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Angry Birds Need Not Apply: A Perspective on the Flexible form and Multifunctionality of Avian Vocal Duets

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Abstract

Research into avian vocal duets has revealed much about the social interactions of mated pairs, including how communication signals mediate important components of fitness such as reproductive success and resource-holding ability. Excellent reviews have been written on avian duets, but none have quantified the prevalence of different duet features and functions, or tested for potential links between structure and function. Here we have compiled a thorough list of studies at the species level and investigated whether there are trends in duet form, trends in duet function and matches between form and function. We have also provided recommendations for reporting of duet structure to help standardize future data collection and facilitate comparative analyses. We found that duet vocalizations are typically tightly coordinated (69% of 33 species), initiated by both partners (80% of 35 species), and have sex-specific contributions (73% of 48 species). Duets vary substantially in structure both across and within species, and this flexibility in duet form may contribute to their use in multiple contexts. Among the well-studied species (functions well supported by experimental evidence and studied post-1983), duets are usually multifunctional, with functions including joint resource defence, signalling commitment, maintaining contact, ensuring reproductive synchrony and mate-guarding. Levels of support for different hypotheses have changed over time as theory within the field developed, but overall, the best-supported function of duets across avian species (81% of 26 species) has been joint resource defence. In all but one of these 26 species, duets are sometimes cooperative (meaning that duet participation benefits both duetting partners), and they often produce multiple benefits. We found associations between form and function, in that duets directed to non-pair individuals have higher amplitude and are more likely to have sex-specific notes than duets directed within the pair. We see the field moving away from labelling duets as representing 'cooperation' or 'conflict' and moving towards a general multifunctionality framework within which researchers test multiple hypotheses for duet function under the assumption that both duet form and function can vary moment to moment and that such flexibility can provide multiple benefits.

Introduction

Vocal signals are critical for mediation and regulation of many animal interactions, thus by studying such signals, researchers can learn how animal social

systems form and are maintained. Throughout the animal kingdom, many communication events involve one sender signalling to one or more receivers (Endler 1993; McGregor 2005; Bradbury & Vehrencamp 2011). A subset of communication events

include simultaneous signal production by multiple individuals who may also be signal receivers. The latter situation is exemplified in over 360 avian species that produce vocal duets and choruses, in which two or more individuals coordinate their vocalizations (Thorpe 1972; Farabaugh 1982; Hall 2004, 2009). Duets are created when an individual (the responder) produces a series of vocalizations with a characteristic form and timing relative to another individual's (the initiator) ongoing vocalizations. These vocalizations appear to be a more complex behaviour than signalling alone, as they involve spatial and temporal coordination, increased attentiveness and potentially additional practice (Hall 2009). The complex nature of duet signals raises intriguing questions about how duets differ in form and function from solo vocalizations (Hall 2004, 2009; McGregor 2005; Dahlin & Wright 2012). For this reason, duets have become an area of intense interest in the last couple of decades, with more than 60 new avian publications since 1990 alone (of more than 90 in the field overall). The recent publication of so many focused studies provides an opportunity to look for overall patterns in avian duet form and function. Excellent reviews by Hall (2004, 2009) provide information on the history of avian duet research. Here we hope to add to the discussion with a quantitative overview of descriptive data regarding duet form and function among duets given by mated pairs of birds. We ask: 'Are there trends in duet form?' 'Are there trends in duet function?' and 'Does form match function?' We also discuss the history of hypothesis development in the field and assess how conclusions about function have changed over time.

Several life-history characteristics have influenced the formation of functional hypotheses regarding avian duets. These include primarily sedentary lifestyles, monogamy (Farabaugh 1982; Benedict 2008; Price 2009), and the fact that duets are always given by members of a mated pair or other cooperative social group. These characteristics led early duet researchers to conclude that duet singers coordinate their vocal outputs as a cooperative signal benefitting the interests of both partners (Wolf 1977; Serpell 1981; Short & Horne 1983). In other words, answering a partner's vocalization would provide fitness benefits to both the initiator and the responder. Duets might benefit the interests of both vocalizing individuals if they are directed to other individuals to help defend shared resources, or if they are directed internally to signal commitment to the partnership, to allow partners to locate each other or to improve reproductive synchrony (Table 1) (Hall 2004, 2009).

Table 1: Hypotheses for duet function assessed from the literature

Hypothesis	Receiver	Conflict or cooperation?
MG – mate-guarding – Individuals respond to their mate's vocalization to illustrate their mated status, discourage rivals and defend their own position within a partnership	Extra-pair	Conflict
RD – joint resource defence – Duets are used to advertise the presence of multiple signallers and their readiness or ability to defend their territory	Extra-pair	Cooperation
SC – signalling commitment to the pair bond – An individual's duet contribution indicates commitment to the mate and partnership	Within-pair	Cooperation
MC – Maintaining contact and recognition – Duets allow pairs to locate and identify each other, thereby preventing misdirected aggression	Within-pair	Cooperation
RS – ensuring reproductive synchrony – Duetting helps partners to synchronize their reproductive efforts	Within-pair	Cooperation

Researchers have found support for all of these functions among duetting species (Hall 2004, 2009). For the last 30 yr, researchers have also recognized that duets may be conflict based if the responding bird who creates the duet receives fitness benefits that the sender does not. In 1983, Sonnenschein and Reyer initiated this shift by hypothesizing that duets could represent conflict between mates if duets are formed when a bird responds to its partner's vocalization to signal the mated status of the partner (Sonnenschein & Reyer 1983). Thus, the duet contributions are directed to receivers external to the pair (Table 1). Mate-guarding as a function has subsequently been documented in multiple species (Levin 1996a,b; Rogers et al. 2007; Tobias & Seddon 2009). Evidence of mate-guarding spurred a series of studies looking for duets representing either conflict or cooperation. Most recently, work is moving away from viewing this as a dichotomy, as researchers recognize that many duets may be used in both types of situations (Benedict 2008; Mennill & Vehrencamp 2008).

The variation in duet function appears to be matched, if not exceeded by variation in the structure of duets, including features such as timing, amplitude and frequency. Across scientific disciplines, it is widely recognized that form and function are linked, especially in the field of bird song where vocalization

features vary in conjunction with context and usage patterns (Emlen 1972; Morton 1975). Although links between form and function have been elegantly demonstrated for signals given by individual animals (Klump & Shalter 1984; Gyger et al. 1987), little to no effort has been exerted to find such patterns in duets. At the population or species level, researchers can make strong predictions that take into account knowledge of a species' natural history. At larger levels, variations in evolutionary history and ecology may make patterns less consistent, and we expect that some of the extensive structural variation found in duets is likely due in part to taxonomic diversity (Ryan & Brenowitz 1985; Hall 2009). Simultaneously we expect that species-specific duet features are shaped by ecological and life-history traits in accordance with their evolutionary history (Farabaugh 1982; Benedict 2008; Hall 2009; Mann et al. 2009), and that across species, duet form will show predictable features. For example, most hypotheses for duetting suggest that duet contributions should be sex specific because duet receivers (whether within-pair or extra-pair) would benefit from quickly recognizing the sex of each duetting partner. Additionally, following the definition of the behaviour, most duets are expected to have relatively high temporal coordination (Hall 2009). Some duet features may vary with function. Species communicating primarily within-pair are predicted to use low-amplitude duets, while species communicating with extra-pair receivers are predicted to use high-amplitude duets. Duet response rates (e.g. answering) are also a defining feature on which evolution may act. The act of responding to another bird is what turns an individual vocalization into a duet, and the timing and precision of the responder and the sex of both the initiator and responder may provide insight into the function of a duet and the motivation of each sex. For example, it is predicted that species in which one sex uses duets to guard mates will likely produce duets consistently initiated by the guarded sex. In contrast, species that use duets for joint resource defence or signalling commitment to a partner are expected to produce duets initiated by both sexes.

To assess trends in duet form and function in conjunction with general life-history characteristics across avian species, we reviewed the literature for relevant descriptions. We found journal articles by conducting Web-based-searches including all years since 1970, and we traced older articles using reference sections from articles found in our original search. We used online search engines including SciSearch, OPPIE, Medline, Zoological Record Web of

Science and Google Scholar, and our keywords included 'duet', 'duet structure' and 'duet function'. We found over 70 articles on 59 species that included details about both duet structure and function (summarized in Appendix S1). We pulled most of the reported information on structural elements and functional significance directly from the articles with little interpretation. We also included information on life-history traits, including whether or not each species is sexually monomorphic, is monogamous, holds year-round territories and lives in groups. We analysed the data to determine general trends in structure and function and also to look for associations between structural variables and function, but did not use a meta-analysis-based approach. We believe that our literature search was comprehensive, but if we missed some relevant articles, we would welcome corrections and additions to the data compiled here.

We categorized the structure of duets for each species using multiple criteria. The following variables were examined: (1) the sex of the duet initiator (categorized as single sex initiation when $\geq 95\%$ were initiated by one sex), (2) the sex of the duet terminator (categorized as single sex termination when $\geq 95\%$ were terminated by one sex), (3) whether or not notes are sex specific, (4) whether or not duets are pair specific, (5) a general estimate of the temporal precision of the duet, which was categorized as high when the response latency was < 200 ms and/or had synchronous note timing, and otherwise categorized as low (6), how notes or phrases from the two partners are delivered; simultaneously, antiphonally, or overlapping, (7) the number of note types used by females, (8) the number of note types used by males, (9) the length of the duet, (10) whether or not duets are sometimes associated with visual displays, (11) a general estimate of duet amplitude; high or low and (12) whether note structure is tonal, broadband or variable. Raw data and more complete descriptions of how structural variables were categorized are included in the Appendix S2.

We assigned duet function to one of five hypotheses (Table 1) based on the author's stated conclusions in their article(s). Our definitions (Table 1) follow those of Hall (2004, 2009) with modifications. In Table 1, we indicate whether each hypothesis is generally taken to represent conflict or cooperation between partners, and we indicate whether the primary receiver is within or external to the pair for each function. Because authors varied in their methodology, we also assigned a level of support to identified hypotheses as follows: 0 indicates unsystematic observations or anecdotes alone, 1 indicates conclusions based on

tests of predictions using systematic observational or descriptive data, 2 indicates conclusions based on results of experimental data such as playbacks or partner addition/removal experiments and 3 indicates conclusions based on multiple lines of evidence.

We did not encounter contradictory evidence in terms of well-supported (2 or 3 on our scale above) duet structure among publications. Different studies on a single species would occasionally differ in the number of functional hypotheses that were supported. We included every function that received support in Appendix S1, and indicated the support for each based on the experimental methods that were used.

Results and Discussion

Life-History Characteristics

Previously published descriptions of the life-history characteristics of duetting species are supported by our data (Farabaugh 1982; Hall 2004, 2009). Of the 59 species in our table, 83% are monomorphic in size/colour, while 17% are sexually dimorphic in one or both attributes. The majority of duetting species are socially monogamous, with 96% of 54 species exhibiting monogamy. Duetting species are also quite sedentary, with 88% of 43 species exhibiting year-round territoriality. There is greater variation in group size. Of 51 species, 72% live as pairs, while 27% of species have the potential to live in larger groups. Group sizes consisting of more than two birds are found in three orders, and of those three orders, the largest proportion of group-living species are found in

Piciformes, in which 85% of barbet species are found in groups.

Form

The most obvious conclusion that we make regarding duet form is that it varies widely among species (Appendix S1, Table 2). This observation is not new, and in fact, it is well known that even closely related species may differ substantially in song or duet form (Mann et al. 2009). A second conclusion is that authors report information about duet structure in highly inconsistent ways. We echo Hall's (2009) call for more quantitative descriptive data regarding duet form, and we have provided recommendations regarding such reporting below. In particular, while some features such as note timing were fairly well reported, many aspects of structure were unavailable for a majority of species. Nevertheless, some patterns are emerging as more and more species are studied in detail. We report all data in the Appendices and summarize the data in Table 2, which indicates sample sizes and how structural variables break down across species and orders. Duets are typically characterized as precise, and we found that 69% of duets had high precision. Duets tend to be loud, with 63% exhibiting relatively high amplitude and 27% exhibiting low or variable amplitude. The duet contributions of different sexes also tend to be distinctive across groups. In 73% of species ($n = 48$), male and female notes differ, making it clear to receivers which portion of the duet comes from which individual. Sex specificity allows for recognition of the initiating sex, and we found that

Table 2: Summary of duet structure characteristics

Structure characteristic	Number and percentage of species with data (%)	Number of orders	Percentages and ranges of duet structure characteristics			
Sex-specific initiation	35 (59%)	8	Male or Female: 80%	Male only: 17%	Female only: 3%	
Sex-specific termination	20 (34)	6	Male or Female: 75%	Male only: 0%	Female only: 25%	
Sex-specific notes	48 (81)	9	Yes: 73%	No: 27%		
Individual or pair specific?	20 (34)	5	Yes: 55%	No: 45%		
Temporal Precision	33 (56)	5	Low: 27%	High: 69%	Variable: 3%	
Note timing	51 (86)	9	Antiphonal: 29%	Overlap: 31%	Simultaneous: 2%	Multiple ways: 37%
Female no of note types	22 (37)	7	Range: 1 to 20+			
Male no of note types	25 (42)	7	Range: 1 to 40+			
Duet length	25 (42)	8	Range: 2 to 40+			
Amplitude	19 (32)	5	Low: 26%	High: 63%	Variable: 1%	
Sometimes associated with visual display?	20 (34)	5	Yes: 84%	No: 16%		
Note structure	31 (52)	8	Tonal: 45%	Broadband: 23%	Variable: 32%	

in 80% of species, duets are initiated by members of both sexes ($n = 35$). Males always initiate duets in 17% of species, and females always initiate duets in only 3% of species. These results suggest that among most species, duet initiation behaviour is flexible. Many species are also flexible in the way that individuals combine duet elements: 29% of species always organize duet notes antiphonally, 31% always overlap notes, only 2% always duet using simultaneous notes and the remaining 37% of species organize elements in multiple different ways in different duets ($n = 51$). Thus, antiphonal and overlapping duets are represented roughly equally and are much more common than simultaneous singing. Individual or pair specificity in duets is found in 55% of species ($n = 20$), but analyses of pair-specificity are usually based on measurements of duet form, not discrimination by individuals or pairs. Playback experiments testing recognition of duets are relatively rare, and more studies of this type would be informative (Wiley & Wiley 1977; Odom & Mennill 2010). There was a great deal of variation in the length of duets among species, and we observed single phrase duets that ranged from two to over 20 notes. In addition, 32% of species have duets that consist of repeated phrases. Physical displays associated with duets are also common, with 84% of 19 species exhibiting physical displays. Physical displays may help emphasize acoustic signals, and such multimodal signals may also more effectively transmit messages to receivers than signals with a single modality (Hebets & Papaj 2005).

We think future meta-analyses and interspecies comparisons will be greatly enhanced by improved consistency in the reporting of duet structural data in new publications. To facilitate that goal, we offer the following recommendations for reporting of vocal duet structure.

Duet initiation and termination

Report the percentage of duets that are initiated by males and females.

Sex specificity

Report the percentage of note types that are sex specific.

Pair specificity

Indicate whether duets are pair specific using the following criteria: I. Pairs give duets with unique combinations of notes, or II. Within-pair acoustic

variation is significantly less than among pair acoustic variation.

Temporal precision

We recommend that authors report the response latency between male–female notes as an indication of temporal precision. We define response latency as the length of time from the beginning of one partner's note to the beginning of the subsequent note by the other partner.

Categorize duets with <200 ms between male and female notes or simultaneous singing as high precision and all other duets as low precision.

Duet length

Provide the average number of notes within a duet as well as the duration of the duet (in seconds). When duets consist of repeated phrases of notes, provide both the mean \pm SE of notes within each phrase and the mean \pm SE of phrases.

Amplitude

Report the amplitude in dB as recorded from a standard distance of 50 m.

Note timing

Categorize duets as antiphonal, overlapping or simultaneous when >90% of duets are given in such a fashion. Report the percentage of duets that are given with each type of timing.

Note structure

Report the percentage of notes within duets that are tonal, broadband or variably structured and provide illustrative spectrograms for each note and/or phrase type.

Function and Associations Between Function and Structure

When we examined functional hypotheses for duetting, we found, as expected, that all studies conducted prior to 1983 found cooperative functions for duetting. These functions included joint resource defence, signalling commitment, maintaining contact and ensuring reproductive synchrony (Dilger 1953; Payne 1970; Wolf 1977; Huxley & Wilkinson 1979). These functions of duetting were also identified in studies

conducted after 1983, as was mate-guarding. We examined 59 species for which duet function conclusions were reported, and for 26 of these species (hereafter referred to as 'well-studied species') the results were given a confidence rating of 2 or 3 on the scale reported above and were collected after 1983, after the mate-guarding hypothesis was introduced. By reporting results for this limited group of species, we ensured that all accepted functions were well supported and that all currently accepted hypotheses were included. The most commonly supported function was joint resource defence (88% of all species, 81% of well-studied species), while the least commonly supported function was ensuring reproductive synchrony (8% of all species, 4% of well-studied species). Using data only from well-studied species, we found that most (65%) are known to use duets to communicate only with extra-pair receivers. Twelve percent of well-studied species are known to use duets only for within-pair communication, and 23% use duets for both within- and extra-pair communication. We examined the data for correlations between duet form and function depending on whether the duets were directed internally or externally to the pair using the well-studied data set. We found that receiver identity correlates with duet amplitude, such that species using duets for extra-pair communication are more likely to produce high-amplitude duets than species using duets for intrapair functions (Percentage of high-amplitude duets: 100% of seven species with externally directed duets, 33% of three species that give both internal and external duets, and 0% of one species that give internal duets) ($n = 11$, $\chi^2_1 = 0.1$, $p = 0.01$). We also found that duets used solely for extra-pair communication are more likely to consist of sex-specific notes (Percentage of sex-specific notes: 86.7% of 15 species with external duets, 57.1% of seven species with both internal and external duets, and 0% of one species with internal duets) ($n = 24$, $\chi^2_1 = 7.6$, $p = 0.02$). We found no relationship between temporal precision, sex and/or pair specificity of duets, or patterning of notes (antiphonal vs. overlap as synchrony was rare) and whether duets are directed internally or externally ($p > 0.05$). Other variables were deemed to have too low a sample size for analysis.

The patterns we observed between structure and function are understandable from an evolutionary perspective. Duets that are used more heavily for intrapair communication do not need to travel as far in the environment and thus can be lower in amplitude. The duets of the African Robin-Chat (*Cossypha heuglini*), who have multiple duet types, exhibit

similar patterns: African robin-chat duets given with familiar individuals and within a pair are lower in amplitude than duets given to external receivers (Todt et al. 1981).

The relationship between sex specificity of notes and communication with extra-pair receivers makes sense given different receiver identities. When duets are used within a pair, receivers (partners) are likely to recognize distinctive features of their mate's calls, and thus sex-specific call types may be unnecessary. In an extra-pair communication context receivers may not recognize individuals, so signallers would benefit from giving notes that are clearly indicative of sex. If used for resource defence, sex-specific duet notes illustrate the presence of two distinct signallers who are joint resource-holders. In a mate-guarding context sex-specific signals indicate who is being guarded and who is conducting the guarding.

To assess the usefulness of the historic conflict-cooperation dichotomy, we determined the number of species within which there is support for an exclusively conflict-based duet function (mate-guarding), the number of species within which there is support for an exclusively cooperation-based (multiple hypotheses) duet function, and the number of species within which there is support for both conflict-based and cooperation-based functions. We report those data, along with rates of duet multi functionality in Table 3. As a rough control for phylogenetic effects, we also report data broken down by family, as duets are thought to have arisen independently in each family (Benedict 2008). Each family was assigned the trait shown by the majority of species within the family.

In most avian species, duets were concluded to have multiple functions. These functions may represent both conflict and cooperation between duetting partners, or they may represent multiple cooperative functions. For example, California towhees use duets to defend resources, to maintain contact with mates and to signal commitment to a partnership (Benedict 2010). Rufous-and-white wrens use duets for all of the same functions as California Towhees, as well as for guarding mates (Mennill & Vehrencamp 2005, 2008; Mennill & Rogers 2006; Osmun & Mennill 2011). When we eliminate species studied before 1983 (when conflict-based duet functions were not tested) and conclusions that are not strongly supported by experimental results, we find that rigorous recent work has provided evidence for conflict-based mate-guarding duet functions and negates the idea that duets are purely cooperative. Nevertheless, almost all well-studied avian species (96%) use duets

Table 3: Duet multifunctionality and support for functions based on cooperation or conflict

	% With multi-functional duets (%)	% Where duets represent only cooperative functions (%)	% Where duets represent only conflict functions (%)	% Where duets represent both cooperation and conflict (%)
All species and all functions with confidence >0 (n = 55)	65	78	0	22
Species with well-supported conclusions (confidence >1) post-1983 (n = 26)	54	54	4	42
Families with well-supported conclusions post-1983 (n = 16)	56	59	6	34

in cooperative contexts. Fewer (44%) well-studied species use duets to defend mates, and only one of these, the Eastern Whipbird, uses duets exclusively for mate-guarding (Mennill & Rogers 2006; Rogers et al. 2006, 2007; Osmun & Mennill 2011). Across all species studied post-1983, researchers have found 41 examples of experimental support for cooperative duet functions (in 33 species) and 12 examples of experimental support for mate-guarding (in 12 species). Among cooperative functions, the one that received the most support was resource defence. One possibility for this pattern is that the most prominent function for duets is indeed resource defence, but other functions may also be underreported because they are less obvious or are more difficult to study. Future research should endeavour, whenever possible, to test for multiple cooperative functions of duets.

Our analyses of patterns in duet function confirmed that the field has undergone a shift from the time when researchers considered duets to be purely representative of cooperation between partners. Following the introduction of the mate-guarding hypothesis (Sonnenschein & Reyer 1983), researchers began to classify duets as representing conflict between mates (i.e. Levin 1996a,b). Such a shifting trajectory is not uncommon among scientific inquiry, and it exemplifies how important it is for researchers to generate and test alternative hypotheses. Importantly, the data strongly support multiple hypotheses for duet function: the majority of species that use duets for mate-guarding also use duets in other contexts, including for joint resource defence, maintaining contact, and signalling commitment to the partnership. It is worth noting that all possible duet functions were not tested for every 'well-studied' species examined in this study. We predict that more comprehensive study of each species would only increase support for duet multifunctionality.

We think it is important that nearly all well-studied species show at least one cooperative function for duets. It is no coincidence that duetting partners are always mates or members of a cooperative social group (i.e. male manakins displaying cooperatively for females) (Trainer et al. 2002). From an evolutionary perspective, the additional effort involved in coordinating one's vocalizations with another individual makes it more likely that such signals would evolve only if they provided significant advantages over vocalizing individually. All evidence suggests that duets have evolved to advance the interests of a joint partnership. Even the mate-guarding hypothesis rests on the premise that duetting partners cooperate to raise young. When individuals use duets to guard mates they are enforcing cooperation from their partners. Thus, future experiments should not be designed to ask whether duets function in conflict *or* cooperation in favour of recognizing that duets usually function in cooperation, and occasionally function in conflict as well. Furthermore, as mate-guarding is the only well-supported hypothesis for duet function that posits conflict between mates, a conflict vs. cooperation dichotomy essentially pits one hypothesis against multiple hypotheses. Better, more recent, research approaches discuss all hypotheses on their own merits and recognize multi-functionality in all forms, including the presence of multiple cooperative functions (for examples see Mennill & Vehrencamp 2008 and Benedict 2010).

The traditional manner in which the conflict vs. cooperation dichotomy has been addressed should also be re-examined in the light of our results. The traditional experimental design contrasts the sex-specific responses of a mated pair to duet and single-sex playbacks, with the prediction that pairs will either respond more strongly to duets or equally strongly to all playbacks if they serve a cooperative, resource

defence function, while responses to same-sex playback will be higher if duets serve a mate-guarding function (Levin 1996a; Hall & Magrath 2000; Hall & Peters 2008; Benedict 2010; Douglas & Mennill 2010; Dahlin & Wright 2012). In some cases, support for a mate-guarding hypothesis has stemmed from strong intrasexual responses by females to solo vocalizations, while males respond equally to solos and duets (Rogers et al. 2006; Koloff & Mennill 2011). For example, in a study of eastern whip-birds, *Psophodus olivaceus* by Rogers et al. 2006; a territory defence hypothesis was discounted due to higher female intrasexual responses, despite equivalent responses by males to both solo and duet playbacks. This study represents the single example of duets functioning purely in mate-guarding with no additional cooperative function. Another possibility that warrants consideration is that females have a stronger intrasexual response because they are avoiding conflict with potentially larger and more aggressive males during territory defence (Logue & Gammon 2004). More complete descriptions of life-history and physical characteristics such as dimorphism might provide additional insights into duet function among species where mate-guarding is a possibility.

The amount of experimental support for different functional hypotheses has changed over time, but our long-term overview suggests that the most common function of duets is joint resource defence. More striking, however, is the result that duets given by mated pairs of birds are most often multifunctional and directed at multiple receiver types. This fact, coupled with the taxonomic diversity of duetting species, may help to account for the vast range and flexibility of avian duet structures.

Conclusions

Avian duets are typically tightly temporally coordinated and include sex-specific elements. Duet amplitude and the sex specificity of notes vary with receiver type, consistent with both within-pair and extra-pair functions of duets. Beyond these conclusions, however, we found very few evident trends in duet form related to individual functional hypotheses. The lack of strong links between duet form and function across species may result from several factors. The simplest explanation is that analyses are hampered by a lack of data on duet form and the fact that all possible hypotheses regarding duet function have not been tested in each species. Another possibility is that associations between form and function were difficult to observe because of two striking and likely related patterns: many duets are multifunctional and

variable in their form both among and within species. Given that we reviewed duets in species representing a large number of families, variation in structure is expected. We were more surprised that duet structure frequently exhibited variation in form within species. If individuals use duets in multiple contexts when signalling to multiple receivers, however, then we would predict that duets should be flexible in form to match variable function. This is supported by the finding that among most species, duets may be initiated by either partner. Similar flexibility is found in duet timing, which may vary within a single species to include antiphonal overlapping and simultaneous note structures. When function varies from moment to moment, form may do so too. Research into duet form continues to bloom, and we hope that our conclusions and the data reported here will serve as a resource for further investigation. We expect that more advances in the field will come as researchers make strides in better describing duet structures and in simultaneously testing multiple functional hypotheses for the vast and fascinating array of avian vocal duets.

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Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's website:

Appendix S1: Table with duet function data, life history data and duet structure data broken down by species.

Appendix S2: Measurements and definitions.

Appendix S3: References of Appendices S1 and S2.