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REVIEW

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A review of hypotheses for the functions of avian duetting

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Abstract Avian duets are striking for the remarkable precision with which duetting partners sometimes coordinate their songs. Duetting species are taxonomically diverse, and the form of their duets varies. The reasons some birds duet when most do not remains unclear despite numerous hypotheses for its function. I review work done so far on duetting, discuss evidence for and against hypotheses for its functions, and highlight approaches useful for future research. The four hypotheses that appear most promising are that individuals join their partners' songs to form duets: (1) to avoid being usurped from a partnership, (2) to prevent their partner being usurped, (3) as a collaborative display in defence of some resource, or (4) to signal commitment to their partner. These hypotheses are not mutually exclusive, and duetting is likely to have multiple roles both within and among species. However, much basic research is still required. Characteristics of duets have rarely been quantified in detail, and information about variability among species in the precision of duetting is necessary, not only to test hypotheses about function, but also to define duetting more precisely. Quantifying the relative frequencies of alternative vocal strategies (for example, remaining silent when a partner sings versus joining in to form a duet) between species and in different contexts will help to determine why partners coordinate their songs to form duets. Furthermore, social systems and sex roles in duetting species are poorly understood, yet understanding these is critical to determining the functions of avian duetting.

Keywords Avian duetting · Hypotheses

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Introduction

Avian duets are joint acoustic displays where two birds coordinate their songs with a degree of temporal precision (Farabaugh 1982). There is tremendous diversity among duetters, both taxonomically and in the form of their duets. The independent evolution of duetting in phylogenetically distinct groups suggests that selection for duetting is strong (von Helversen 1980). Nevertheless, the function of avian duets remains poorly understood, partly as a consequence of the historical focus of research on birds of the northern temperate regions where females often do not sing and duetting is rare (Langmore 1998).

The form of duetting varies considerably among species, but has seldom been quantified in detail and consequently the definition of duetting is still debated (Langmore 2002). I define duets as overlapping bouts of vocalisations given by paired individuals such that their elements within those bouts have a high level of alternation, or a low coefficient of variation of the intervals between their elements, or both (adapted from Farabaugh 1982). Duet partners are usually a paired male and female, though there are exceptions, like the male–male duos that duet to attract females in lekking blue-backed manakins (*Chiroxiphia* spp, Snow 1977). In many species, one or both sexes sing independently of their partner in addition to duetting (Harcus 1977). Duet initiation and the elements comprising duets are sex specific in some species, but not others (Wickler and Seibt 1982). Within the coordinated bouts of vocalisations comprising duets, the level of alternation between partners' elements varies, elements may be produced synchronously or antiphonally, and the temporal precision with which partners coordinate their contributions to the duet also varies (Payne and Skinner 1970). Variation in

Table 1 A few examples of species that duet, illustrating both taxonomic diversity and variation in form of duetting behaviour[a], including relative use of duets and solos, sex-specificity of duet initiation and elements, whether elements within duets overlap or not, and how precisely they are coordinated

Family[b] (Subfamily)	Species	% Vocalisation in duet		% Duets initiated by female	Elements sex-specific	Elements overlap or alternate	Precision[d]	Source
		Male[c]	Female					
Anatidae (Anatinae)	Canada goose (*Branta canadensis*)	Some	Most	Few	Yes	Alternate	–	(Whitford 1996)
Psittacidae	Yellow-naped amazon (*Amazona auropalliata*)	Most	Most	40–60	Yes	Alternate	10–40	T. Wright, personal communication
Mesitornithidae	Subdesert mesite (*Monias benschi*)	>90	60–90	>90	Yes	Alternate	10–40	(Seddon 2002)
Corvidae (Cinclosomatinae)	Eastern whipbird (*Psophodes olivaceous*)	40–60	>90	<10	Yes	Alternate	10–40	(Watson 1969)
Corvidae (Dicrurinae)	Australian magpie-lark (*Grallina cyanoleuca*)	60–90	60–90	40–60	No	Alternate	<10	M. Hall, unpublished data
Corvidae (Malaconotinae)	Bokmakierie (*Telophorus zeylonus*)	40–60	>90	40–60	Yes	Overlap	>90	M. Sawyer, personal communication
Muscicapidae (Turdinae)	White-browed robin-chat (*Cossypha heuglini*)	10–40	Most	<10	Yes	Alternate	10–40	(Todt et al. 1981)
Certhiidae (Troglodytinae)	Bay wren (*Thryothorus nigricapillus*)	>90	>90	>90	Yes	Alternate	<10	(Levin 1996a)
Passeridae (Ploceinae)	African forest weaver (*Ploceus bicolor*)	–	–	–	No	Overlap	–	(Wickler and Seibt 1980)
Fringillidae (Emberizinae)	Red-shouldered blackbird (*Agelaius assimilis*)	10–40	10–40	40–60	No	Alternate	10–40	(Whittingham et al. 1992; Whittingham et al. 1997)

[a] Qualitative data are presented verbally, and quantitative data in broad categories (<10, 10–40, 40–60, 60–90, >90%) as I frequently had to estimate values from data presented in different forms, for example, the estimate of precision in white-browed robin-chats is based on coordination coefficients [(M–SD)/M] of approximately 0.6–0.8 in Fig. 5 from Todt et al. (Todt et al. 1981).

[b] Classification follows Sibley and Monroe (Sibley and Monroe 1990)

[c] (Number of duets)/(number of duets+number of male solos)

[d] Precision is the variability in response intervals between partners' elements; the standard deviation expressed as a percentage of the mean (Levin 1996a)

some of these parameters is illustrated in Table 1 with a few duetting species from different taxa. However, key features of duets have been quantified in so few species that we have little idea of the range and any natural dichotomies in, for example, temporal precision or the percentage of vocalisations that occur in duets. Though Farabaugh's (1982) broad definition of duetting encompasses a continuum of diverse duetting styles, which may or may not be functionally distinct, reaching a more restricted definition of duetting that is meaningful is not yet possible. Detailed quantifying of duet characteristics, not only among species, but also within species in different contexts, is therefore necessary to more narrowly define duetting, as well as for testing hypotheses about function.

Though duetting has attracted interest over several decades and generated numerous hypotheses for its function (von Helversen 1980), it remains unclear why pairs of birds coordinate their songs to form duets in some species when, in the vast majority of the world's birds, they do not. In part, this is because duetting has only recently been viewed from an evolutionary perspective. Many early hypotheses treated duetting similarly to male solo song, and did not ask why temporally coordinated songs should be more effective than songs sung independently (Wickler 1980). Further, duetting pairs were regarded as a unit, and individual interests and the influence of conflict between the sexes were often not explicitly considered (Levin 1996a). Now when we ask "Why duet?" we ask why an individual (male or female) joins its partner's songs to form duets rather than merely singing independently of it. Early hypotheses, for example that duetting functions in pair-bond maintenance and territorial defence, need to be re-evaluated from this individual perspective.

Avian duetting is of interest because precise duetting is unusual, and understanding its function could shed light on other joint signalling displays produced in different taxa, in other modalities, and by more than two individuals. Farabaugh (1982) reported 222 bird species that duet (at less than 3% of species worldwide, it is about as common as inter-specific brood parasitism or cooperative breeding, Stacey and Koenig 1990; Davies 2000). This is no doubt an underestimate, particularly if a broader definition of duetting is used, but very precisely coordinated duetting is nevertheless relatively rare. Duetting has evolved in several other taxa (for a recent review of insect duets, see Bailey 2003), and similar principles or approaches can often usefully be applied across taxa (for example, the impact of conflict or cooperation between individuals on their signalling interactions, Greenfield 1994). The functions of duetting may be similar across taxa where social contexts are similar (for example, some birds and primates, Geissmann 1999). The vocal choruses produced by more than two individuals in group-living birds and other animals may have functions similar to duets (Reyer and Schmidl 1988; McComb et al. 1994; Seddon 2002). Likewise, coordinated acoustic displays may be functionally equivalent to synchronised visual displays (Malacarne et al. 1991).

Understanding the function of duetting also has broader relevance to other fields of study including the neural basis of behaviour, interactive communication, and conflict and cooperation between the sexes. Much is known about the neural bases of song production and song perception (Margoliash 1997), but how the two systems are linked is poorly understood. Duetting birds synchronising their songs need to integrate song production with song perception on a scale of milliseconds, and provide a good system for investigating the neural basis of interactive communication. Similar interactive communication occurs in other contexts on a slower timescale, for example when countersinging territorial songbirds sing in response to one another. Studies of communication are increasingly recognising the complexity of communication networks, and singing interactions between territorial male songbirds have provided a good model system for animal communication systems (Dabelsteen and McGregor 1996). Duetting adds a further level of complexity because vocal interactions occur on a fine temporal scale between partners, as well as on the broader temporal scale between counter-duetting pairs (Todt and Naguib 2000). Duetting represents an apparently cooperative interaction between the sexes, raising the question of whether this is the case and, if so, how and why traditional conflict between the sexes is resolved and how cooperative partnerships are maintained. The evolution of cooperative partnerships is of interest in fields as diverse as behavioural ecology and economics (Sherratt and Roberts 2002; Watson 2002).

Historical overview

When William Thorpe visited Africa from England for the first time, he was fascinated and astonished by the extraordinary precision of antiphonal singing in tropical bird species. Thorpe's (1963) work on auditory reaction times stimulated similar work by others (Grimes 1965; Payne and Skinner 1970), and culminated in a monograph, which surveyed all known duetting species, relating duetting to ecology and behaviour (Thorpe 1972). He concluded that duetters were predominantly tropical and monomorphic, occupying dense vegetation where visual displays were ineffective. He suggested that duetting functioned for mutual recognition and maintenance of contact between partners, as well as mutual stimulation, reassurance after disturbance, and aggressive territory maintenance (Thorpe 1972).

Todt and his co-workers conducted one of the most detailed single-species studies on duetting, showing the value of using a variety of approaches to study duetting in detail. They analysed the structure of antiphonal duets by white-browed robin-chats (*Cossypha heuglini*) to reveal four categories of duets performed in different contexts, for example long, loud, well-coordinated duets performed from exposed perches that served as territorial advertisements (Todt et al. 1981). Robin-chat partners usually approach one another before duetting, and duetting rates decreased when partners were separated experimentally (Todt et al. 1981). Experiments with model birds suggested that increasing spatial proximity of duetting partners increased the level of threat signalled by the territorial display (Hultsch and Todt 1984). Shared territory occupancy and mate familiarity seem to be important prerequisites for duetting in this species (Todt 1975). Experiments on captive birds showed that newly introduced partners only started duetting together after aggressive interactions decreased (Todt et al. 1981). Deafening or muting one pair member to modify or prevent duetting did not end partnerships but prevented reproduction, suggesting that duetting is not necessary for pair-bond maintenance, though perhaps for successful reproduction (Todt and Hultsch 1982). They concluded that robin-chat duets function primarily as territorial displays, with some intra-pair function (Todt and Naguib 2000).

In 1980, Wickler spurred research on duetting by attempting to explain what complex pair-specific duets might achieve that other song could not, as well as by clarifying pair-bond maintenance and making specific predictions. The term "pair-bond" had been used rather intuitively (Armstrong 1963) and could refer to a variety of concepts (Black 1996). Wickler clarified the concept of a pair-bond by linking it with previously suggested hypotheses for the function of duetting. He suggested that duetting might strengthen the pair-bond by (1) maintaining contact between partners, (2) synchronising reproductive physiology or (3) advertising mated status. However, he also highlighted the inadequacy of these hypotheses in accounting for the complex pair-specificity of duets in some species. He proposed the "coyness" hypothesis that pair-specific duets might require new partners to invest a lot of time learning to duet with one another, deterring philanderers and making desertion less common (Wickler 1980). He also noted that "pair-bond strength" should be quantified, and the benefits of strong pair-bonds determined by measuring reproductive success. The hypothesis and predictions he outlined generated both theoretical discussion (Serpell 1981) and experimental tests (Arrowood 1988; Levin 1996a; Geissmann 1999).

Farabaugh (1982) reviewed work on duetting, and developed methods for quantifying variation in features of duets. She reiterated early views that duetting functioned in territorial defence and maintenance of long-term pair-bonds (Armstrong 1947; Robinson 1949). Her comparison of birds of North America and Panama showed that duetting was more common in the tropical than in the northern temperate region, and that duetting was not associated with plumage monomorphism. However, she also highlighted the lack of knowledge about duetters and duetting. For example, pair-bond duration was rarely known because there had been so few long-term studies on colour-banded birds (Farabaugh 1982). Diversity in duetting behaviour remains poorly described two decades later, and the characteristics identified by Farabaugh are still useful for quantifying this variation (for detailed methods, see Farabaugh 1982):

1. Type of sound: song, call or non-vocal sound, whether sounds are sex-specific, and what parts of the vocal repertoire are used in duets.
2. Percentage of vocalisations that occur in duets: the relative participation of partners in duets and solo singing.
3. Order of elements: who initiates duets, the degree of alternation between partners (e.g. MFMFMFMF vs MMFFMMFF or MMMMFFFF), and the amount of overlap.
4. Temporal precision: a key feature of duets, the variability of time intervals between the onset of an element and the onset of the partner's previous element (coefficient of variation of response intervals, or reaction times, between partners).

Levin (1996a) highlighted the importance of an evolutionary approach to duetting, taking an individual perspective and considering the effect of conflict between the sexes on interactions between partners. Her study on bay wrens (*Thryothorus nigricapillus*) was one of few to have used individually marked birds to that time (Tingay 1974; Brown and Lemon 1979; Farabaugh 1983; Levin 1988), allowing individual behaviour to be quantified in more detail. She also used laparotomy to distinguish the sexes. Her results challenged two assumptions about duetting species: bay wren partnerships were not long lasting and nearly all duets were initiated by the female (Levin 1996a). She also showed that new pairs did not have to invest time learning to produce precise, pair-specific duets, refuting Wickler's (1980) hypothesis. Sex-specific responses to playback led Levin (1996b) to argue that males and females defended their territory independently of one another, and hence that duetting was unrelated to territorial defence. Having challenged the traditional view that duetting was a cooperative display for maintaining pair-bonds and territories, she suggested instead that duetting might be a consequence of conflict between the sexes. She argued that bay wren duets were a consequence of male behaviour (joining female songs to form duets), and had the potential to be used for mate guarding (Levin 1996b).

Hypotheses

Many different functions that are not mutually exclusive have been suggested for avian duetting (Table 2). Duetting probably has several functions in single species and

Table 2 Hypotheses for the function of avian duets categorised according to whether a bird joining its partner's song to form a duet is signalling to its partner or to outsiders, what information it conveys, and whether the vocal interaction may involve conflict between partners. See text for detailed explanation and discussion of individual hypotheses

	Receiver	Information conveyed	Conflict
Primary functions			
1. Maintaining contact (Cobb 1897)	Partner	Location, individual identity	No
2. Ensuring reproductive synchrony (Dilger 1953)	Partner	Readiness to breed	No
3. Mate guarding (Stokes and Williams 1968)	Same-sex outsiders	Sex, mated status, location	Yes
4. Guarding paternity (Sonnenschein and Reyer 1983)	Same-sex outsiders	Sex, mated status, location	Yes
5. Preventing a partner being usurped	Opposite-sex outsiders	Sex, mated status, location	No
6. Joint resource defence (Seibt and Wickler 1977)	Outsiders	Location, fighting ability, mated status	No
7. Signalling quality (Smith 1994)	Partner, outsiders	Quality	Yes
8. Signalling commitment (Wickler 1980)	Partner	Commitment	Yes
Secondary functions			
9. Sex recognition (Hooker and Hooker 1969)	Partner	Sex	No
10. Maintaining reproductive isolation (Diamond and Terborgh 1968)	Partner	Species identity, sex	No
11. Ritualised appeasement (Kunkel 1974)	Partner	Individual identity	No
12. Protection from predation (Harcus 1977)	Predator	Not location	No

different functions in different species (Harcus 1977; Todt et al. 1981; Sonnenschein and Reyer 1983). Similar functions may be achieved in different ways, for example pair-bonds may be maintained by maintaining contact, ensuring reproductive synchrony, mate guarding, preventing a partner being usurped, or guarding paternity. Central to understanding the function of a signal is knowing who the signaller and recipient are, what information the signaller is conveying, and whether sender and recipient have congruent interests (Bradbury and Vehrencamp 1998). Though both birds have both roles in duets, it is the second bird that creates the duet by responding to the duet initiator—if it did not join its partner's song, there would be no duet but rather a solo. Hypotheses for the function of duetting can therefore be categorised with regard to who this second bird is signalling to when it joins its partner's song to form a duet, what information it conveys, and whether its interests conflict with those of its partner (Table 2).

The acoustic properties of duets, the responses they elicit, and the contexts in which they occur suggest that duets function as both intra- and extra-pair signals. A few species produce low-amplitude duets that may function solely for within-pair communication (Todt et al. 1981; Morton and Derrickson 1996). However, many duetting species produce duets that carry well beyond their territory boundaries, suggesting that they are directed at outsiders (Seibt and Wickler 1977). Nevertheless, signals may be louder than necessary for effective transmission (Maynard Smith and Harper 1995), so although quiet duets refute long distance communication, loud duets do not preclude an intra-pair function. Birds joining their partners' songs to form duets elicit responses from both their partners and outsiders. Duet initiators modify the timing or structure of their vocalisations when their partner joins in, in Canada geese (*Branta canadensis*), Australian magpie-larks (*Grallina cyanoleuca*) and sub-desert mesites (*Monias benschi*, Whitford 1996; Hall 2001; Seddon 2002). Duets are given in contexts of intrusion and of interactions with neighbouring pairs (Wickler 1976; Harcus 1977; Wiley and Wiley 1977). Further, simulated intrusion influences the proportion of their partners' songs that individuals join to form duets (Levin 1996b; Hall 2000). Some playback experiments have shown that duets elicit a different response from solo songs (Harcus 1977; Appleby et al. 1999; Hall 2000; Grafe and Bitz 2003), indicating that duetting itself (not just song) elicits a response from extra-pair birds.

Hypotheses for the function of duetting differ in the information they suggest duets convey. Information about species, sex, and individual identity, or the location of the signaller is probably conveyed in the structure and acoustic properties of the song each individual contributes to the duet, in much the same way that this information is conveyed in non-duetting species. Of more interest in explaining the evolution of duetting is information conveyed by the coordination of songs to form duets. For example, if both partners reveal their locations by their song, then the duet may reveal to outsiders how far apart partners are. Such information could be important in, for example, mate guarding and joint resource defence. During interactive communication between territorial male songbirds, the timing and choice of song type used in responses can communicate aggressive intent (Vehrencamp 2001). The vocal interaction between duetting partners occurs on a much faster timescale, but the precision of temporal coordination (Thorpe 1963) and the non-random choice of song elements (Vencl and Soucek 1976), are also likely to convey information between duetting partners or to other birds. For example, the apparent effort required to achieve precise temporal coordination with a duetting partner may indicate an individual's quality or its commitment to a partnership (Wickler 1980; Smith 1994). Precision may also signal to outsiders that partners are close together, if close proximity allows for greater precision of duets. In addition, duets and choruses may reveal the number of individuals participating in the display. The context of duetting may also convey information, for example the likelihood that an individual will answer its partner to form a duet may vary at different stages of the breeding cycle and indicate readiness to breed, ensuring synchrony through the cycle.

Levin's (1996b) suggestion that duetting was a consequence of conflict between the sexes challenged early assumptions that duetting was a cooperative display between partners (Thorpe 1972). However, it is becoming apparent that there is no clear dichotomy between cooperation and conflict, rather that duetting involves elements of both (Seddon et al. 2002). Nevertheless, hypotheses make different predictions about which is likely to predominate (Table 2). For example, duetting is a cooperative display if it functions in joint resource defence, and a result of conflict between the sexes if it functions in guarding paternity. Conflict would underly duetting behaviour if it were used to signal commitment, though the extent of conflict between partners would vary depending on individual quality and the availability of higher quality mates.

The extent of conflict or cooperation between partners depends on the costs and benefits of alternative vocal strategies to each individual. Individuals face two kinds of contexts, and in each they have the choice to sing or remain silent. If an individual's partner is singing, it can choose not to sing, resulting in a solo song by the partner, or it can join in to form a partner-initiated duet. Alternatively, if its partner is not singing, then it can also remain silent, or it can start singing independently of its partner. In this latter case either a solo song or duet initiation could result, with the outcome of the individual's choice of strategy depending on the subsequent choice by its partner to join in or not. The interplay between partners continues because, if its partner chooses to join in, the individual has a further choice of whether to stop singing and cut the duet short, or continue and prolong the duet. Further choices about timing and element type determine the precision and type of the resulting duet.

Table 3 Predictions regarding the form, context, and social and ecological correlates of duetting, of the eight major hypotheses listed in Table 2

Hypotheses	Maintaining contact	Ensuring reproductive synchrony	Mate guarding	Guarding paternity	Preventing a partner being usurped	Joint resource defence	Signalling quality	Signalling commitment
Duet structure								
Loud	–	–	Yes	Yes	Yes	Yes	–	–
Locatable	Yes	–	Yes	Yes	Yes	Yes	–	–
Sex-specific elements	–	–	Yes	Yes	Yes	–	–	–
Female initiates	–	–	–	Yes	–	–	–	–
Responsiveness related to quality	–	–	Yes	Yes	Yes	Yes	Yes	Of mate
Precision related to quality	–	–	–	–	–	Yes	Yes	Of mate
Duet context								
Distance between partners	Far	–	–	–	–	Close	–	–
Intrusion	–	–	Yes	Yes	Yes	Yes	–	Yes
Same sex more threatening	–	–	Yes	Yes	No	–	–	Yes
Solos more threatening	–	–	Yes	Yes	Yes	No	–	Yes
Duets more threatening	–	–	No	No	No	Yes	–	No
Timing	All year	Before nesting	All year	Fertile	All year	All year	All year	All year
Social and ecological correlates								
Visually occluded habitat	Yes	–	–	–	–	–	–	–
Similar sex roles	–	–	–	–	–	Yes	–	Yes
“Two better than one”	–	–	–	–	–	Yes	–	Yes
Low extra-pair paternity	–	–	–	–	–	–	–	Yes

Quantifying variation in the form of male and female duetting behaviour between species and in different contexts gives an indication of the relative payoffs of alternative strategies. The fact that some strategies are not used in some species suggests that the payoffs of different strategies vary among species. For example, comparing species from Table 1, most white-browed robin-chat duets are initiated by males and female solo song is rare, suggesting that the payoff to females for singing in coordination with their partner is greater than for singing independently. In contrast, female bay wrens initiate most duets but seldom sing solo songs, suggesting that the payoff to males of joining female song to form duets is greater than leaving them to sing alone. Magpie-larks and male buff-breasted wrens (*Thryothorus leucotis*) sing for longer when their mate joins in to form a duet than when they sing alone (Farabaugh 1983; Hall 2001), while male slate-coloured boubous (*Laniarius funebris*) stop singing sooner if their partner responds (Sonnenschein and Reyer 1983), suggesting that the payoffs to duet initiators of having partners join their songs differs between species. Male and female element types are tightly linked in plain wrens (*Thryothorus modestus zeledoni*) and tropical boubous (*Laniarius aethiopicus*) so the type used by one bird strongly influences the type that its partner uses in response (Grafe et al. 2003; Mann et al. 2003).

I will discuss hypotheses individually below, outlining predictions and presenting evidence for and against each to identify those that are most promising for future research. Predictions can be made at a variety of levels, from the form of duetting, to the contexts in which duetting occurs, and the social and ecological factors associated with duetting. Some predictions of the major hypotheses are summarised in Table 3. The secondary hypotheses are not so much hypotheses for the evolution of duetting as beneficial side-effects or consequences of duetting, and are only discussed briefly.

Maintaining contact

Partners could use duetting cooperatively to maintain contact with one another in situations where visibility is limited, for example by dense habitat (Thorpe 1963; Cobb 1897). If this were the case, then duetting would be more common among species living in visually occluded habitats and, within a species, individuals would answer more of their partners’ songs to form duets when they were out of sight. Duetting would occur throughout the year, and the acoustic properties of duets would allow the signaller to be easily located and identified individually.

Contact maintenance cannot provide a general explanation for the evolution of duetting because many species maintain contact with calls that are not coordinated (Wickler 1980). However, a precisely timed response may allow for more efficient maintenance of contact. By responding immediately to its partner, and making use of the "silent window" following its partner's song, the answering bird minimises the amount of time its partner has to devote to being attentive. This would not explain the evolution of prolonged bouts of coordinated song, but only duets comprising a simple, well synchronised call and answer.

There is evidence that contact maintenance may be important in a few species, but it is not a widespread function of duetting. In some species, partners routinely duet from some distance apart, consistent with this hypothesis (Lewis 1982; Sonnenschein and Reyer 1983). Duets formed when male bar-headed geese (*Anser indicus*) respond to the calls of partners searching for lost goslings probably function in cooperative contact maintenance by reducing the amount of time females have to be attentive to their partners (Lamprecht et al. 1985). Female Steere's babblers (*Liocichla steerii*) respond to a higher proportion of their partners' songs to form duets in dense than in open habitat (Mays, Yao and Yuan, unpublished data). Early comparative studies suggested that duetting was associated with dense habitats and therefore likely to be important for maintaining contact (Thorpe 1972), but a more recent comparative analysis that considered phylogeny did not find an association with dense habitat (Malacarne et al. 1991). Furthermore, partners in many species are usually perched close together and in visual contact when they duet (Kunkel 1974). Magpie-larks are less likely to answer their partners' songs to form duets with increasing distance apart (Hall and Magrath 2000).

Ensuring reproductive synchrony

Partners may use duetting cooperatively to help synchronise their reproductive physiology (Armstrong 1947). Kunkel (1974) argued that duetting was more common in the tropics because there were fewer external cues for sexual synchronisation between mates. If duetting functions in ensuring reproductive synchrony, then individuals should be most likely to answer their partner's songs just before the start of nestbuilding, and duetting should be necessary for successful reproduction.

The fact that many species duet throughout the year even though they breed seasonally (for example Harcus 1977) precludes this being the sole function of duetting (even in the tropics most bird species breed seasonally when their food is most abundant, for example, early in the rainy season Farabaugh 1982; Stiles and Skutch 1989). Nevertheless, male song in non-duetting species stimulates females to build nests and lay eggs in addition to its roles in territorial defence and mate attraction (Kroodsma 1976). Furthermore, coos that female ring doves (*Streptopelia risoria*) produce in response to male courtship displays cause endocrine changes leading to ovulation (reviewed in Cheng 1992). In duetting species, partners may stimulate and synchronise reproductive behaviour more effectively by coordinating their songs to form duets than by singing independently of one another.

There is some evidence consistent with this hypothesis, though experimental testing is challenging because of the difficulty of eliminating duetting between partners without eliminating solo singing or song perception. Slate-coloured boubous were more likely to answer their partners' songs to form duets at the start of the breeding season and before successive breeding attempts, than after the start of nestbuilding (Sonnenschein and Reyer 1983). Todt and Hultsch (1982) showed that cutting a nerve controlling the left syrinx to modify the vocal output of the male of a captive pair of robin-chats caused the male to duet with the female less often, and prevented nestbuilding and breeding activity. Investigating the relationship between duetting and hormones (Schwabl and Sonnenschein 1992) may prove a useful approach to determining whether duetting is more effective than solo singing at stimulating and synchronising the production of hormones associated with reproduction.

Mate guarding

By answering its partner's song in duet, an individual could advertise the mated status of its partner to outsiders and repel potential rivals attracted to its partner's solo song (Stokes and Williams 1968; Wickler 1980; Sonnenschein and Reyer 1983; Levin 1996b). Although there is consensus on the basic definition of this hypothesis, also called mate defence, there are various ways in which it might operate. An individual may prevent same-sex rivals copulating with its partner or pairing with its partner. In the latter case, it may avoid being usurped itself, or maintain monogamy by preventing its partner taking additional mates (Sonnenschein and Reyer 1983; Langmore 1998). Deterring a partner from deserting could be a form of mate defence (Seddon et al. 2002), as could protecting a partner from being usurped (Appleby et al. 1999). These latter cases do not fit within the initial definition because the duetting response is directed not at same-sex rivals, but at the partner or opposite-sex outsiders respectively. I separate the various forms of mate guarding because their assumptions and predictions differ. The hypothesis that an individual duets to prevent same-sex rivals pairing with its partner is discussed here, and the remaining hypotheses in separate sections below (guarding paternity, signalling commitment, and protecting a partner from being usurped).

Duetting may prevent same-sex rivals pairing with a partner by advertising its mated status (Sonnenschein and Reyer 1983; Langmore 1998). If the partner sings to attract additional or alternative mates, then duetting is a consequence of conflict between partners. Songs should be loud, and reveal the sex and location of the singer (Table 3). Individuals should join more of their partners' songs to form duets in the presence of same-sex outsiders. Levin (1996b) and Seddon et al (2002) predicted that unpaired birds should be attracted to solo song playback of the opposite sex and repelled by paired intruders, while birds with partners should perceive same-sex intruders as more of a threat than intruders of the opposite sex, and solitary intruders as more of a threat than paired intruders. Of these latter predictions, the first three are also consistent with duetting functioning in joint resource defence, and it is only the fourth prediction that distinguishes the two hypotheses (Table 3), because solitary intruders represent more of a threat than paired intruders to a partnership, but less of a threat to the resource.

Some evidence supports a mate guarding function, though as yet few data show that individuals faced with same-sex outsiders will join more of their partners' songs to form duets. Male California quail (*Lophortyx californicus*) separated from their mates respond antiphonally to the female's separation call with an aggressive call, especially when unmated males also call in response to the female (Stokes and Williams 1968). Many playback studies found stronger responses to same-sex solo playback for at least one measure of response by at least one sex, but few measured subjects' likelihood of joining their partners' songs to form duets during playback (Morton and Derrickson 1996; Levin 1996b; Hall 2000; Seddon et al. 2002; Grafe and Bitz 2003). Consistent with mate guarding, male tropical boubous join a higher proportion of their partners' songs to form duets during male solo than male-initiated duet playback (Grafe and Bitz 2003). In addition, tropical boubous show a novel form of mate guarding, jamming a rival's song, if their partner responds to male solo playback by duetting with it (Grafe and Bitz 2003). Also, male magpie-larks join a higher proportion of their partners' songs during solo than duet playback, suggesting that solitary intruders are more threatening, but, by contrast, they initiate more vocalisations in response to playback of duets than playback of solos (Hall 2000). Furthermore, contrary to the predictions of the mate guarding hypothesis, magpie-larks are equally likely to join their partners' songs to form duets regardless of the sex of solo playback (Mulder et al. 2003). Further tests of the effect of sex of solo playback, and of solo and duet playback, on the likelihood of duetting with a partner are necessary in other species to determine whether birds duet with their partners in contexts where they risk being usurped from a partnership.

The idea that duetting is important in preventing polygamy (Sonnenschein and Reyer 1983; Langmore 1998) has not yet been tested comprehensively, though Farabaugh (1982) noted a contrast between polygynous non-duetting and monogamous duetting populations of house wrens (*Troglodytes aedon*) and red-winged blackbirds (*Agelaius phoeniceus*). Since most duetting species are monogamous, a comparative approach is required to fully test this.

Guarding paternity

Males may answer their partners' songs to form duets to repel rival males that are attracted to female song seeking extra-pair copulations (Sonnenschein and Reyer 1983). In this form of mate guarding, duetting is a consequence of conflict between the sexes over mating. Predictions are that females initiate duets, and that males answer more of their partners' songs to form duets when females are fertile. Also, vocalisations should be loud, easily located, and sex-specific. Male elements may follow female elements more closely or overlap female elements. Male responsiveness (likelihood of answering female song to form duets) may be related to the quality of both partners and of rival males. Since it is lone males that are a threat to paternity, in the context of playback (or intrusion) males should be more responsive to their partners during male than female solo playback, and during male solo than duet playback. Paternity guards reduce loss of paternity (Komdeur et al. 1999), but low extra-pair paternity may also be associated with an absence of paternity guards (Robertson et al. 2001), perhaps because females do not pursue extra-pair copulations. It is therefore not possible to predict extra-pair paternity rates if duetting were used to guard paternity.

This hypothesis cannot account for duetting at times when females are not fertile, and so cannot provide a single, general explanation for the evolution of duetting. Though females may make choices about mating over longer periods, especially in sedentary species with stable neighbourhoods, it is only when their partner is fertile that males risk losing paternity. Males responding to their partners' songs to form duets outside the fertile period could signal commitment to their partners to assure paternity (see discussion that follows). A further problem with this hypothesis is that, in addition to advertising the mated status of their female to rivals by duetting, males also reveal their location relative to the female. This is likely to be costly to males when a vocal alternative to physical mate guarding might be useful, for example when the male is far from the female or in visually occluded habitat.

There are few tests of this hypothesis, but so far most evidence is against it (Hall and Magrath 2000). Though female bay wrens initiate nearly all duets (Levin 1996b), the likelihood of males answering their partners' songs to form duets does not increase when females are fertile (Levin 1988, p. 34). When magpie-lark females are fertile, they initiate fewer songs and males join a smaller proportion of these songs to form duets, indicating both that fertile females do not sing to attract extra-pair copulations and that males do not use duetting as a paternity guard (Hall and Magrath 2000). No playback experiments have yet quantified variation in the likelihood of males answering their partners' songs to form duets during playback of male or female solos or duets at different stages of female fertility. In several species male elements follow female elements in duets more closely than vice versa (Wright, personal communication; Whitford 1996; Seddon 2002). This may indicate guarding paternity, or a more generalised form of mate guarding (discussed previously) that is sex-specific for some reason, for example, if a male-biased sex ratio causes greater competition for mates among males than females.

Preventing a partner being usurped

Duetting may be used to prevent a partner being usurped. In this cooperative form of mate guarding, the bird forming the duet directs the signal at intruders of the opposite sex that may pose a threat to its partner. The prediction of this hypothesis is that solitary intruders (or solo playback) of the opposite sex should increase likelihood of duetting with a partner. Further, individuals would only benefit from preventing their partners being usurped in species where social or ecological factors meant that a familiar mate was better than an unfamiliar bird capable of usurping the mate.

Male tawny owls respond as intensely to female playback as to male playback, and males that have bred successfully with their partner respond more intensely to female playback than males that have been unsuccessful, consistent with males protecting a valuable mate from being usurped by a female intruder (Appleby et al. 1999). However, though the overall response of males to playback is consistent with the predictions of the hypothesis, their likelihood of joining their partners' songs to form duets was not measured, so it is unclear whether duetting is used for mate defence. Magpie-larks are equally likely to answer their partners' songs to form duets during playback of opposite- and same-sex songs (Hall 2000; Mulder et al. 2003), suggesting that preventing a partner being usurped is as important as avoiding being usurped. No duetting species have been studied in sufficient detail to draw firm conclusions about the benefits of mate familiarity. Magpie-larks may benefit from maintaining long-term partnerships (Hall 1999). However, bay wrens do not have long lasting partnerships (Levin 1996a), and dusky antbirds (*Cercromacra tyrannina*) frequently swap mates and territories (Morton et al. 2000), indicating that there is likely to be variation among duetting species.

Joint resource defence

Duetting may function as a cooperative display to outsiders, advertising and defending territory ownership (Robinson 1949) or access to resources (Black and Owen 1988). If this is the case, then duets should be easily located and loud enough to be transmitted to outsiders. Both sexes should participate in defence, and partners should defend the resource jointly rather than independently, for example by approaching outsiders together. Furthermore, partners should be more likely to coordinate their songs into duets than to sing alone when faced with outsiders. There is no simple prediction regarding the sex-specificity of responses to outsiders; a lack of sex-specificity is likely, but sex-specificity may be introduced by factors like sexual size dimorphism or variation in sex ratio that cause differences between the sexes in the relative threat of male and female outsiders. If likelihood of duetting and duet precision are related to individual quality, then they may signal ability to defend the resource to outsiders. Some authors consider joint defence the evolutionary origin of duetting (Wickler 1980; Todt and Naguib 2000). A key prediction in this case is that, by coordinating their signals, partners produce a display that is more effective than separate solo signals at excluding potential intruders and maintaining territories or access to resources.

Most work on duetting has focused on territorial songbirds and, though there are a few species where duetting, or at least some low amplitude duet types, does not have a territorial function (Todt et al. 1981; Morton and Derrickson 1996), much evidence is consistent with this hypothesis. There are not many data from non-territorial systems, but work on parrots, geese and swans also suggests that duets serve as a collaborative display in defence of some resource (Arrowood 1988; Black and Owen 1988; Kraaijeveld and Mulder 2002). In the discussion of evidence below, I focus on territorial systems.

There are numerous features of duetting that are consistent with a territorial function, but do not distinguish duetting from solo song. Many species duet throughout the year and are believed to defend territories year-round (Farabaugh 1982). Like male territorial song, duets are often loud, easily located, and performed from prominent places, during dawn border patrols, in counter-singing interactions with neighbours, and in response to intrusion and playback (Payne 1971; Harcus 1977; Seibt and Wickler 1977). Duetters are also able to distinguish the duets of their neighbours from unfamiliar duets, responding less aggressively to duets by neighbours (Wiley and Wiley 1977; Galeotti and Pavan 1993; Hall 2000; Grafe and Bitz 2003).

Both sexes respond to territorial intrusion in duetting species, but further work is needed to determine whether this response, particularly the vocal response, is collaborative. Females as well as males respond to playback in all species tested (Wickler 1976; Harcus 1977; Levin 1996b; Morton and Derrickson 1996; Appleby et al. 1999; Hall 2000; Seddon et al. 2002; Grafe and Bitz 2003). Paired tropical boubous will simultaneously attack a dummy, consistent with joint territorial defence (Grafe and Bitz 2003). Bay wrens and dusky antbirds respond more intensely to same-sex playback, leading to the suggestion that partners defend the territory independently of one another (Levin 1996b; Morton 1996; Morton and Derrickson 1996). However, to determine whether this is the case, the responses of individuals in relation to their partners have to be quantified. Overall measures of response such as approaching the speaker and initiating songs are less important than how likely individuals are to join their partners' songs to form duets. Unpaired white-browed robin-chats are repelled by paired model intruders (Hultsch and Todt 1984), indicating the importance of the physical proximity of duetting partners. Magpie-lark partners approach the speaker together rather than alone in 80% of playback trials, they are more likely to duet than to sing alone, and individuals are equally likely to join their partners' songs to form duets regardless of the sex of solo playback, suggesting a coordinated response to simulated intrusion (Hall 2000).

If territorial defence is not collaborative and duetting is a consequence of mate guarding (Levin 1996b; Morton 1996), we can make several predictions about the kind of vocal response expected to playback. During female playback, female solos should be common and male solos rare (if males sing, their partners should join in to form duets for mate guarding). Likewise, during male playback, male solos should be common and female solos rare. Further, female-initiated duets should be rare during female playback (because males would not need to guard against female intruders), and male-initiated duets rare during male playback. So far, few published experiments have distinguished these different kinds of response. Further research, distinguishing male and female vocal strategies (initiating song versus joining a partner to form duets) in response to playback, is necessary to determine whether territorial defence is collaborative in a range of duetting species.

The prediction that duets are more threatening territorial displays than solo songs, central to the argument that duets evolved for joint resource defence, as well as for distinguishing joint resource defence from mate defence, has limited support so far (see Mate guarding section), but should be tested in other species. An experiment comparing responses to playback of duets and playback of solo songs, using songs by the same two birds is yet to be conducted. This playback experiment could be associated with removal experiments, where a paired male and female are removed and replaced with two speakers playing either their duets or their solo songs, and intrusion rates monitored. If two birds achieve a more threatening display by coordinating their songs to form duets than by singing independently of one another, then duet playback would be more effective at preventing intrusion than playback of solos. Removal experiments can also be used to determine whether a solitary individual is able to maintain all of its territory without the assistance of its partner, though results are likely to be influenced by population density and the number of floaters. Solitary bay wrens are able to maintain territories, indicating that duetting in that species is not essential to territorial defence (Levin 1996a).

Signalling quality

The way an individual duets, for example its speed of answering, may be an indicator of individual quality (Smith 1994). The ability to duet with great precision may serve as an indicator of individual quality if integrating sound perception and production rapidly enough to produce precisely coordinated duets is difficult and related to individual quality. This could be underpinned by early neural development, analogous to the proposal that the ability of males to learn repertoires may allow females to assess male quality as determined by early development (Catchpole 1996; Nowicki et al. 1998). If precise duetting signals individual quality, then how well an individual coordinates with its partner's song should be related to measures of individual quality such as lifetime reproductive success and survival, as well as to mate choice in pair formation, divorce or extra-pair mating. However, assessment of mate quality has limited power to account for ongoing duets and other mutual displays performed after pair formation by monogamous species with little opportunity for mate choice because of long-term partnerships and low levels of divorce and extra-pair mating (Wachtmeister 2001). The precision of duets may also indicate quality to outsiders in the context of resource defence, and be related to success of a pair in aggressive interactions over resources.

The relationship of precision in duetting to individual quality and mate choice has only been investigated in one species so far. Evidence from the unusual case of male–male duetting partnerships in lekking long-tailed manakins (*Chiroxiphia linearis*) supports this hypothesis. Male duos that match the sound frequencies of their songs most closely attract more females, suggesting that the ability of a male to match frequencies with his duetting partner may be an indicator of quality (Trainer and McDonald 1995). Well-matched duets take years of practice to achieve, implying that perhaps females prefer males that live long enough to form long-term cooperative partnerships (Trainer and McDonald 1995; Trainer et al. 2002).

Signalling commitment

The effort required to achieve coordination with a partner's song could signal commitment to the partner (Wickler 1980). I take "commitment" to mean willingness to invest, or put effort into, parental care, territorial defence, or other aspects of the partnership. Signalling commitment is important when the benefit to an individual of being in a partnership depends on both its own and its partner's investment, so that it will not pay an individual to invest unless its partner also invests. By signalling its own willingness to invest, therefore, an individual attempts to elicit reciprocal investment from its partner. If there is conflict between partners, an individual may use duetting deceptively to elicit more investment from its partner so that it can reduce its own level of investment (Wachtmeister 2001). In species with long-term partnerships and repeated interactions between partners, counter-adaptations to deception are likely to evolve and deception is likely to be limited and difficult to detect.

Between species, duetting should be more likely when sex roles are similar, such that males and females both invest in one or more aspects of the partnership, for example, parental care, predator vigilance, territorial defence, etc. If duetting represented an honest signal of willingness to invest in a partnership, then measures of duetting should be related to mate quality within species such that individuals with high quality mates duet more, or more precisely, and duetting should be associated with low levels of extra-pair mating and divorce. In the context of intrusion, the predictions of this hypothesis are the same as for mate defence (evidence already discussed), as a solitary intruder of the same sex represents a rival with which the partner might desert. Aspects of duetting that might signal commitment include the likelihood that an individual will answer its partner's song in duet, and the speed or pair specificity of its response, if these relate to the attentiveness or proximity of their partner (Wickler 1980; Smith 1994; Levin 1996a).

The social systems of most duetting species, and the importance of commitment and mutual investment by partners to individual fitness are poorly understood, despite their importance for understanding the function of duetting. Duetting species are thought to be monogamous, a belief supported by the few species where mating systems have been investigated and DNA fingerprinting revealed little or no extra-pair paternity (Fleischer et al. 1997; Lawless et al. 1997; Hall and Magrath 2000). The belief that duetting species have long-term pair-bonds is not supported by data from bay wrens or dusky antbirds (Levin 1996a, p. 1095; Morton et al. 2000). However, in magpie-larks, partnerships are usually long-term, divorce and extra-pair matings are rare, and biparental care may be essential to successful reproduction (Hall 1999; Hall and Magrath 2000). Few studies have quantified male and female contributions to parental care in duetting species (Whittingham et al. 1996; Hall 1999), and little is known about the extent of conflict between the sexes over relative parental investment. Morton (1980) suggested that sex roles are more similar in species with more precisely coordinated duets, based on comparison of four species of *Thryothorus* wrens. The association of duetting with plumage monomorphism (Thorpe 1972; Malacarne et al. 1991; but see Farabaugh 1982) could be a consequence of sexual selection operating similarly on both sexes, if sex roles in duetting species are more similar than in non-duetting species. Large-scale comparative analyses controlling for phylogeny will be useful for testing hypotheses when more is known about the social context of duetting and relative investment by males and females. For example, are more precisely coordinated duets associated with social systems that depend more on cooperation between the sexes?

Duetting may signal commitment during the process of pair formation. Duetting rates are low in new pairs but increase as they become established (Todt et al. 1981; Arrowood 1988), consistent with the idea that cooperative relationships develop through gradual increases in investment (Roberts and Sherratt 1998; Sherratt and Roberts 2002). Wickler (1980) suggested that duetting could signal commitment if a coy individual requires that a new partner invest time in learning precisely coordinated, pair-specific duets. Making potential partners invest time learning to duet with a new partner could be a way of eliminating philanderers and reducing the risk of desertion. This "coyness hypothesis" was proposed to explain the unusual duetting of the African forest weaver (*Ploceus bicolor*) where partners sing the same song in unison (Wickler 1980; Wickler and Seibt 1980). Long-tailed manakins have a similar type of duet, with pairs of males singing the same song virtually in unison, and they take years of cooperation to perfect the duets necessary to attract females for copulations (Trainer and McDonald 1995; Trainer et al. 2002). However, African forest weaver songs do not change once they have been learned, and two birds with different song types paired in captivity reproduced successfully, but never modified their song types to produce a unison duet (Seibt et al. 2002). Furthermore, antiphonally duetting species do not require long periods of time to learn to duet with a new partner (Farabaugh 1983; Arrowood 1988; Levin 1996a; Hall 2001). Nevertheless, even when duetting with a new partner does not have to be learned, duetting could still indicate commitment because both pair members make on-the-spot adjustments to achieve coordination of their songs into a duet (Hall 2001; Seddon 2002).

Willingness to invest may change with circumstances, so individuals should continue signalling commitment after mate choice and pair formation to elicit ongoing investment from their partners. The idea that the speed of answering a partner's song could be used to assess attentiveness (Smith 1994) has not yet been tested. However, a few studies have measured responsiveness; the proportion of their partners' songs that individuals join to form duets. Resident male bay wrens that experienced a mate change were less responsive to new partners than established partners; and they were also less responsive to new partners than males in new partnerships that had joined a resident female, gaining a territory as well as a mate, consistent with the idea that answering a partner's song to form a duet signals willingness to invest (Levin 1996a). Heavier subdesert mesites are more likely to participate in duets and choruses (Seddon 2002), perhaps indicating a greater willingness to invest by individuals in better condition or with more to lose.

Secondary functions

Sex recognition

Plumage monomorphism is a common characteristic of duetting species (Malacarne et al. 1991), and duetting may allow recognition of sex by means of vocal dimorphism (Hooker and Hooker 1969). This hypothesis does not explain the evolutionary origins of duetting, as it is the sex-specificity of the song itself, whether sung solo or in duet, that facilitates sex recognition. Some duetting species produce sex-specific contributions to duets while others do not (Wickler and Seibt 1982). Even in species where sex-specificity of song is not obvious to humans, conspecifics may be able to identify sex (Yamaguchi 1998). Although recognition of sex does not explain the evolution of duetting, vocal sex recognition is a prerequisite for other hypotheses that may account for the evolution of duetting.

Maintaining reproductive isolation

Diamond and Terborgh (1968) suggested that maintaining reproductive isolation could be an incidental or additional role of duetting in some species. Song characteristics reveal species identity, and duetting would add another level of distinctiveness between species. If this were the case, the presence of vocally similar close relatives would be associated with an increase in the likelihood or complexity of duetting behaviour. Consistent with this hypothesis, sympatric congeneric barbets have very divergent duetting behaviour, while taxa occurring allopatrically have similar duets (Short and Horne 1983). Further, duets differ in both the form and timing of notes (Short and Horne 1983).

Ritualised appeasement

Kunkel (1974) noted that aggressive behaviour was often associated with duetting, and suggested that duetting represented a ritualised appeasement of aggression between partners. However, the aggression he described was not between duetting partners, but rather against other conspecifics, consistent with duetting functioning in joint defence. Furthermore, observations on experimentally established new pairs of captive birds indicate that new partners only start to duet together after aggression has declined and affiliative interactions begun (Todt et al. 1981), indicating that duetting is a consequence rather than cause of reduced aggression between partners. Nevertheless, duetting in Cuban grassquits (*Tiaris canora*) may serve as a form of appeasement between partners (Baptista 1978).

Protection from predation

Duets are sometimes given in response to disturbance or potential danger, and Harcus (1977) suggested that duetting may provide protection from predation by alerting the partner and confusing predators. The predictions of this hypothesis are unclear. It seems unlikely that the bird forming the duet (by joining its partner's song) would be alerting the partner initiating the duet. Whether the fact that duets come from two locations confuses predators is yet to be tested. Orange-chinned parakeets (*Brotogeris jugularis*) duet in response to both intruding parakeets and a predator (Power 1966), and it seems most likely that duets used as cooperative threat displays towards conspecifics are sometimes also used against predators. If they confused the predator, this would be an incidental effect rather than a major function.

Conclusions and future directions

In conclusion, there are several hypotheses that may explain why birds duet. However, further descriptive and experimental data are necessary to test these more widely. Variation in the form of duetting behaviour needs to be quantified in a range of species and contexts. This will allow a more precise and, if appropriate, narrower definition of duetting, as well as allowing variation in duetting to be related to social context and to evolutionary history to identify function. Aspects of duetting like the function of repertoires and proximate causes of duetting are areas that have so far remained largely unexplored.

Some existing hypotheses do not provide general explanations for the function of duetting, but others warrant further research. So far, theory and evidence suggest that duetting is unlikely to be used to guard paternity or to signal quality during mate choice. The reproductive synchrony hypothesis is yet to be tested, and is limited to accounting for duetting in a specific phase of the reproductive cycle, but may nevertheless be part of the function of duetting. Maintaining contact may be a function of simple call-answer duets, but this hypothesis cannot explain more complex duetting behaviour. The remaining hypotheses are those most likely to provide broadly applicable explanations of the evolutionary function of duetting:

1. Avoiding being usurped from partnership—advertise own mated status to same-sex outsiders.
2. Preventing partner being usurped from partnership—advertise partner's mated status to opposite-sex outsiders.
3. Joint resource defence—collaborative display to outsiders in defence of territory or other resource.
4. Signalling commitment—duet to indicate willingness to invest and elicit reciprocal investment from partner, which may be used deceptively if partners are in conflict over relative levels of investment.

Part of the difficulty in distinguishing hypotheses is that they are not exclusive, and duetting, like male song, is likely to have more than one function. For example, individuals that benefit from forming an alliance to defend access to resources cooperatively would value their partnership, so mate defence should follow from joint resource defence. Similarly, an individual investing in joint territorial defence with its partner, may thereby indicate commitment and elicit investment from its partner. Efforts to prevent a partner being usurped could also indicate commitment to the partner and reduce the risk of being deserted.

Testing these hypotheses requires descriptive and experimental data relating variation in duetting behaviour to different contexts both within and between species. Individuals can be readily sexed in monomorphic species using molecular sexing methods, so that male and female vocal roles can be identified with certainty (Slater et al. 2002; Grafe et al. 2003). Duet characteristics need to be systematically quantified using the methods described by Farabaugh (1982). The relative frequencies of alternative vocal strategies can be documented, particularly the proportion of their partner's vocalisations that each sex joins to form duets, and how these change in different contexts, for example with changing breeding stages or territorial intrusion. Playback experiments can be used to test the influence on duetting of the sex and number of intruders, whether their songs are coordinated into duets or not, and how precisely they coordinate their songs. Though composite measures of response to playback are useful as overall measures of intensity of response (McGregor 1992), in assessing the role of duetting it is essential to distinguish different kinds of vocal responses so that relative frequencies of alternative strategies can be compared.

In addition to variation in whether partners coordinate their songs to form duets, there is also variation in how they do so. The temporal precision of duets varies with species and contexts, and factors influencing duet precision are poorly understood and warrant further investigation. In many duetting species, males and females each have repertoires of elements, which they combine in stereotyped ways to form different duet types (Farabaugh 1983). How the sexes choose types in relation to the types their partners and neighbours use, and the significance of these choices, is yet to be investigated. Some species use different duet types in different contexts, indicative of functional differences (Sonnenschein and Reyer 1983; Grafe et al. 2003). Song matching has been studied in countersinging territorial males, and probably also occurs in duetting species such as tropical boubous (Grafe and Bitz 2003), Eastern whipbirds (*Psophodes olivaceous*, Amy Rogers, personal communication), black-bellied wrens (*Thryothorus fasciatoventris*; David Logue, personal communication), and yellow-naped amazons (*Amazona auropalliata*; Jack Bradbury, personal communication). These complex territorial interactions within and between pairs, involving both sexes, have not yet been explored in detail.

Variation in duetting behaviour needs to be related to social and ecological factors to evaluate the fitness consequences to individuals of using alternative vocal strategies. Detailed studies on individually marked populations are necessary to determine the duration of partnerships and the frequency of divorce and extra-pair mating in a range of duetting species, to determine whether more coordinated duetting is associated with long-term cooperative partnerships as predicted by some hypotheses. The relative investment of males and females in aspects of the partnership such as territorial defence and parental care need to be quantified in duetting species to determine whether sex roles are similar, and to what extent an individual's fitness is influenced by its partner's investment. Knowledge of social context is also important for designing and interpreting experiments. For example, in species that maintain territories year-round, unfamiliar intruders are likely to be prospecting for a territory, so playback of unfamiliar duets will only be realistic if pairs form before territory establishment.

More data are needed to determine whether duetting is in fact a tropical phenomenon. Farabaugh (1982) compared bird species of North America and Panama and concluded that duetting was more common among tropical than temperate species, independent of the greater species richness of the tropics. However, Robinson (1949) noted that duetting is more common in southern than northern temperate regions, perhaps because more species do not migrate, but maintain pair-bonds and territories throughout the year. A systematic comparison of the frequency of duetting in southern temperate regions with tropical and northern temperate regions, relating duetting to differences in life histories, male–female interactions, etc. in the different regions is necessary to determine whether duetting is more common in the tropics.

So far, evolutionary history has rarely been considered in assessing the current function of duetting, and there are two approaches that may be useful in redressing this. First, single species studies that focus detailed research on duetting species from non-duetting groups may allow the function of duetting to be identified while eliminating ancestry as a cause of duetting. Much of the work on duetting has been conducted in groups where duetting is common, such as the bush shrikes (subfamily Malaconotinae) and new world wrens (genus *Thryothorus*), and there is a need for this to be related to the phylogenies of these groups. Second, there is a need for comparative studies that take phylogeny into account. To date, only one comparative study has taken relatedness into account, by analysing at both species and genus levels (Malacarne et al. 1991).

As well as assessing the function, or survival value, of duetting and its evolutionary history (ultimate questions), the question of why birds duet can also be assessed in terms of development and causation (Tinbergen 1963; Krebs and Davies 1993). Though song learning has been well studied in male songbirds, learning in female songbirds is poorly understood (for a review, see Riebel 2003) and little is known about the ontogeny of duetting (Wickler and Sonnenschein 1989). There has been some work on the hormonal (Schwabl and Sonnenschein 1992) and neural (Brenowitz et al. 1985) bases of duetting, but further research is needed. Such research could also be useful for assessing some of the hypotheses for the function of duetting, for example, that duetting helps partners achieve reproductive synchrony.

Avian duetting is a fascinating phenomenon that continues to stimulate interest and research. Understanding why duetting partners coordinate their vocalisations will have relevance to research in other areas including different kinds of joint signalling displays, as well as more broadly in understanding complex communication systems and interactions between the sexes.

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