
COOPERATIVE DEFENCE IN DUET SINGING BIRDS

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ABSTRACT

In many species of birds, pair mates sing duet songs. It has been hypothesized that coordinated singing is an adaptation to mediate conflict with rivals that would usurp territory or replace one of the pair mates. Duets should be more effective than solo songs at deterring rivals if duet songs signal that pair mates will defend cooperatively. While it has been argued that cooperative defence is incompatible with males pursuing their own fitness interests, counter arguments suggest several conditions in which cooperation may benefit both males and females. Data from observational studies of duetting birds provide some evidence of cooperative defence, but more quantitative studies are needed. Experimental removals of one pair mate have failed to demonstrate that being paired reduces the risk of territory loss. These experiments, however, have not been conducted over the relevant time scales and appear prone to Type II error. A meta-analysis of 19 song playback and decoy presentation experiments reveals that duetting species are significantly more cooperative (i.e. respond with a weaker same-sex bias) than non-duetting species. In summary, empirical evidence supports the hypothesis that duetting pair mates defend their territories and/or one another cooperatively, but fails to link cooperative defence to fitness benefits.

KEY-WORDS: *cooperation, sex roles, duetting, antiphonal song, tropical birds*

INTRODUCTION

In most north-temperate birds only males sing, but in tropical and south-temperate latitudes it is not unusual for both sexes to sing (Stutchbury & Morton, 2001). In over 200 species (Farabaugh, 1982), pair mates coordinate their songs in time, producing a joint vocalization called duet song. Duet singing has evolved numerous times (Wickler, 1980), primarily among socially monogamous species that remain paired throughout the year (Farabaugh, 1982).

While it is clear that duet song serves more than one adaptive function (reviewed in Hall, 2004), virtually all duetting species use duets to mediate

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agonistic encounters with extra-pair conspecifics (Logue & Gammon, 2004). There exists much debate over exactly how duetting functions during these encounters. It has been suggested that participating in vocal duets (as opposed to singing solo) staves off extra-territorial pairs that might attempt to usurp part or all of the territory (Wickler, 1976). Similarly, participating in vocal duets may reduce the likelihood that the actor and/or his mate will be usurped from their position on the territory (Hall, 2000; Hall, 2004). All of these hypotheses, which I will refer to collectively as "cooperative defence hypotheses," are appealing because they link signal structure with function: temporally coordinated songs intrinsically signal that two individuals are present, they are more-or-less close to one another (as communicated by the relative timing and points of origin of the contributions), and at least one of them has made a choice to emit a signal in coordination with the other. All three of these intrinsic messages are expected to deter intrusion more than solo song if it is likely that the duetting pair will defend cooperatively, i.e. both pair mates will act to expel an intruder from the territory.

Indeed, a key assumption of the cooperative defence hypotheses is that pairmates must back up their signals by cooperating to fight off intruders. Ample evidence (discussed in detail below) supports the conclusion that both males and females defend against same-sex intruders. The contentious issue, and the focus of this chapter, is whether pair-mates regularly exhibit aggression toward opposite-sex intruders. In the following section, I offer a theoretical treatment of this question. I then review the empirical evidence, beginning with observational data and moving through various types of experiments. Included in this section is a meta-analysis comparing levels of cooperative defence among duetting species versus non-duetting species. The chapter ends with general conclusions and recommendations for additional research.

SHOULD PAIR MATES DEFEND COOPERATIVELY?

Compared to exclusively same-sex defence, cooperative defence may be more effective at deterring usurpation or encroachment (Hultsch & Todt, 1984; Farabaugh, 1982). Individuals that cooperate to defend might enjoy a fitness advantage over non-cooperative individuals if cooperation improves their ability to remain on the territory or include important resources within the territory borders.

Cooperative defence may also benefit an individual by reducing the likelihood that its mate will be injured or usurped (e.g. Sunde & Bølstad, 2004), a type of defence Hall (2000, 2004) deems "preventing a partner being usurped." There are a variety of circumstances in which an individual that cooperates with its mate to expel an opposite-sex intruder should expect higher Darwinian fitness than an individual that allows its mate to defend alone and passively accepts the winner of opposite-sex encounters as a mate. First, the duration of the actor's pair bond with its mate could positively influence the actor's reproductive success (Appleby et al., 1999; Black, 2001). Second, the probability of succeeding in a current reproductive effort could be compromised if the mate is usurped or injured

(Llambías & Ferretti, 2003; Logue & Gammon, 2004). Third, if competitive ability is an imperfect predictor of parenting ability or other desirable traits (Forstmeier et al., 2002), an individual could benefit from retaining its current mate even if the mate is an inferior territorial competitor. The hypothesis that cooperative defence is adaptive because it prevents the partner being usurped or injured provides a theoretical link between cooperative defence and year-round pair bonds. Specifically, if individuals do not re-mate each year they may reap long term rewards from investing (e.g. by defending intersexually) in the current mate.

The main theoretical argument against cooperative defence is that males should not reject additional females on the territory because a male's fecundity is limited by the number of females with which he mates (Bateman, 1948; Farabaugh 1982, 1983; Arcese, 1989; Slagsvold, 1993; Mays & Hopper, 2004). Under this paradigm pair mates are viewed as living in a state of conflict, with males attempting to attract additional mates and females attempting to repel them (Hurly & Robertson, 1984; Levin, 1996b). This appears to be an accurate appraisal of the relationship between pair mates in polygynous species like the Red-winged Blackbird (*Agelaius phoeniceus*, Hurly & Robertson, 1984). Polygyny does not appear to be common in most duet singing birds (exceptions documented in Galeotti et al., 1997; Whittingham et al., 1997; Maller & Jones, 2001). Duet singing birds tend to be minimally ornamented and form territories in visually occluded habitat (Hooker & Hooker, 1969; Thorpe, 1973), suggesting that males rarely mate polygynously. In species where polygyny is impossible or highly improbable males may behave to maximize success with one mate rather than attempting to acquire additional mates (e.g. Matthews, 2002). It is also possible that birds cooperate facultatively, allowing the coexistence of polygyny and cooperative defence. For example, a male may maximize his fitness by accepting two mates, which he then helps to defend against other intruding females.

DO PAIR MATES DEFEND COOPERATIVELY?

Observational studies

Observations of duet singing in free living birds are generally consistent with the hypothesis that duet participation signals cooperative defence. It is well established that duet songs are often delivered at high amplitude (e.g. Wickler, 1976; Grafe et al., 2004) and from prominent places (e.g. Sonnenschein & Reyer, 1983), as would be expected if pair mates were cooperating to prevent territorial challenges. These characteristics, however, are also consistent with some other hypothesized duet functions, most notably acoustic mate guarding (Sonnenschein & Reyer, 1983; Levin, 1996b; Hall, 2004). More compelling evidence comes from the finding that at least some species sing duets throughout the year (Sonnenschein & Reyer, 1983; Hall & Magrath, 2000; Logue, 2004) but breed seasonally (e.g. Hall & Magrath, 2000; Gill et al., 2005). This pattern supports a role for duet song in cooperative defence but not in acoustic mate guarding (Farabaugh, 1982). The

strongest observational evidence linking duet singing to cooperative defence are the numerous records of heightened duet levels during pairwise territorial encounters (e.g. Wickler, 1976; Farabaugh, 1983; Sonnenschein & Reyer, 1983; Grafe et al., 2004).

Observations of non-vocal behaviour in free-living birds have provided some evidence for cooperative defence in duetting birds. Due to the difficulty of obtaining large sample sizes of naturally occurring intrusions and the speed at which such interactions typically occur, reports of such observations tend to be vague. For example, in Slate-coloured Boubous (*Laniarius funebris*; Sonnenschein & Reyer, 1983), Tropical Boubous (*L. aethiopicus*; Grafe et al., 2004) and Great Kiskadees (*Pitangus sulphuratus*; Llambías & Ferretti, 2003) both pair members are reported to be active in territory defence, but it is not clear from the reports whether defence is cooperative or strictly intrasexual. Other reports suggest that intrasexual defence is the norm among Buff-breasted Wrens (*Thryothorus leucotis*; Farabaugh, 1983) and Subdesert Mesites (*Monias benschi*; Seddon et al., 2003), but provide no quantitative evidence to support these conclusions. Careful observation of the dichromatic Dot-winged Antwren (*Microrhoptias quixensis*; Greenberg & Gradwohl, 1983) revealed that territorial displays were usually "oriented toward birds of the same sex," although territorial females were repeatedly observed chasing solitary male intruders. Sunde and Bølstad (2004) used radio telemetry to track mated pairs of the duet singing Tawny Owl (*Strix aluco*). They found that as territorial conflicts between two individuals escalated from vocal signalling to chasing and fighting, the pair mates of the fighting birds usually joined the mêlée, "backing up" their partners. These birds were no more likely to direct aerial displays or chases at same-sex versus opposite-sex rivals.

Removals

To my knowledge, three removal experiments have been conducted on duet singing birds. These experiments bear on the presumed adaptive outcome of cooperative defence, but do not actually test whether defence is cooperative. Their premise is that if cooperative defence is adaptive because it reduces the risk of territory loss, then birds whose mates are removed should be expected to lose part or all of their territories. Levin (1996a) removed five male and five female Bay Wrens (*Thryothorus nigricapillus*); Morton and his colleagues (2000) removed 12 male and ten female Dusky Antbirds (*Cercomacra tyrannina*); and Fedy and Stutchbury (2004) removed ten male and seven female White-bellied Antbirds (*Myrmeciza longipes*). Morton et. al. (2000) removed at least one bird for nine days, but over all three studies most removals lasted less than 48 hours. In nearly all cases, after one member of a pair was removed, the remaining member maintained the territory until a replacement mate arrived or the study ended (the exception was a male White-bellied Antbird, who switched territories after his mate was removed). The results have been interpreted to suggest that paired defence is not critical for territory maintenance in these species.

The results of removal experiments provide the strongest evidence against the hypothesis that cooperative defence facilitates the maintenance of territory borders against expansionists or usurpers. Importantly, however, these removal experiments do not tell us whether territory borders would remain stable and whether the resident would maintain ownership over a longer timescale with only one pair member to defend (Grafe & Bitz, 2004), nor whether the remaining bird would have enjoyed higher fitness with the removed mate versus the replacement mate. The timescales over which experiments are conducted most are necessarily much shorter than those over which individuals can maintain residency on a territory (at least six years in the case of the Black-bellied wren, D.M.L. unpublished data). If territory ownership is an important determinant of fitness and intrusion pressures vary over time (e.g. stronger when neighbours are prospecting for nest sites, or when juveniles are dispersing), relatively brief removals might not show any increase in the risk of usurpation even if there is strong selection for cooperative defence in the long term.

The strongest empirical support for a territorial monogamous species preventing the mate from being usurped comes from experiments on a crustacean, the snapping shrimp *Alpheus angulatus*. Mathews (2002) staged territorial intrusions and discovered that females of this species are significantly less likely to be usurped if they are paired. She ran many staged usurpation attempts (28 single female trials, 32 single male trials, plus controls) to show that the presence of a mate reduces the risk of usurpation in female snapping shrimp. In the bird studies, sample sizes were fairly small (see above), and because usurpations were not staged, it is not clear that potential intruders were motivated to usurp at the time of the experiment. Large sample sizes and staged usurpation attempts are impractical in bird studies, but speaker replacement studies may provide a more feasible means of examining the role of duet songs in mediating territory intrusion (see Conclusions and Recommendations).

Song playback and decoy presentation experiments

Methods

Playback experiments in which male solo song and female solo song are played to paired birds have revealed a great deal about the roles of the sexes in territory defence. A review of the results from such experiments is complicated by variable reporting practices. Most authors compare the responses of each sex to male versus female song playback, but a few compare the responses of males versus females to each sex of playback. While both types of comparison are interesting, concision and clarity generally require authors to focus on one type of comparison. I recommend comparing the responses of each sex to male versus female playback. This type of analysis focuses on alternative strategies available to an individual bird, resulting in a relative weighting of intersexual versus intrasexual defence.

Pair-versus-pair conflict is common in many species of duet singing birds (e.g. Greenberg & Gradwohl, 1983; Sonnenschein & Reyer, 1983; Sunde and Bølstad, 2004). Pairwise territorial intrusions have been simulated by playing duet songs through a single speaker (Wiley & Wiley, 1977; Levin 1996b; Morton & Derrickson, 1996; Appleby et al., 1999; Hall, 2000; Seddon et al., 2002; Fedy & Stutchbury, 2005). Monophonic duet playback (i.e. broadcasting both the male and female components of a duet through one speaker) is useful for attracting birds and for comparing male and female responses generally, but yields little specific information on sex roles in territory defence. With this in mind, my colleague and I used a computer to separate duet songs into their male and female components, pasted the songs into the two channels of a stereo recording while maintaining their temporal relationship to one another, and played the recordings through separate speakers (Logue & Gammon, 2004). We call this technique *stereo duet playback*.

Stereo duet playback offers several advantages over monophonic duet playback. First, a dual sound source more closely resembles a natural stimulus and should therefore elicit a response that is closer to the birds' natural response to a pairwise intrusion. Rogers and her colleagues (2004) tested this hypothesis by playing stereo and mono duet stimuli to Australian Magpie-larks (*Grallina cyanoleuca*). They found that birds of both sexes responded more strongly to stereo duet playbacks, as measured by flights toward the speakers. Second, by playing the male and female contributions through separate speakers, it is possible to separately measure each bird's minimum approach distance to the male and female speakers during the trial. One can then calculate each bird's bias toward the same-sex speaker as a proxy of intrasexually biased aggression and so quantified the roles of the sexes during pairwise conflicts (Logue & Gammon, 2004; Mennill in press).

Four studies presented live (Hau et al., 2004; S. Gill unpublished data) or stuffed (Hultsch & Todt, 1984; Grafe et al., 2004) decoys to duet singing birds. Results of these experiments can be compared to results from similar experiments on non-duetting species in which females do not regularly sing, and so are not amenable to song playback experiments.

Physical responses to simulated territory intrusions

I conducted a meta-analysis aimed at providing a quantitative answer to the question of whether duetting species show a greater tendency to defend cooperatively versus non-duetting species (Tables 1 & 2). The meta-analysis includes only data from experiments in which both male and female stimuli were presented. Stimuli could come in the form of playbacks or of live or dead decoys, and could be presented sequentially or simultaneously, but must have originated from separate sources (i.e. mono duet playbacks were not included because they do not allow comparison of response to same-sex versus opposite-sex stimuli). One experiment was omitted because the playback songs were recorded from neighbouring birds, which are known to elicit weak responses in this species

(Cooney & Cockburn, 1995). Another was omitted because only comparisons of male versus female responses were presented (Morton & Derrickson, 1996). All of the experiments included in the analysis were conducted on free-living birds.

I included physical responses but not vocal responses in the meta-analysis. The primary justification for omitting vocal responses is that non-duetting species are incapable of answering song and females of many of these species sing little or not at all. I would therefore be limited to looking at only male song initiation, which would make the comparisons with males different from those with females. Further, song rate is a poor indicator of aggression across species because most species increase song output during periods of intense aggression, but others actually reduce song output (e.g. Fig. 2 in Logue & Gammon, 2004). Finally, until the significance of song initiation and song answering are better understood, it is impossible to draw firm conclusions about cooperative defence based on patterns of singing.

The eight response variables used in the analysis were (1) closest approach to the stimulus in meters, or if that was not given, time spent in proximity of the stimulus, (2) whether or not the bird approached the stimulus, (3) latency to approach the stimulus in seconds, (4) number of attacks on the decoy, (5) bias in closest approach during stereo duet playback, (6) number of flights or flights toward the speaker or flights over the speaker (7) duration of response (8) composite aggression score. I included all available data for variables one through seven. To avoid counting the same data twice, I did not include both univariate and composite responses from a particular species. Univariate measures were used whenever possible, but in two cases I included composite measures because univariate measures were not reported.

Data were converted to bias scores by dividing each mean response to the same-sex stimulus by the sum of the mean responses to the same-sex and the opposite sex stimuli. This produced scores with a possible range of 0-1, for which scores >0.5 indicated same-sex bias (subjects responded more strongly to stimuli of the same-sex) and scores <0.5 indicated opposite sex bias (subjects responded more strongly to stimuli of the opposite-sex). For variables in which low values indicate strong aggression (closest approach, latency to approach), bias scores were made comparable to those from other variables by subtracting the values from one.

If tests were conducted in more than one phase of the breeding cycle bias scores were calculated for each phase and then averaged across phases. Scores were then averaged across response variables, resulting in one mean bias score for each sex, for each species (these are the numbers in bold in Tables 1 & 2). These mean scores represent composite measures of cooperativity, and are the only values used in the statistical tests described below. The only congeners in the data set are the four *Thryothorus* species, all of which sing duets. Because this genus was highly over-represented in the data set, the scores from the *Thryothorus* species were averaged to generate a single score for each sex. Data were not normally distributed so Mann-Whitney U-tests were used to compare the degree of cooperation among species that sing duets versus those that do not. Statistical tests

were conducted in SPSS (Version 11.0, 2001). Scores presented in the text below represent medians with interquartile ranges in parentheses.

Males of species that sing duets scored 0.52(0.055) while those from species that do not duet scored 0.80(0.10). This difference is statically significant (Mann-Whitney U test: $N_1=8$, $N_2=5$, $U=6.5$, $P=0.045$), indicating that compared to males of non-duetting species, males of duetting species behave more cooperatively during playback and decoy experiments (Fig. 1). Females of duetting species also scored more cooperatively than their non-duetting counterparts (Fig. 1; duetting females: 0.53(0.072); non-duetting females: 0.71(0.17); Mann-Whitney U test: $N_1=8$, $N_2=7$, $U=5.0$, $P=0.006$). Results for both tests remained significant when the four *Thryothorus* wrens were counted separately.

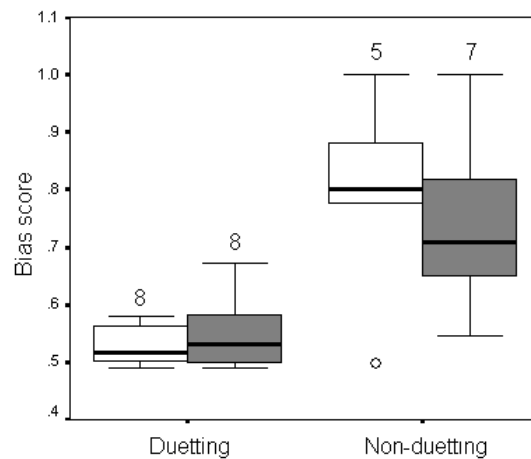


Figure 1. Box plot of non-vocal responses to playback and decoy experiments by males (open boxes) and females (shaded boxes) of duetting and non-duetting species. Bias scores greater than 0.5 indicate that birds' responses were biased toward stimuli of the same sex; scores lower than 0.5 indicate responses biased toward the opposite sex. Central bars represent medians, boxes represent the interquartile range, whiskers represent the range of values, and an open circle represents an outlying data point. Numbers above the boxes indicate sample sizes. Data from four wrens in the Genus *Thryothorus* were averaged to contribute one value to the duetting male box and one value to the duetting female. Please see the text for statistical comparisons.

The results of the meta-analysis support the hypothesis that cooperative defence is more important among duet-singing species than among non-duetting species. Mean scores were generally greater than 0.5, indicating that both non-duetting and duet-singing birds defend more strongly against members of the same sex. This conclusion is not surprising; same-sex intruders pose a direct threat to an individual's territory ownership and mated status (Appleby et al., 1999). Usurpation by a same-sex intruder can be expected to result in negative fitness consequences, whereas the consequences of the mate being usurped will depend on the fitness costs and benefits expected with the current mate versus those expected with the potential usurper.

Table 1. Summary of experimentally derived male roles in territory defence. The possible range of scores is 0-1. Scores above 0.5 indicate that defence is biased toward same-sex stimuli, scores below 0.5 indicate a bias toward opposite-sex stimuli and the deviation from 0.5 indicates the strength of the bias. Scores in italics are based on written statements of 'no difference' in cases where mean values were not reported. Please see the text for statistics.

Species and reference	Duet	Design ^a	Closest approach	Approach stimulus (y/n)	Latency to approach	Attacks on decoy	SDP ^a bias	Flights	Response duration	variate score	Mean score
Tawny Owl ¹	Y	SP	0.54	0.46	0.46			0.55			0.50
Scops Owl ²	Y	SP	0.33	0.53	0.68	1		0.43	0.50		0.58
Slaty Antshrike ³	Y	SP + SDP	0.57				0.54	0.55			0.55
White-bellied Antbird ⁴	Y	SP			0.46				0.52		0.49
Spotted Antbird ⁵	Y	LD + SP	<i>0.5</i>	0.53	0.78	-		<i>0.5</i>			0.58
Buff-breasted Wren ^{6b}	Y	LD + SP				0.44					0.44
Black-bellied Wren ^{7b}	Y	SP + SDP	0.47				0.48				0.47
Rufous-and-white Wren ^{8b}	Y	SDP					0.68				0.68
Bay Wren ^{9b}	Y	SP	0.43					0.52			0.47
Australian Magpie-lark ^{10,11}	Y	SP + SDP		<i>0.5</i>			0.5	0.54			0.51
Subdesert Mesite ¹²	Y	SP	0.50								0.50
Eastern Bluebird ¹³	N	DD		0.83		0.93					0.88
Great Tit ¹⁴	N	LD	0.84			0.71					0.78
Kestrel ¹⁵	N	LD + PB							0.8		0.8
Yellow-breasted Chat ¹⁶	N	DD				1					1
Rufous-collared Sparrow ¹⁷	N	LD							0.50		0.50

^a SP = Solo male and female playback; LD= Live decoy presentation; SDP = Stereo duet playback; DD = Dead decoy presentation

^b Treated as a single data point in statistical tests

References: 1-Appleby et al. 1999; 2-Galeotti et al. 1997; 3-D.M.L. unpublished data (N=15 pairs); 4-Fedy & Stutchbury 2005; 5-Hau et al. 2004 and M. Hau pers. comm.; 6-S. Gill pers comm.; 7-Logue & Gammon 2004; 8-Mennill in press; 9-Levin 1996b; 10-Hall 2000; 11-Mulder et al. 2003; 12-Seddon et al. 2002; 13-Gowaty 1981; 14-Slagsvold 1993; 15-Wiklund & Village 1992; 16-Mays & Hopper 2004; 17-Busch et al. 2004.

Table 2: Summary of experimentally derived female roles in territory defence. Please see the text for statistics and Table 1 for abbreviations and references.

Species and reference	Duet	Design	Closest approach	Approach stimulus (y/n)	Latency to approach	Attacks on decoy	SDP bias	Flights	Response duration	Multi-variate score	Mean score
Tawny Owl ¹	Y	SP	0.57	0.79	0.54			0.51			0.60
Scops Owl ²	Y	SP	0.59	0.47	0.44	-		0.67	0.54		0.54
Slaty Antshrike ³	Y	SP + SDP	0.52				0.47	0.51			0.50
White-bellied Antbird ⁴	Y	SP			0.54				0.50		0.52
Spotted Antbird ⁵	Y	LD + SP	0.5	0.71	0.66	1		0.5			0.67
Buff-breasted Wren ^{6a}	Y	LD + SP				0.56					0.56
Black-bellied Wren ^{7a}	Y	SP + SDP	0.65				0.52				0.58
Rufous-and-white Wren ^{8a}	Y	SDP					0.44				0.44
Bay Wren ^{9a}	Y	SP	0.63					0.71			0.67
Australian Magpie-lark ^{10,11}	Y	SP & SDP		0.5			0.5	0.47			0.49
Subdesert Mesite ¹²	Y	SP	0.5								0.5
Eastern Bluebird ¹³	N	DD		0.84		0.69					0.77
Great Tit ¹⁴	N	LD	0.82			0.92					0.87
Kestrel ¹⁵	N	LD + PB								0.60	0.60
Yellow Warbler ¹⁸	N	DD	0.43			0.62		0.59			0.55
Yellow-breasted Chat ¹⁶	N	DD				1					1
Rufous-collared Sparrow ¹⁷	N	LD								0.70	0.70
European Starling ¹⁹	N	LD	0.71								0.71

^a Treated as a single data point in statistical tests

References 1-17 are same as in Table 1; 18-Hobson & Sealy 1990; 19-Sandell & Smith 1997.

Despite my efforts to choose comparable experiments, the studies contributing to the data set used different sample sizes, experimental designs, etc., and reported different response variables (Tables 1 & 2) which may have influenced the results. Also, it is important that readers recognize that this analysis demonstrates a correlation but does not show causation. There are several

potentially confounding factors (e.g. latitude, taxonomy, territorial system, mating system) that may form causal links between duet singing and cooperative defence.

CONCLUSIONS AND RECOMMENDATIONS

Observational and experimental approaches have produced convergent data indicating that in duet singing birds, pair mates of one or both sexes regularly act to exclude both same-sex and opposite-sex intruders from their territory. This finding stands in contrast to the bulk of the data collected from non-duetting species and supports a critical assumption of the cooperative defence hypotheses of duet function. Recall that according to these hypotheses, duet participation functions to deter extra-pair individuals from expanding into the actor's territory, usurping the actor, and/or usurping the actor's mate (Hall, 2004). Selection may favour more cooperative strategies in species that maintain pair-bonds throughout the year because returns on investment in the current mate pay off over longer time scales than the breeding season of a seasonally paired bird.

The most direct way to measure the importance of cooperative defence in nature is to observe the roles of males and females during naturally occurring territorial conflicts. In particular, the field would benefit from quantitative observational studies of the roles of male and female territory owners during territorial interactions (e.g. Freed, 1987; Sunde & Bølstad, 2004).

While observational and playback experiments have demonstrated that cooperation exists among duetting birds, removal experiments have failed to show that cooperation yields the predicted benefit of increased tenure on the territory. The results of these removal experiments, however, must be interpreted cautiously because they were conducted over very short time scales relative to the potential tenancy of a pair on a territory, relied on small numbers of samples, and occurred under unknown pressures from extra-territorial intruders. Speaker replacement studies (Krebs et al., 1978) offer an alternative means of testing the territorial function of duet song versus solo songs, and may be more viable than standard removals of many birds over long time scales. In speaker replacement studies, territory holders are removed from their territory and replaced with speakers broadcasting song. Territories are then monitored for intrusion by male and female conspecifics. If male duet participation reduces the rate that the female will be usurped, we would expect that females would be slower to intrude during playback of duet song versus playback of solo male song and solo female song (and vice versa for female participation). Researchers could control for intrusion pressures by using matched pairs of control (solo male and solo female song) and experimental (duet song) plots.

This report shows that female song playback evokes strong responses from males of duetting species. Many authors, including myself, interpret this pattern as evidence for cooperative defence by males. It is possible, however, that these responses are driven by sexual motivation rather than agonistic motivation. Future

playback experiments should be designed in such a way that males' responses can be clearly interpreted as either aggressive or sexual. This can be accomplished in several ways. Stereo duet playbacks and pair-wise decoy presentations simulate a scenario in which the territorial male is in imminent risk of losing his territory and should be expected to prioritize defence over courtship. These techniques could be used simultaneously for maximum effect. Presentation of dead decoys allows the observer to note attacks, courtship displays, and attempted copulations, but not all species respond well to dead decoys. Finally, one can test males that are involved in a breeding effort. Males with eggs or young are expected to pay reproductive costs if they lose their current mates (Logue & Gammon, 2004).

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