for a much-needed re-evaluation of the current male-centric definitions within the field of avian vocalisations. However, our proposed solutions require a detailed understanding of the ultimate and proximate causes of vocalisations, respectively, which means that they have their own operational limitations. Fortunately, our understanding of the functions of avian vocalisations has grown rapidly in recent years (e.g. Cain & Langmore, 2015; Hall *et al.*, 2015; Amy *et al.*, 2018) as has our knowledge of the neurological mechanisms involved in their production (e.g. Farrell *et al.*, 2015; Benichov *et al.*, 2016; Shaughnessy *et al.*, 2019), so we are increasingly well equipped to meet these operational challenges.

VI. CONCLUSIONS

(1) It is clear that female vocalisations can be the same, similar or very different to those of males, and that these similarities and differences are likely determined by the contexts in which the vocalisations are used (see Table 1a and b). One key ecological difference between males and females is that most female birds are more involved with caring for young than males (Lack, 1968). Therefore, female vocalisations in the context of the nest are key for understanding the differences in vocalisations between the sexes and present an exciting albeit challenging opportunity for future research. Recordings of females and young at the nest can be difficult to obtain, and observing and recording interactions becomes more challenging once young have left the nest. However, these points of interaction are likely to hold important clues for both ultimate and proximate understandings of female and male vocalisations and are thus a necessary target of study.

(2) Investigations of the ultimate causes of female vocalisations are required for a comprehensive understanding of the evolution of vocal communication in *both* sexes. Possible functions of female vocalisations are diverse and may be the same or different from males. However, while there are now several case studies that identify the function of female vocalisations, few quantify the associated fitness benefits (Riebel *et al.*, 2019). Fitness benefits are not always easy to determine and may vary with species and ecological context; nevertheless, more empirical testing of hypotheses focusing on fitness implications for females and their offspring would be beneficial (Riebel *et al.*, 2019; see also Hall & Langmore, 2017).

(3) Future work on the proximate causes of female vocalisations could help shed light on the ontogeny of vocalisations in *both* sexes. Such work would greatly benefit from focusing on the development of vocalisations during female-specific activities, rather than simply comparing female vocal behaviours directly with those of males. Given the substantial resources females invest in rearing young, it is likely that female vocalisations play an important role in vocal production and perception learning in both male and female offspring. More broadly, we will likely gain valuable insight into song development by investigating vocal learning in female (and male) parrots and hummingbirds in addition to vocal learning in oscine passerines.

(4) In this review, we have demonstrated that the terms 'song' and 'call' continue to inform current understanding of avian vocalisations, despite an undue reliance of their definitions on functional characteristics of vocalisations in males. We have shown that the term 'song' is inadequate for the broad range of complex vocalisations produced by females that operate in contexts well beyond the 'traditional' contexts of mate

attraction and territory defence. We propose two parsimonious, inclusive solutions to this conundrum, intended as useful starting points for much-needed further debates within the field of avian vocalisations. In the first, we offer a functional definition of 'song' that includes all vocalisations resulting from intra- and/or intersexual selection. This solution would render the definition of song functionally coherent and immune from restrictions based on sex and taxonomic affiliation. In the second, we suggest a purely mechanistic definition in which 'song' encompasses only learned, typically complex vocalisations. This solution would also remove ambiguity associated with the classification of vocalisations, and is inclusive of songbirds that may defend year-round territories. These two proposed definitions focus exclusively on functional and mechanistic characteristics of vocalisations, respectively, and so can help resolve 'false debates' that result from conventional understandings that mix ultimate and proximate levels of analysis (MacDougall-Shackleton, 2011).

(5) The shift away from a male-biased perspective on avian vocalisations now seems complete. The discovery that song production by both sexes is ancestral in oscine passerines (Odom *et al.*, 2014) has precipitated a change in our understanding of the selection pressures that give rise to complex vocalisations in oscines and other avian taxa more broadly. To make progress, we advocate for a more inclusive, evidence-based approach that takes account of the diversity of avian vocalisations, across sexes, taxa, and ecological contexts.

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