Title: Duetting behavior varies with sex, season, and singing role in a tropical oriole (*Icterus icterus*)

Abbreviated title: Duetting varies with sex, season and role

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Data Accessibility Statement

Analyses reported in this article can be reproduced using the data provided by Odom et al. (2017).

Data will be archived in Dryad before publication and the following reference added:

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Lay summary

Many birds sing with their mates, forming duets that could serve many functions. We found that duetting behavior varied between the two sexes and between the breeding and non-breeding season. Both females and males answer their mate's songs in both seasons to defend territories and maintain contact with each other. Males also answer their mate during the breeding season, possibly to guard their paternity. Thus duetting functions in both breeding and non-breeding activities.

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Abstract

Females and males of many animals combine their vocalizations into coordinated acoustic duets. Duets can mediate both cooperation and conflict between partners, and are common in tropical, sedentary species that may use duets for multiple functions year-round. To elucidate the full range of duet functions, we need to study the individual-level behaviors that generate duets throughout the year. We evaluated multiple functions of duetting behavior in female and male Venezuelan troupials (*Icterus icterus*) during the breeding and non-breeding seasons, including territory defense, maintaining contact with a mate, and paternity guarding. In both sexes during both seasons, song initiation rates were predicted by conspecific solo and duet rates. However, troupials were more likely to answer their mate to form duets after conspecific duets than after conspecific solos, supporting a territory defense function of duets. Troupials that answered their mate to form duets were also more likely to move toward their mate (than duet initiators and soloists), suggesting that duet participation also functions to maintain contact. During the breeding season, males were particularly likely to fly toward their mate after answering to form a duet. This finding may indicate that males answer to guard paternity, although other predictions of paternity guarding are not supported. Examining individual-level behaviors during both the breeding and non-breeding season revealed multiple functions of troupial duets. Our results are consistent with social selection acting on females and males to maintain contact and territories year-round, and possibly sexual selection on males for functions tied to the breeding season.

Keywords: Duet function, bird, song, territory defense, contact maintenance, paternity guard

Many animals produce elaborate vocal duets in which mated females and males combine their vocalizations (Farabaugh 1982; Hall 2004; Mann et al. 2009; Logue and Hall 2014; Odom et al. 2015; Tobias et al. 2016). Duet participation probably serves multiple adaptive functions, which vary among sexes, species, and the individuals' role in the duet (Dahlin and Benedict 2014; Hall 2009; Logue and Krupp 2016). Most duet research indicates that duetting benefits both partners by facilitating territory defense or maintaining contact with a partner (Logue 2005; Mennill and Vehrencamp 2008; Dahlin and Benedict 2014). Duetting may also emerge from conflict between pair members if the initiating bird benefits from attracting a replacement or extra-pair mate, but its mate repels potential rivals by answering (Marshall-Ball et al. 2006; Seddon and Tobias 2006; Hall and Peters 2009). Thus, it is important to study duets in ways that allow multiple functions of duets to be detected on the individual-level (Dahlin and Benedict 2014; Logue and Krupp 2016).

When studying duets on the individual-level, it is valuable to consider the selection pressures that act on each sex. Elaborate traits, like bird song, are most often studied in males and are thought of as sexually selected to attract or compete for mates (Andersson 1994). Elaborate female traits are more common than previously thought, however, and may evolve through broader social or natural selection pressures (Amundsen 2000; Odom et al. 2014). Because females are often limited by the number of offspring they can produce, female elaborate traits are more likely to function primarily in territory defense versus mate attraction (West-Eberhard 1983; Lebas 2006; Rosvall 2011; Tobias et al. 2012). Therefore, the specific benefits that each sex receives from duetting could also differ based on the benefits that females and males receive from holding a territory (Lebas 2006; Rosvall 2011; Tobias et al. 2012). Studying sex differences in selection pressures is especially relevant in tropical, duetting species, as many of these species hold year-round territories (Stutchbury and Morton 2001; Odom et al. 2016; Tobias et al. 2016).

Duet evolution is tied to year-round territoriality (Tobias et al. 2016). However, almost no studies have examined duet function entirely outside of the breeding or pre-breeding season (exceptions include: Sonnenschein and Reyer 1983; Hall 2000). To understand the full range of duet functions, it is important to examine duets both during and outside of the breeding season (Odom et al. 2016). Whereas animals may use duets in contexts pertaining to breeding activities during the breeding season, they may also use duets in different or broader contexts outside of the breeding season (West-Eberhard 1983; Tobias et al. 2012).

We conducted behavioral observations of mated pairs of Venezuelan troupials (*Icterus icterus*) during both the breeding and non-breeding seasons. Our previous research on troupial song rates and structure showed that pairs regularly duet in the breeding and non-breeding season (Odom et al. 2016). In the current study, we assessed which of a suite of variables were related to duetting behavior. All our models included sex and season, allowing us to assess whether duetting behavior differs between females and males or the breeding and non-breeding season. In addition, we included a variable for vocal role in our analyses. This allowed us to determine if there are behavioral differences between soloists (birds who sing and are not answered by their mate) versus duet initiators (birds who sing first in a duet and are answered by their mate), as well as between birds that answer their mate to form a duet (answerers) versus birds that do not answer their mate (non-answerers).

We tested three leading hypotheses for the functions of duet participation: (1) territory defense – duets signal to conspecifics that both pair members are present and prepared to defend a territory, (2) maintaining contact – duets help pair members coordinate activities or locate each other, and (3) paternity guarding – answering the mate's song serves as a paternity guard by signaling to conspecifics that the mate is not available during female fertile periods (Hall 2004; Logue and Gammon 2004; Mennill and Vehrencamp 2008; Tobias and Seddon 2009). These hypotheses offer distinct predictions about the birds' behavior before and after vocalizing. Based on the territory defense and paternity guarding hypotheses (hypotheses 1 and 3), song answering should be associated with interactions with extra-pair conspecifics. Territory defense (hypothesis 1) would be supported if troupials duetted in response to other pairs of troupials (e.g., potential territory competitors), and if song answering were common throughout the year. In contrast, paternity guarding (hypothesis 3) predicts that a bird is more likely to answer its mate in the presence of one other troupial (e.g., a potential extra-pair mate), and should be biased toward males during the breeding season. Based on the maintaining contact hypothesis (hypothesis 2), we predicted that pair members would move toward each other after a duet. Paternity guarding (hypothesis 3) could also be associated with reducing distance between pair mates, particularly if males move toward their mate after they answer during the breeding season.

Our main goal was to determine duet function by assessing which behaviors are associated with troupials that answer their mate to form duets. We also examined the behaviors of initiators and non-answerers, especially in contrast to answerers. We had two main sets of analyses: (1) we tested for behaviors that predict initiating and answering, and (2) we compared the subsequent behaviors of soloists, duet initiators, answerers, and non-answerers. We discuss our findings with respect to the current functions of duets and the selection pressures that shape vocal behavior in females and males.

Methods

Study species

Troupials are sexually monochromatic, socially monogamous, solitary nesting New World orioles that regularly sing solos and duets (Jaramillo and Burke 1999; Odom et al., 2016). Mated pairs maintain year-round territories and both sexes participate in territory defense (KJ Odom, unpublished data). Female and male troupials both sing long (6-8 s) series of 1-3 alternating notes, which can be combined into simple (one phrase) or more complex (multiple phrase) note combinations (Odom et al. 2016; Odom 2016). Both female and male troupials overlap their mate's songs to form duets. The songs within duets usually overlap considerably, but both the duration and extent of note overlap can vary among duets within a pair. Male and female songs are structurally similar, but their song output differs. Males have increased rates of solo singing before dawn during the breeding season whereas females solo during the day at slightly higher rates than males year-round. Female and male initiated duets occur at similar rates in the breeding and non-breeding season, but duet rates overall are highest in the non-breeding season (Odom et al. 2016).

Field site and data collection

Fieldwork was conducted in the dry forests of Cabo Rojo National Wildlife Refuge in southwestern Puerto Rico (17°590N, 67°100W). We recorded troupial behavior over three field seasons from 16 May – 29 June 2013, 19 May – 01 July 2014, and 17 November – 18 December 2014. The breeding season for troupials in the dry forests of Puerto Rico coincides with the wet season, which begins in late April to early May. The dry, non-breeding season occurs from October to April. Therefore, our observations included two breeding seasons and one non-breeding season. Our non-breeding research was conducted during the first half of the dry season to avoid pre-breeding activities.

All observations were conducted on mated, territorial pairs of troupials. Each season we observed 13-16 pairs of troupials, most of which we observed all three field seasons. Mate and territory turnover between seasons resulted in a final sample size of 19 males and 18 females (see supplementary Table S1 for sample sizes for each analysis). As described in Odom et al. (2016), all troupials were banded with individual and sex-specific color bands. Sex was assigned in the field using wing length measurements and later confirmed by breeding behavior and molecular sexing (Griffiths et al. 1998). For the breeding and non-breeding seasons of 2014, we fitted focal birds with VHF radio transmitters to aid in locating and identifying individuals (radio transmitter models Pip Ag386 and Ag393 manufactured by Biotrack). We recorded birds with a Marantz PMD 661 recorder and Sennheiser ME67 shotgun microphone with K6 power module. All field methods and protocols were approved by the University of Maryland, Baltimore County IACUC committee (approval KO010531215).

Study design

We conducted multiple one-hour observation sessions for each pair of troupials, in each field season. We noted all solos and duets by the focal pair as well as any other, non-focal troupial solos or duets we heard. Troupial songs are loud signals that carry far and duets often overlap extensively, such that we could unequivocally identify solos and duets 200-300 m away. Troupial territories are roughly 200 m in diameter, so our audible range seemed reasonable to detect vocalizing conspecifics that might pose a territorial threat (KJ Odom, unpublished data). We noted which sex soloed, initiated a duet, or answered a duet. Songs for which we were unable to assign singing roles were not included in the analyses. We categorized songs as duets if there was any degree of overlap between the focal pair member's songs, or if their songs occurred within one note-length of each other. Individual troupials almost never sing solos in quick succession, so we are confident in our scoring of solos and duets. Immediately following a solo or duet, we dictated notes on the focal birds' behaviors, and on any non-focal troupials present. All observations were conducted by two observers so that each observer could focus on one pair member. We conducted three observation sessions within the first four hours after sunrise each morning and cycled through each pair before re-observing a pair so that all pairs were observed at least once per week. Observations were balanced, such that each pair was observed a similar number of times each hour of the morning relative to sunrise.

When our focal birds soloed or duetted, we gathered the following information about the event: (1) Occurrence of songs and song type (solo, duet, or none) by other, non-focal troupials in the two minutes prior to focal singing (troupials can take a minute or more to react to intrusions, Odom, 2016). (2) Mate distance – the distance between the focal pair members, estimated to the nearest meter when pair members were within 10 m of each other or to the nearest 10 m when pair members were greater than 10 m apart. (3) Number of other troupials present – defined as the number of non-focal troupials seen within 60 m of the focal pair at the time of, immediately prior to, or immediately following the focal song (troupials regularly interact with conspecifics within 60 m and we could reliably visually scan up to 60 m). (4) Immediate behavior – the behavior immediately following song (details below). (5) Reaction direction with respect to mate – the first direction that each pair member moved with respect to their mate. If the bird did not move within two minutes we scored no movement. Prior to conducting observations each season, we practiced estimating distances using measured flagging tied at 1, 5, and 10 m intervals for up to 100 m and during observations estimates were frequently corroborated between observers.

In the field, we noted all behaviors; however, prior to analysis, we collapsed similar behaviors into fewer categories and excluded any categories with fewer than 14 instances to preserve statistical power (models with fewer than 14 instances of a response variable category failed to converge). We also removed any behaviors from our analyses that did not occur in all levels of sex, season, and role. This excluded several instances of display and calling behavior, which were given primarily by initiators, and foraging behavior, of which we had no instances for female duet initiators; most instances of foraging occurred in non-answerers. The behaviors included in the final analyses were fly, hop/look up, and perch. We combined hop and look up into a single category because they are both vigilance behaviors. Hop up involved birds making several quick, successive jumps to higher branches in the canopy followed by a back and forth scanning motion of the head. Look up was an abrupt straightening of posture with a vigorous, sweeping, side-to-side head movement.

Analysis design

We analyzed troupial singing behavior in two ways. Our predictive behavior analyses evaluated the focal animals' singing behavior based on prior behavior and context, whereas our subsequent behavior analyses evaluated the focal animals' behavior after one or both members of the focal pair sang. All models for these analyses are summarized in Table 1.

<u>*Predictive behavior analyses*</u> - For the predictive behavior analysis, we ran separate models for initiators and answerers (Table 1). We averaged values for each individual for the initiator analysis and used the model to predict the number of initiations based on the following

fixed effects: number of prior solos by nearby non-focal conspecifics (hereafter, “others”), number of prior duets by others, mate distance, number of others present, sex, season, and role (soloist or duet initiator). We also included all two-way interactions between sex, season, and role, and each of the behavioral variables as fixed effects. The answerer analysis included role (answerer or non-answerer) as a binomial response variable, and the fixed effects prior song type, mate distance, and number of others, as well as sex, season, and their interactions with the behavioral explanatory variables. The initiator analysis used a continuous rather than a binomial response variable because we did not have data for when no focal birds sang to compare to initiation behavior.

<u>*Subsequent behavior analyses*</u> – To assess how troupials behave after singing, we treated each subsequent behavior (immediate behavior and reaction direction to mate) as its own response variable in a separate univariate model. Each model included sex, role, and season as well as their interaction terms. Because the subsequent behaviors for each individual of a mated pair could vary independently (unlike in the predictive models), our subsequent behavior models included all four possible roles: soloist, duet initiator, answerer, and non-answerer. All analyses included ID as a random effect, except the predictive initiator analysis, since initiation rate was averaged by individual.

Statistical analyses

Prior to analysis, we evaluated the structure of our data to eliminate outliers and correlated explanatory variables (Zuur et al. 2010). When two variables were correlated, we included the variable that we expected to be more biologically relevant. When data were missing, we omitted the entire case. All scalar explanatory variables were scaled and centered in R (R Development Core Team 2015).

All models were run using the MCMCglmm package in R (Hadfield 2010a; R Development Core Team 2015). We chose this package because it allows multinomial response variables (used in the subsequent behavior analyses) and random effects. MCMCglmm allows GLMM structures to be carried out in a Bayesian context, so it is subject to many assumptions of the Bayesian framework (Hadfield 2010 a,b; Kery 2010). All models were run for 360,000 iterations, using a burn in of 10,000 iterations and no thinning for a final sample size of 350,000. Models for immediate behavior required longer runs to reach stationarity, so we ran them for 900,000 iterations, using a burn in of 100,000 iterations, and no thinning for a final sample size of 800,000. We used vague priors as recommended for our model structure (Hadfield 2010b). We examined trace plots for all variables of all models to verify that models were well-mixed, and we used Geweke's and Heidelberger and Welch's diagnostics to assess convergence of all final models (Heidelberger and Welch 1983; Geweke 1992). All final models had Geweke's values less than one Z-score (2 standard deviations) and Heidelberger and Welch's diagnostics with p-values greater than 0.05, which are consistent with the null hypothesis that the Markov chain is from a stationary distribution.

We initially ran full models for all analyses, which included all fixed effects and their two-way interactions with sex, season, and role, where applicable (full models in Table 1). We then reduced our models by dropping any two-way interactions that did not contribute considerably to variation in the full models (see reduced models in Table 1). Variables with a Bayesian p-value less than or equal to 0.05 were considered to contribute substantially to variation in each model.

Results

Predictive behavior analyses

Troupial singing behavior was influenced by prior singing by other, non-focal troupials (Table 2, Figures 1 and 2). Song initiation rates increased with both increased prior solo and prior duet rates by non-focal troupials (Table 2, Figure 1). Answering behavior, more specifically, was predicted by the type of prior song sung by non-focal troupials: troupials were more likely to answer their mates after non-focal duets than after non-focal solos (Table 2, Figure 2a). Sex was also an important predictor of answering. Females and males answered an approximately equal number of songs to form duets, but males left a greater proportion on their mates' songs unanswered than did females (Table 2, Figure 2b).

Subsequent behavior analyses

After focal troupials sang, their most common subsequent immediate behavior was perch, followed by fly, and then hop/look up (Table 3, Figure 3 & 4). Immediate behavior also varied with sex, season, and singing role. Males were less likely to remain perched than were females (Figure 3a). Troupials were less likely to remain perched during the breeding than the non-breeding season (Figure 3b). Answerers were more likely to remain perched than duet initiators and non-answerers (Figure 3c). A significant sex × role interaction indicated that the likelihood of perching after both initiating or non-answering was higher in males than in females; males tended to fly more than females after answering or solo singing (Table 3, Figure S1a). A significant role × season interaction indicated that the likelihood of perching was greater for answerers compared to non-answerers in the non-breeding season (Table 3, Figure S1b). This result appears to be due to a higher incidence of flying after answering, initiating, and solo singing in the breeding season.

After one or both focal birds sang, focal individuals were more likely to move toward their mate or stay in the same position rather than move away from their mate (Table 4). Compared to soloists, answerers were more likely to move toward than away from their mate (Table 4, Figure 4). Duet initiators were more likely to stay the same distance than move away from their mate compared to answerers (Table 4, Figure 4). A sex × role interaction indicates that male duet initiators were more likely to remain in the same position than move away from their mate compared to female duet initiators (Table 4, Figure 5a). A sex × season interaction indicates that during the breeding season, males were more likely than females to move toward, as opposed to away from, their mate (Table 4, Figure 5b).

Discussion

Our results indicate that troupials participate in duets to defend territories and maintain contact. We found mixed support for paternity guarding. Below, we discuss the evidence from our results for each hypothesis. We also examine the differences we observed between female and male duetting behavior and discuss their implications for selection pressures acting on female and male song.

Territory defense

Our results support key predictions of the hypothesis that troupials duet to defend their territories from other troupials. Both song initiating and answering increased with prior singing by other, non-focal troupials, but song answering, in particular, increased following duets by non-focal pairs. Our findings are consistent with other studies that have concluded that avian duets function in territory defense (e.g., Hall 2000; Logue and Gammon 2004; Mennill 2006; Benedict 2010; Templeton et al. 2011; Dowling and Webster 2015). In addition, song answering behavior was consistent in the breeding and non-breeding season, and duetting is common in troupials in both seasons (Odom et al. 2016). Thus, we also provide support that song answering functions in territory defense during both the breeding and non-breeding season.

Our findings also indicate that troupials duet to defend territories specifically from mated pairs of troupials. Only mated troupials duet and troupials duetted at particularly high rates following conspecific duets. Similarly, a playback study showed that troupials approach more rapidly and make more flights toward the playback speaker following duet stimuli compared to solo stimuli (Odom 2016). Therefore, duets of mated pairs elicit a stronger vocal and physical response than solos. This may simply be because duets indicate the presence of two birds, but we suggest this could be because duets specifically indicate the presence of a mated pair (Molles and Waas 2006; Odom 2016). We did not know the identity of non-focal birds, however, we noticed many duets came from predictable locations within the territories of other known pairs. Therefore, we suspect that these other duets were often given by neighboring troupial pairs. Although troupial territories are relatively stable from year-to-year, we witnessed at least three territory expansions and take-overs by mated, neighboring troupials during our three field seasons (KJ Odom, pers. obs.). Thus, even known mated troupials could pose a substantial territorial threat to established mated pairs.

Maintaining contact and duet multifunctionality

Troupial duets also appear to help pair members maintain contact. Troupials tended to move toward their mate after singing. Answerers were more likely to move toward their mate than soloists, as would be expected if duetting allowed birds to acoustically localize one another in space. Maintaining contact could benefit pair members in a number of ways and other studies have also found support for birds duetting to maintain contact with mates (e.g., Mays et al. 2006; Logue 2007; Mennill and Vehrencamp 2008; Benedict 2010).

Other studies that find support for duets being used to maintain contact also often find support for other duet functions, such as territory defense (Logue 2007; Mennill and Vehrencamp 2008; Benedict 2010). While it is recognized that duets in many species are multifunctional (i.e., duets are used to defend territories and maintain contact), Mennill and Vehrencamp (2008) suggested specifically that duet function can vary based on context. In addition, we propose that duets could serve multiple functions in a single duetting event. More specifically, answering your mate to maintain contact could, in itself, have multiple functions. For example, encouraging a mate to stay close could aid in territory defense and prevent the mate from interacting with potential extra-pair mates. Furthermore, such answering could target multiple receivers (e.g., the mate and other troupials, McGregor 2005; Benedict 2010). We frequently observed troupials flying together during or immediately following duets, especially following interactions with non-focal pairs. In these instances, duets may have the dual advantage of indicating the presence of a united front, while keeping pair members together to effectively respond to the territorial threat. In this way, duets could be multifunctional within a single vocal bout.

Male song as a paternity guard

Some of our results are consistent with the hypothesis that male troupials guard their paternity by answering female songs, but some key predictions of that hypothesis were not supported (Hall 2004; Seddon and Tobias 2006; Hall and Peters 2009). Our most compelling evidence for paternity guarding is that males, after answering, are especially likely to move toward their mate during the breeding season. In addition, males are more active than females, more often flying after answering their mate. These protective male behaviors, although not a stipulation of vocal paternity guarding, suggests a link between answering and other paternity guarding behaviors in troupials.

Contrary to other predictions of the paternity guarding hypothesis, we did not find evidence that males answered their mates at higher rates during the breeding season and male answering rates were lower overall than were female answering rates (Seddon and Tobias 2006; Odom et al. 2016). The overlapping structure of troupial duets affords that troupial answering could be used to mask a partners' song (Tobias and Seddon 2009). The extent of overlap varies considerably within a pair, such that troupials could alter their duet structure depending on the cooperative or conflicting context of a particular duet (Tobias and Seddon 2009). Nevertheless, we lack sufficient nesting data to confirm whether male troupials answer their mates in paternity guarding contexts specifically during female fertile periods. Such information is necessary to confidently conclude that troupials answer as a paternity guard, and would be a valuable addition to future studies with troupials or other species. There are other breeding and nest defense activities that occur throughout the breeding season. Male troupials do not participate in nest building or incubation, so an alternative possibility to paternity guarding is that males are contributing more to territory and nest defense while females are occupied with nest building and incubating.

Mate and paternity guarding are often discussed together in the duet literature, yet there are differences in the predictions of when each should occur. In both cases, mates overlap their partners' songs to signal the mated status of their partner. However, mate guarding should happen all year in year-round territorial species and both females and males can benefit from guarding their mate, whereas paternity guarding should occur specifically during the breeding season by males (Benedict 2008; Hall and Peters 2009). Having a mate even in the non-breeding season likely safeguards one's opportunity to breed during the next breeding season and maintaining the same mate for multiple mating attempts could increase success of subsequent broods (Bart and Tornes 1989). Thus, we should expect to see mate guarding year-round, but we found male troupials specifically answer and then move toward their mate during the breeding season, suggesting this behavior is more likely to guard paternity, however, more information on the occurrence of male answering specifically during female fertile periods is needed.

Sex differences in duetting behavior

Female and male troupials differed in their singing and answering behavior, which indicates that their reasons for singing and answering also differ. Combined with our previous findings that males sing the majority of their solo songs at dawn during the breeding season and females solo primarily during the day at consistent rates throughout the year, our results support the idea that social selection pressures act on elaborate traits of females (Tobias et al. 2012). In long-lived, year-round territorial species, having access to adequate resources year-round likely has substantial lifetime fitness benefits (Clutton-Brock 2009; Clutton-Brock and Huchard 2013).

Also, females specifically receive little additional benefit from attracting additional mates (West-Eberhard 1983; Lebas 2006; Rosvall 2011). Thus, females should use their songs primarily to defend territories (Tobias et al. 2012). Conversely, male singing and duetting behavior contributed to both socially and sexually selected behaviors, including defending year-round territories and protecting paternity (Andersson 1994; Tobias et al. 2012). These findings are consistent with an ancestor in which both females and males sang for territory defense, but where song has become co-opted in males to also attract mates and defend paternity. Thus, these behaviors may have arisen from broader selection pressures in both sexes. These results emphasize the importance of considering the evolutionary pressures selecting for duet participation in males and females independently (Hall 2009; Logue and Krupp 2016).

Differences in singing role

We found differences in duetting behavior between answerers and non-answerers, as well as answerers and initiators (including soloists and duet initiators), which we discuss above as lending support to our hypotheses. However, we found very little difference in the singing behavior between soloists (birds who sing and are not answered by their mates) and duet initiators (birds who sing and are answered by their mates). This may be because it is the answering bird that is chiefly responsible for creating a duet (Mennill 2006; Hall 2009; Logue and Krupp 2016). Thus, we might not expect much of a difference between the behavior of initiators, whether they are answered or not. In a previous study, we did see differences in song structure among duet initiators, soloists, and answerers (Odom et al. 2016). Therefore, it seems prudent to design analyses that allow for these roles to be examined independently (Logue and Krupp 2016).

Conclusions

Both female and male troupials answer their mates to form duets to defend territories and maintain contact in the breeding and non-breeding season, but males may also answer their mate during the breeding season in paternity guarding contexts. Troupial answering to form duets is therefore multifunctional, and its function varies with sex and season. We suggest that song answering to form duets may have evolved beyond solo singing (Odom et al. 2015) because duets can uniquely benefit both females and males in multiple and different ways. Our results emphasize the importance of taking into account the individual benefits that each sex receives from answering their mate to form duets, and using methods that allow the multifunctionality of duets to be examined both within and outside of the breeding season (Mennill and Vehrencamp 2008; Tobias et al. 2012; Logue and Krupp 2016).

References

Amundsen T, 2000. Why are female birds ornamented? Trends Ecol Evol 15:149-155.

Andersson MB, 1994. Sexual selection. Princeton, NJ: Princeton University Press.

Bart J, Tornes A, 1989. Importance of monogamous male birds in determining reproductive success. Behav Ecol Sociobiol. 24:109-116.

Benedict L, 2008. Unusually high levels of extrapair paternity in a duetting songbird with long-term pair bonds. Behav Ecol Sociobiol. 62:983-988.

Benedict L, 2010. California towhee vocal duets are multi-functional signals for multiple receivers. Behaviour. 147:953-978.

Clutton-Brock T, 2009. Sexual selection in females. Anim Behav. 77:3-11.

Clutton-Brock T, Huchard E, 2013. Social competition and its consequences in female mammals. J Zool. 289:151-171.

Dahlin CR, Benedict L, 2014. Angry Birds Need Not Apply: A Perspective on the Flexible form and Multifunctionality of Avian Vocal Duets. Ethology. 120:1-10.

Dowling J, Webster MS, 2015. An experimental test of duet function in a fairy-wren (Malurus) with moderate cuckoldry rates. Behav Ecol. 27:228-236.

Farabaugh SM, 1982. The ecological and social significance of duetting. In: Kroodsma DE, Miller AH, Ouellette H, editors. Acoustic Communication in Birds. New York, NY: Academic Press. p. 85-124.

Geweke J, 1992. Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. In: Bernardo J, Berger J, Dawid A, Smith A, editors. Bayesian Statistics. 4th ed. Oxford, UK: Oxford University Press. p. 169-188.

Griffiths R, Double MC, Orr K, Dawson RJ, 1998. A DNA test to sex most birds. Mol Ecol. 7:1071-1075.

Hadfield JD, 2010a. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. J Stat Softw. 33:1-22.

Hadfield J, 2010b. MCMCglmm: Markov chain Monte Carlo methods for Generalised Linear Mixed Models. Tutorial for MCMCglmm package in R:1-25.

Hall ML, 2000. The function of duetting in magpie-larks: conflict, cooperation, or commitment? Anim Behav. 60:667-677.

Hall ML, 2004. A review of hypotheses for the functions of avian duetting. Behav Ecol Sociobiol. 55:415-430.

Hall ML, 2009. A review of vocal duetting in birds. Adv Stud Behav. 40:67-121.

Hall ML, Peters A, 2009. Do male paternity guards ensure female fidelity in a duetting fairy-wren? Behav Ecol. 20:222-228.

Heidelberger P, Welch PD, 1983. Simulation run length control in the presence of an initial transient. Oper Res. 31:1109-1144.

Jaramillo A, Burke P, 1999. New World Blackbirds: The Icterids. Princeton, NJ: Princeton University Press.

Kery, M, 2010. Introduction to WinBUGS for ecologists: Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses. Boston, MA: Academic Press.

Lebas NR, 2006. Female finery is not for males. Trends Ecol Evol. 21:170-173.

Logue DM, 2005. Cooperative defence in duet singing birds. Cogn Brain Behav. 9:497-510.

Logue DM, 2007. Duetting in space: a radio-telemetry study of the black-bellied wren. Proc R Soc B. 274:3005-3010.

Logue DM, Gammon DE, 2004. Duet song and sex roles during territory defence in a tropical bird, the black-bellied wren, *Thryothorus fasciatoventris*. Anim Behav. 68:721-731.

Logue DM, Hall ML, 2014. Migration and the evolution of duetting in songbirds. Proc R Soc B. 281:20140103.

Logue DM, Krupp DB, 2016. Duetting as a collective behavior. Front Ecol Evol. 4:7.

Mann NI, Dingess KA, Barker KF, Graves JA, Slater PJ, 2009. A comparative study of song form and duetting in neotropical Thryothorus wrens. Behaviour. 146:1-43.

Marshall-Ball L, Mann N, Slater P, 2006. Multiple functions to duet singing: hidden conflicts and apparent cooperation. Anim Behav. 71:823-831.

Mays HL, Yao C-T, Yuan H-W, 2006. Antiphonal duetting in Steere's liocichla (*Liocichla steerii*): male song individuality and correlation between habitat and duetting behavior. Ecol Res. 21:311-314.

McGregor PK, 2005. Animal communication networks. Cambridge, UK: Cambridge University Press.

Mennill DJ, 2006. Aggressive responses of male and female rufous-and-white wrens to stereo duet playback. Anim Behav. 71:219-226.

Mennill DJ, Vehrencamp SL, 2008. Context-dependent functions of avian duets revealed by microphone-array recordings and multispeaker playback. Curr Biol. 18:1314-1319.

Molles LE, Waas JR, 2006. Are two heads better than one? Responses of the duetting kokako to one-and two-speaker playback. Anim Behav. 72:131-138.

Odom KJ, 2016. Investigating female songs and duets in songbirds (Oscine passerines) at three evolutionary scales: phylogenetic reconstruction, comparative methods, and field studies. Baltimore, MD: University of Maryland, Baltimore County.

Odom KJ, Hall ML, Riebel K, Omland KE, Langmore NE, 2014. Female song is widespread and ancestral in songbirds. Nat commun. 5:3379.

Odom KJ, Omland KE, McCaffrey DR, Monroe MK, Christhilf JL, Roberts NS, Logue DM, 2016. Typical males and unconventional females: songs and singing behaviors of a tropical, duetting oriole in the breeding and non-breeding season. Front Ecol Evol. 4:14.

Odom KJ, Omland KE, Price JJ, 2015. Differentiating the evolution of female song and male–female duets in the New World blackbirds: Can tropical natural history traits explain duet evolution? Evolution. 69:839-847.

Rosvall KA, 2011. Intrasexual competition in females: evidence for sexual selection? Behav Ecol. 22:1131-1140.

Seddon N, Tobias JA, 2006. Duets defend mates in a suboscine passerine, the warbling antbird (*Hypocnemis cantator*). Behav Ecol. 17:73-83.

Sonnenschein E, Reyer HU, 1983. Mate-Guarding and other Functions of Antiphonal Duets in the Slate-coloured Boubou (*Laniarius funebris*) 1. Z Tierpsychol. 63:112-140.

Stutchbury BJ, Morton ES, 2001. Behavioral ecology of tropical birds. San Diego, CA: Academic Press.

R Development Core Team. 2014. R: a language and environment for statistical computing (reference index, version 3.1.2). Vienna (Austria): R Foundation for Statistical Computing: http://www r-project org.

Templeton C, Rivera-Caceres K, Mann N, Slater P, 2011. Song duets function primarily as cooperative displays in pairs of happy wrens. Anim Behav. 82:1399-1407.

Tobias JA, Montgomerie R, Lyon BE, 2012. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. Phil Trans R Soc B. 367:2274-2293.

Tobias JA, Seddon N, 2009. Signal jamming mediates sexual conflict in a duetting bird. Curr Biol. 19:577-582.

Tobias JA, Sheard C, Seddon N, Meade A, Cotton AJ, Nakagawa S, 2016. Territoriality, social bonds, and the evolution of communal signaling in birds. Front Ecol Evol. 4:74.

West-Eberhard MJ, 1983. Sexual selection, social competition, and speciation. Q Rev Biol. 58:155-183.

Zuur AF, Ieno EN, Elphick CS, 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol. 1:3-14.

Figure captions:

Figure 1. Troupial initiation rates are predicted by prior song rates of other, non-focal troupials. The number of songs initiated by focal troupials increases with number of (a) prior solos and (b) prior duets by conspecifics (Table 2). Values are raw counts for each bird.

Figure 2. Troupial answering behavior is predicted by prior songs by other, non-focal troupials and sex: a) troupials are more likely to answer their mate to form a duet after conspecific duets than after conspecific solos; b) female troupials answer a larger proportion of their mate's songs to form duets than males, who leave a large portion of their mate's songs unanswered.

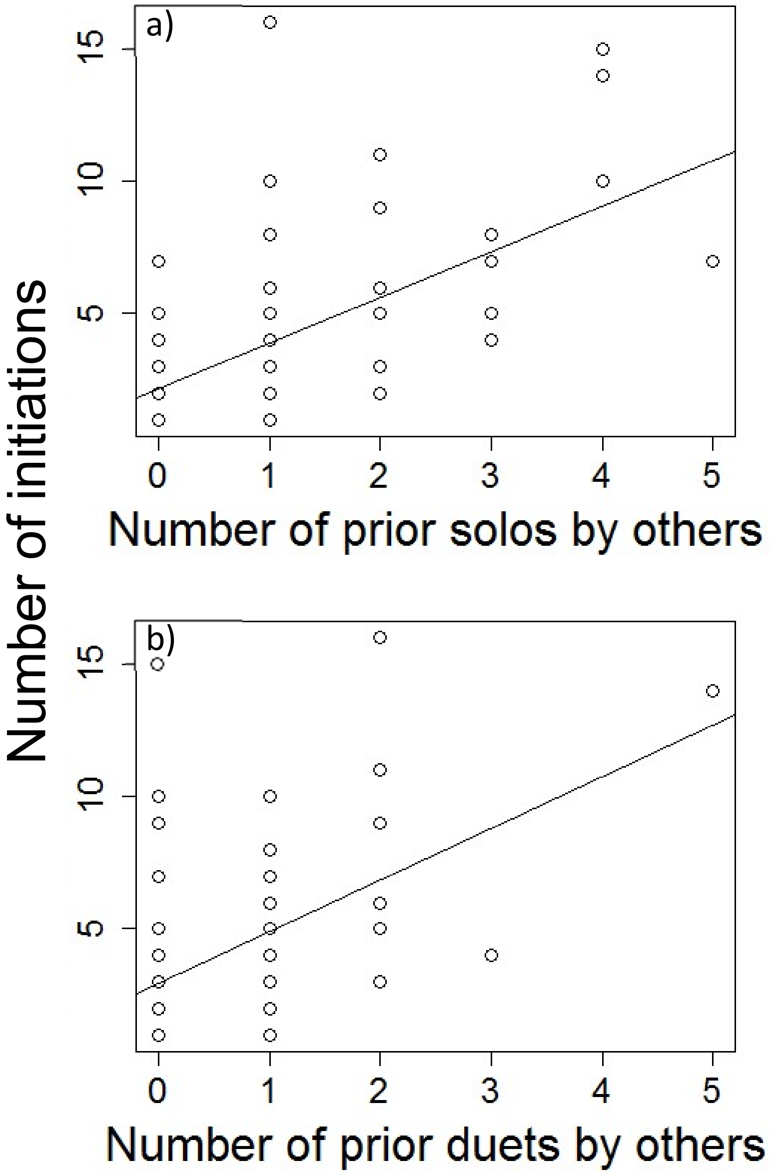
Figure 3. Immediate behavior of troupials following focal songs show that (a) males are less likely to perch than females, (b) troupials are less likely to perch in the breeding than the non-breeding season, and (3) duet initiators and non-answerers are less likely to perch than answerers.

Figure 4. Reaction direction with respect to mate varied with singing role, such that answerers were more likely to move toward their mate than soloists, and duet initiators were more likely to stay the same distance from their mate compared to answerers.

Figure 5. Reaction direction to mate varied with Sex x Role and Sex x Season interactions: a) male duet initiators were more likely to stay the same distance from their mate than female duet initiators, especially compared to answerers; b) during the breeding season, males are more likely to move toward their mate than females.

Figure S1. Immediate behavior following focal songs was influenced by Sex x Role and Season x Role interactions: a) the likelihood of perching after initiating or non-answering was higher in males than females; b) the likelihood of perching was greater for answerers compared to non-answerers in the non-breeding season.

Figure 1.


a)
Number of initiations
5
10
15
0
1
2
3
4
5
Number of prior solos by others
b)
5
10
15
0
1
2
3
4
5
Number of prior duets by others

605 Figure 2.

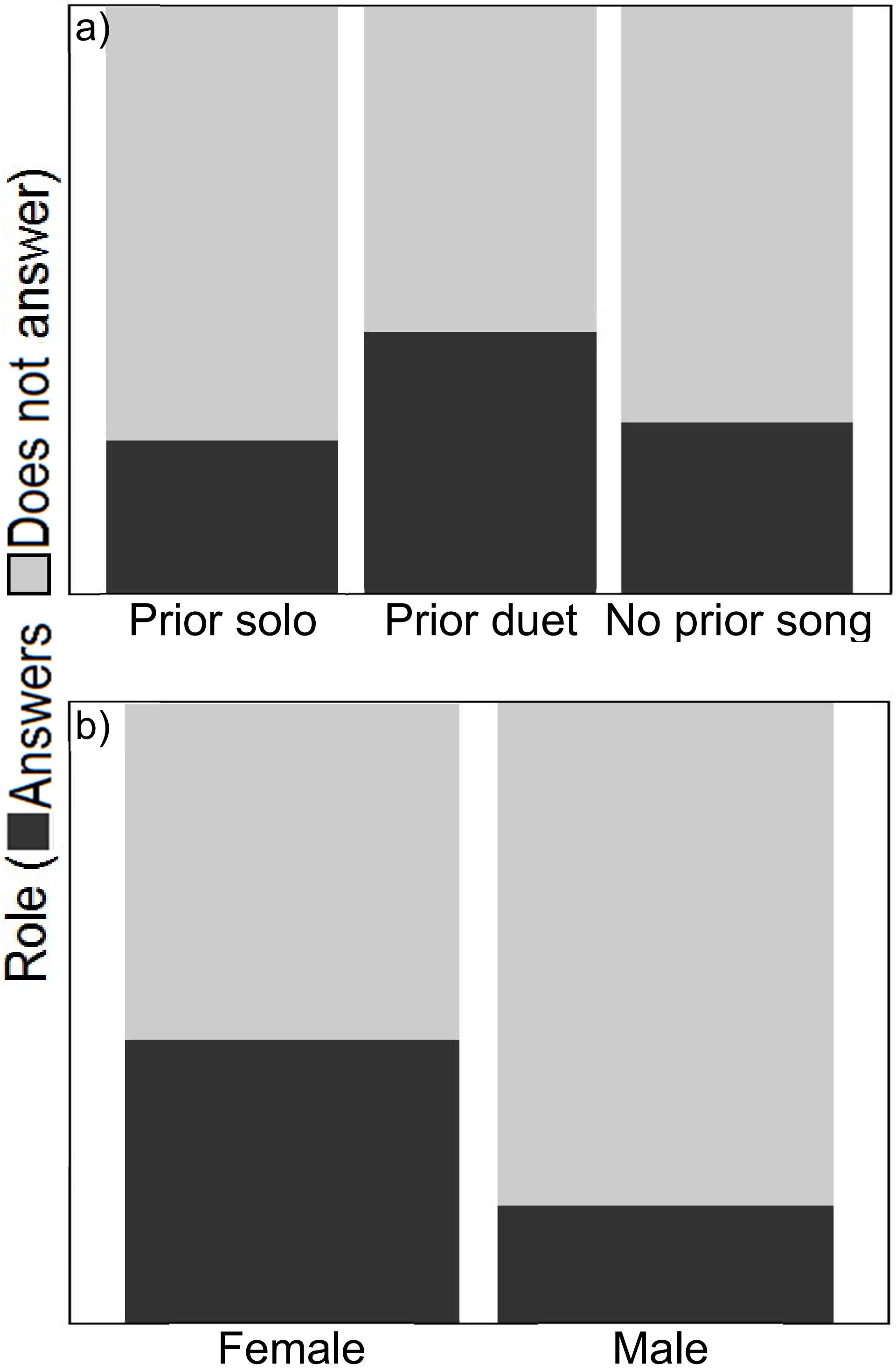

Role (■Answers □Does not answer)
a)
Prior solo
Prior duet
No prior song
b)
Female
Male

Figure 3.

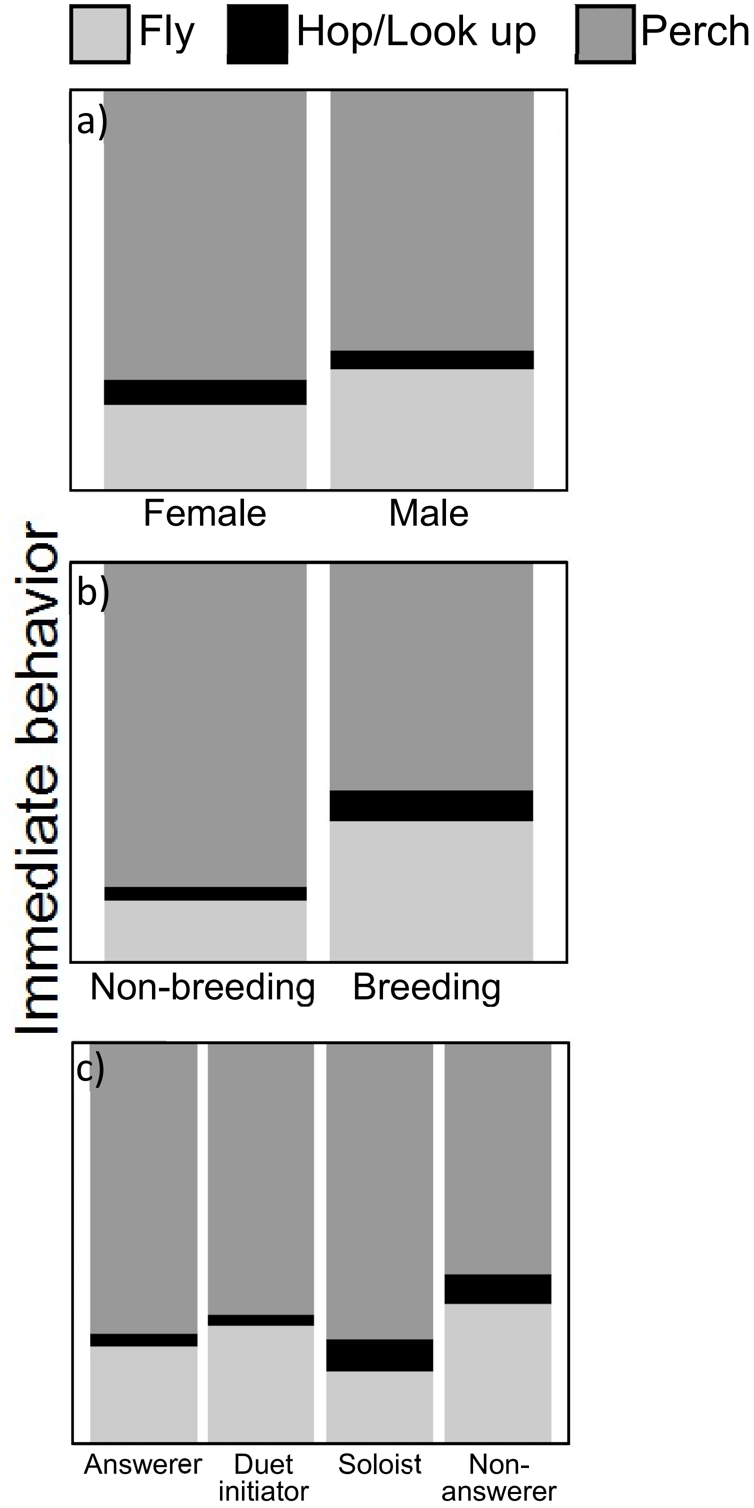
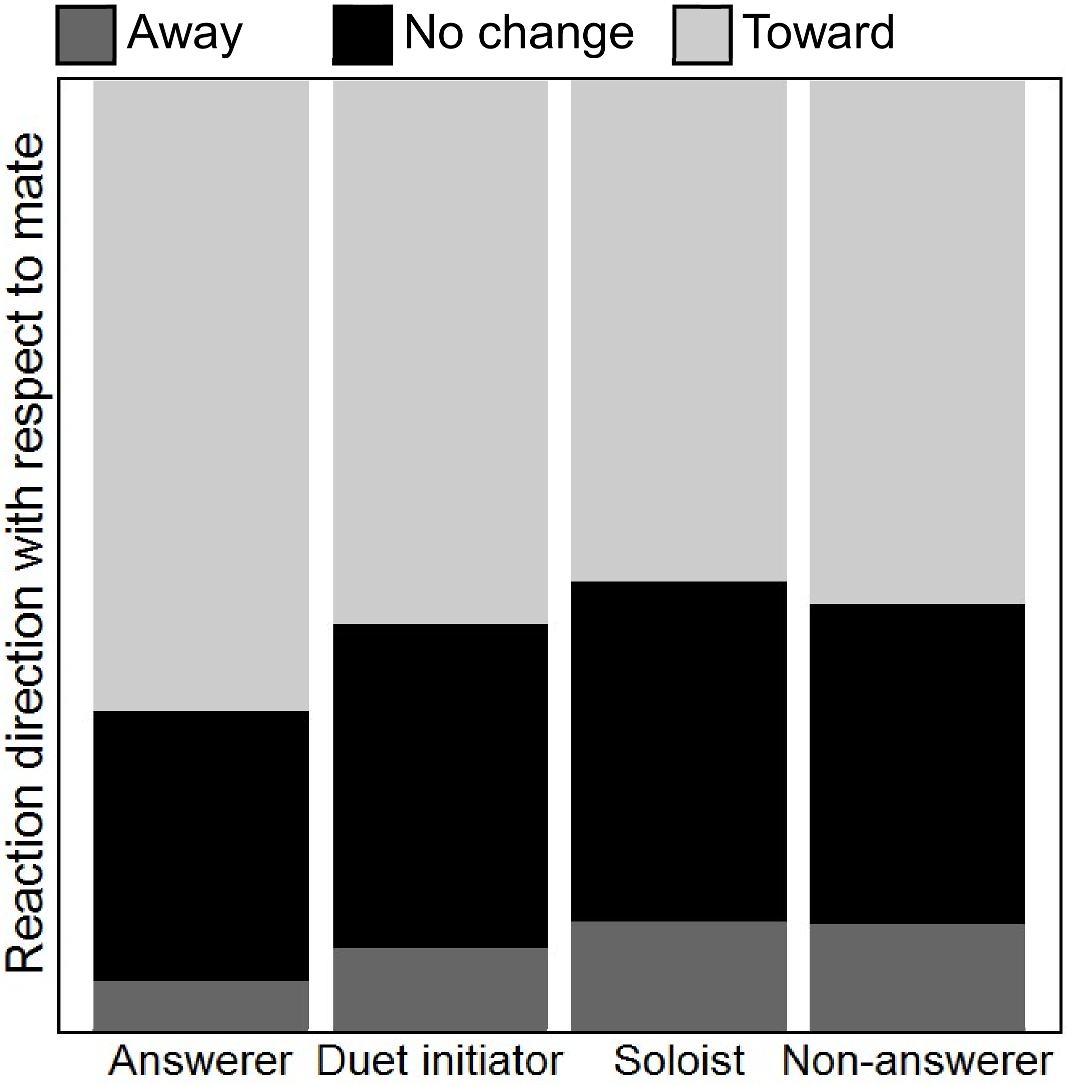

Fly
Hop/Look up
Perch
Immediate behavior
a)
Female
Male
b)
Non-breeding
Breeding
c)
Answerer
Duet initiator
Soloist
Non-answerer

Figure 4.



Away
No change
Toward
Reaction direction with respect to mate
Answerer
Duet initiator
Soloist
Non-answerer

Figure 5.

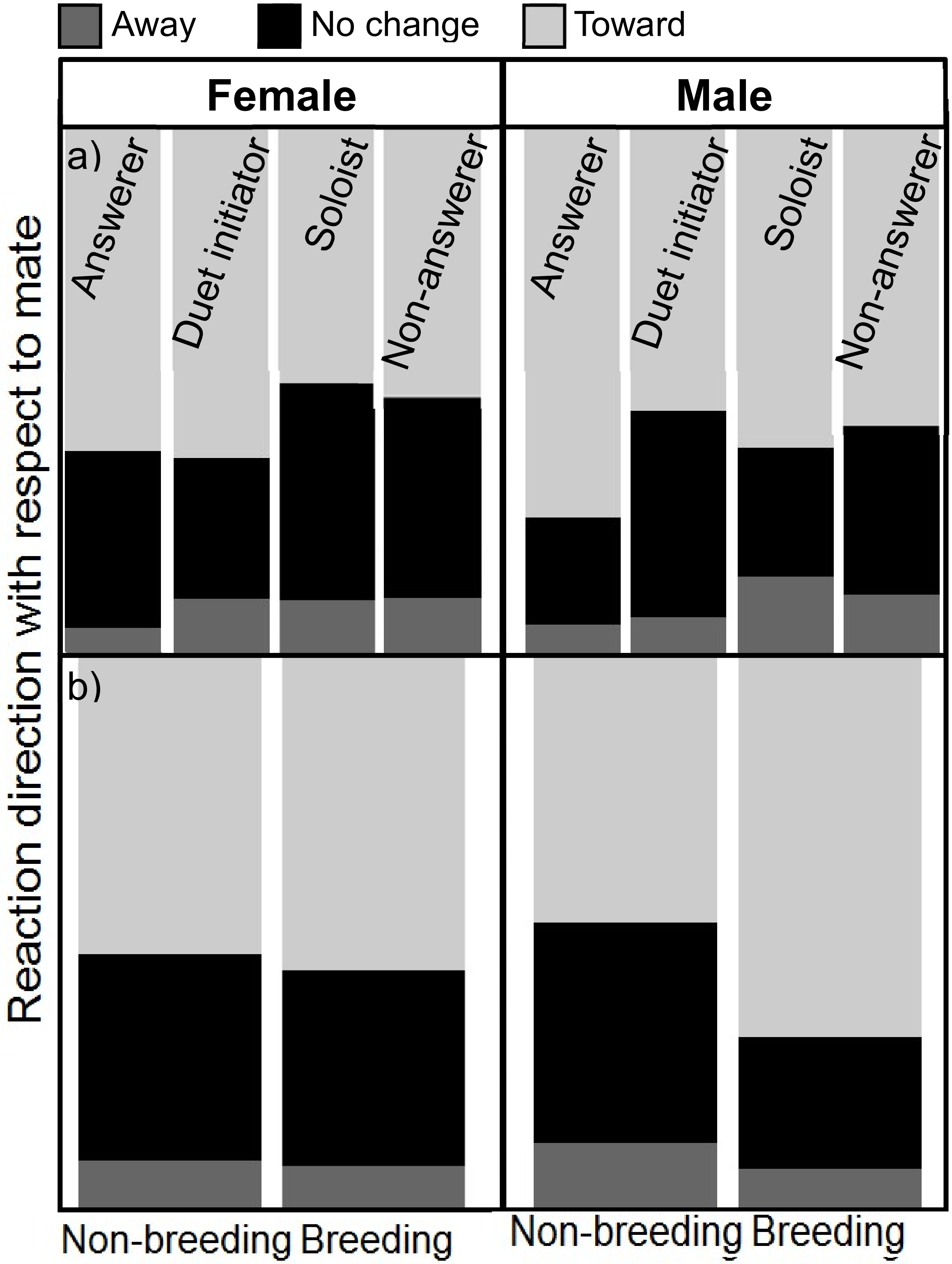

Away
No change
Toward
Female
Male
a)
Answerer
Duet initiator
Soloist
Non-answerer
Answerer
Duet initiator
Soloist
Non-answerer
b)
Reaction direction with respect to mate
Non-breeding
Breeding
Non-breeding
Breeding

Figure S1.

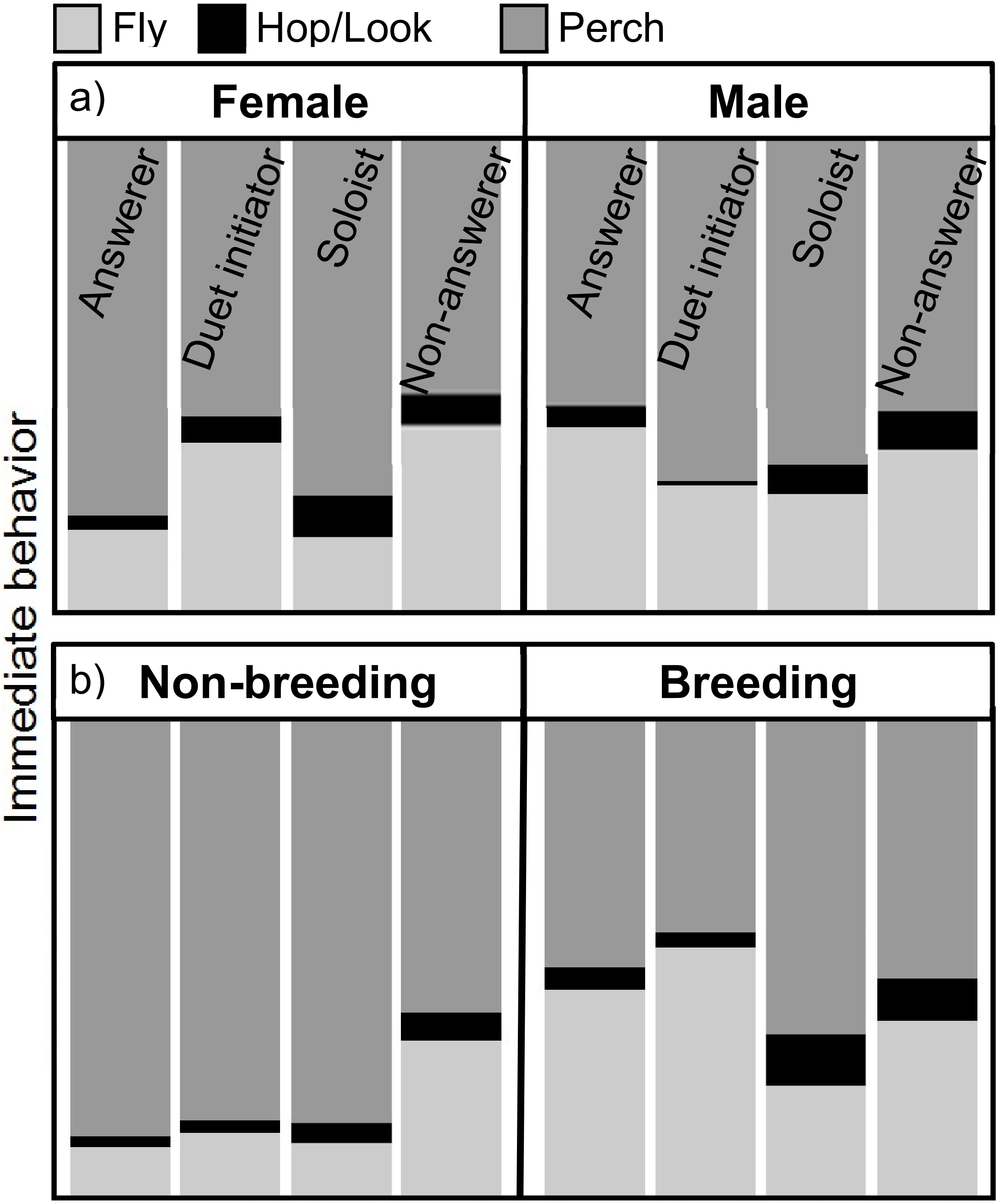

Fly
Hop/Look
Perch
a)
Female
Male
Answerer
Duet initiator
Soloist
Non-answerer
Answerer
Duet initiator
Soloist
Non-answerer
Immediate behavior
b)
Non-breeding
Breeding

Table 1. All full and reduced models analyzed for both the predictive and subsequent behavior analyses, including all response variables included in each model. Interactions are specified by *.

Analysis	Dataset	Response variable	Model version	Explanatory variables
Predictive behavior	Initiators	Initiation rate (averaged by individual)	Full	Prior solos by others + Prior duets by others + Mate distance + Number of others + Sex + Role (Soloist or Duet initiator) + Season + Prior solos*Sex + Prior duets*Sex + Mate distance*Sex + Number of others*Sex + Prior solos*Role + Prior duets*Role + Mate distance*Role + Number of others*Role + Prior solos*Season + Prior duets*Season + Mate distance*Season + Number of others*Season
			Reduced	Prior solos by others + Prior duets by others + Mate distance + Number of others + Sex + Role + Season
	Answerers	Role (Answerer or Non-answerer)	Full	Prior song type by others + Mate distance + Number of others + Sex + Season + Prior song type by others*Sex + Mate distance*Sex + Number of others*Sex + Prior song type by others*Season + Mate distance*Season + Number of others*Season
			Reduced	Prior song type by others + Mate distance + Number of others + Sex + Season
Subsequent behavior	All Roles (Soloists, Duet initiators, Answerers, and Non-answerers)	Immediate behavior	Full	Sex + Role + Season + Sex*Role + Role*Season + Sex*Season
			Reduced	Sex + Role + Season + Sex*Role + Role*Season
		Reaction direction to mate	Full	Sex + Role + Season + Sex*Role + Role*Season + Sex*Season
			Reduced	Sex + Role + Season + Sex*Role + Sex*Season
		Reaction direction to other	Full	Sex + Role + Season + Sex*Role + Role*Season + Sex*Season
			Reduced	Sex + Role + Season + Role*Season

Table 2. Predictive behavior models. Reduced model results for explanatory variables that may predict whether a troupial (1) initiates singing, or (2) answers versus does not answer their mate's song to form a duet. Variables that contribute substantially to variation in each model are in bold (based on a Bayesian p-value ≤ 0.05).

Dataset	**Variable**	**Levels compared**	**Posterior means**	**Lower 95% CI**	**Upper 95% CI**	**Effective sample size**	**Bayesian p-value**
Initiation rate	**Prior solos by others**	-	0.48	0.23	0.75	103444	**< 0.001**
	Prior duets by others	-	0.30	0.06	0.54	129144	**0.016**
	Mate distance	-	0.13	-0.14	0.42	62360	0.356
	Number of others	-	0.01	-0.27	0.29	71604	0.933
	Sex	Female - Male	-0.11	-0.64	0.42	83318	0.673
	Role	Duet initiator - Soloist	0.13	-0.40	0.67	84160	0.627
	Season	Non-breeding - Breeding	-0.24	-0.76	0.28	80370	0.363
Answerers vs Non-answerers	**Prior song type by other**	Duet - None	54.58	-41.08	152.64	33507	0.252
		Duet - Solo	110.76	5.66	221.12	19080	**0.031**
	Mate distance	-	24.80	-3.75	55.61	28185	0.088
	Number of others	-	18.46	-9.75	47.70	32985	0.191
	Sex	**Female - Male**	152.16	48.53	258.99	10530	**0.003**
	Season	Non-Breeding - Breeding	9.60	-49.73	70.57	54270	0.746

Table 3. Subsequent behavior models – Immediate behavior. Final model for immediate behavioral response of troupials to focal songs based on sex, singing role, and season. Levels listed below are with respect to the following levels – Immediate behavior: fly, Sex: female, Role: answerer, and Season: non-breeding. Variables that contribute substantially to variation in the model are in bold (based on a Bayesian p-value ≤ 0.05).

Explanatory variable	**Levels**	**Posterior means**	**Lower 95% CI**	**Upper 95% CI**	**Effective sample size**	**Bayesian p-value**
	Hop/Look up	-2.57	-4.60	-0.61	1241	**0.003**
	Perch	1.78	0.91	2.65	9315	**< 0.001**
Sex	Hop/Look up: Male	-0.88	-3.20	1.42	1617	0.448
	Perch: Male	-1.87	-3.02	-0.76	9439	**0.001**
Role	Hop/Look up: Duet initiator	0.04	-2.67	2.75	1363	0.974
	Perch: Duet initiator	-1.28	-2.39	-0.17	8155	**0.022**
	Hop/Look up: Soloist	0.93	-1.34	3.26	1526	0.433
	Perch: Soloist	-0.60	-1.64	0.45	8041	0.259
	Hop/Look up: Non-answerer	-0.62	-3.40	2.14	1499	0.664
	Perch: Non-answerer	-2.38	-3.56	-1.23	8633	**< 0.001**
Season	Hop/Look up: Breeding	-0.78	-2.92	1.44	1431	0.458
	Perch: Breeding	-2.23	-3.16	-1.30	8086	**< 0.001**
Sex * Role	Hop/Look up: Male-Duet initiator	-0.82	-4.45	2.59	1046	0.653
	Perch: Male-Duet initiator	2.27	0.95	3.58	7988	**< 0.001**
	Hop/Look up: Male-Soloist	-0.22	-2.81	2.38	1945	0.862
	Perch: Male-Soloist	1.12	-0.12	2.37	8565	0.076
	Hop/Look up: Male-Non-answerer	1.47	-1.35	4.42	1826	0.312
	Perch: Male-Non-answerer	1.79	0.44	3.13	8789	**0.008**
Role * Season	Hop/Look up: Duet initiator-Breeding	-0.57	-3.85	2.68	1159	0.719
	Perch: Duet initiator-Breeding	-0.07	-1.34	1.17	8199	0.907
	Hop/Look up: Soloist-Breeding	0.72	-1.83	3.26	1800	0.567
	Perch: Soloist-Breeding	1.11	-0.07	2.29	8524	0.064
	Hop/Look up: Non-answerer-Breeding	0.63	-2.11	3.36	1858	0.648
	Perch: Non-answerer-Breeding	1.79	0.54	3.07	8905	**0.005**

Table 4. Subsequent behavior models – Reaction direction with respect to mate. Final models for the direction focal troupials moved with respect to their mate following focal songs. Levels listed below are with respect to the following levels – Reaction direction: away, Sex: female, Role: answerer, and Season: non-breeding. Variables that contribute substantially to variation in each model are in bold (based on a Bayesian p-value ≤ 0.05).

Explanatory variable	**Levels**	**Posterior means**	**Lower 95% CI**	**Upper 95% CI**	**Effective sample size**	**Bayesian p-value**
	No change	1.48	0.49	2.48	2848	**0.002**
	Toward mate	1.73	0.83	2.66	2434	**< 0.001**
Sex	No change: Male	-1.22	-2.78	0.32	2815	0.120
	Toward mate: Male	-0.62	-1.97	0.73	2818	0.367
Role	**No change: Duet initiator**	-1.33	-2.48	-0.24	2618	**0.019**
	Toward mate: Duet initiator	-0.93	-1.96	0.11	2691	0.079
	No change: Soloist	-0.61	-1.57	0.34	2465	0.201
	Toward mate: Soloist	-1.13	-2.05	-0.20	2380	**0.014**
	No change: Non-answerer	-0.58	-1.67	0.50	2552	0.292
	Toward mate: Non-answerer	-1.04	-2.11	0.01	2643	0.052
Season	No change: Breeding	-0.07	-0.78	0.65	3253	0.863
	Toward mate: Breeding	0.07	-0.63	0.75	3069	0.841
Sex * Role	**No change: Male-Duet initiator**	2.11	0.46	3.79	2359	**0.014**
	Toward mate: Male-Duet initiator	0.42	-1.10	1.96	2663	0.589
	No change: Male-Soloist	0.03	-1.59	1.64	2478	0.975
	Toward mate: Male-Soloist	-0.14	-1.62	1.32	2726	0.855
	No change: Male-Non-answerer	0.54	-1.08	2.16	2476	0.512
	Toward mate: Male-Non-answerer	0.04	-1.48	1.54	2676	0.956
Sex * Season	No change: Male-Breeding	0.07	-0.96	1.11	3148	0.907
	Toward mate: Male-Breeding	0.99	0.00	1.97	3056	**0.049**

Table S1. Number of individuals and number of observations for each sex included in each analysis.

Analysis	Dataset	Season	Sex	Number of individuals	Number of observations
Predictive behavior	Initiators	Breeding	Male	15	81
			Female	16	118
		Non-breeding	Male	12	77
			Female	12	85
	Answerers	Breeding	Male	16	104
			Female	15	76
		Non-breeding	Male	11	79
			Female	12	77
Subsequent behavior	Immediate behavior	Breeding	Male	16	184
			Female	16	199
		Non-breeding	Male	12	136
			Female	12	149
	Reaction direction to mate	Breeding	Male	16	180
			Female	16	192
		Non-breeding	Male	12	154
			Female	12	159
	Reaction direction to other	Breeding	Male	16	91
			Female	15	120
		Non-breeding	Male	11	84
			Female	11	80

Table S2. Full model results for interaction terms not included in the reduced models (those interaction terms that did not contribute considerably to the final models based on a Bayesian p-value ≤ 0.05). Levels listed below are with respect to the following levels –Sex: female, Role: answerer, Season: non-breeding, Immediate behavior: fly, and Reaction direction: away.

Analysis	**Dataset**	**Levels**	**Posterior means**	**Lower 95% CI**	**Upper 95% CI**	**Effective sample size**	**Bayesian p-value**
Predictive behavior model – Initiation rate	Initiators	Prior Solo – Sex: male	-0.19	-0.82	0.44	89648	0.56
		Prior Duet – Sex: male	-0.24	-1.06	0.58	73281	0.57
		Mate Distance – Sex: male	0.27	-0.47	1.01	53831	0.47
		Number of others – Sex: male	-0.65	-1.42	0.12	79385	0.10
		Prior Solo – Role: soloist	-0.39	-1.03	0.26	75453	0.24
		Prior Duet – Role: soloist	0.33	-0.48	1.15	80385	0.43
		Mate Distance – Role: soloist	-0.01	-0.73	0.69	47015	0.96
		Number of others – Role: soloist	-0.37	-0.94	0.22	53231	0.21
		Prior Solo – Season: breeding	0.47	-0.18	1.13	75075	0.16
		Prior Duet – Season: breeding	-0.31	-0.89	0.28	96389	0.29
		Mate Distance – Season: breeding	-0.22	-1.02	0.59	67724	0.59
		Number of others – Season: breeding	0.00	-0.60	0.59	61081	0.99
Predictive behavior model – Answerer vs Non-answerer	Answerers vs non-answerers	Prior song type by others: duet – Sex: male	67.88	-151.65	290.82	49359	0.54
		Prior song type by others: solo – Sex: male	-55.28	-206.71	93.89	55249	0.47
		Mate Distance – Sex: male	7.72	-69.11	82.21	55445	0.84
		Number of others – Sex: male	28.53	-39.32	97.09	52322	0.41
		Prior song type by others: duet – Season: breeding	-19.06	-235.00	200.40	48957	0.86
		Prior song type by others: solo – Season: breeding	7.23	-144.10	159.95	52558	0.93
		Mate Distance – Season: breeding	-37.73	-114.31	40.20	54834	0.33
		Number of others – Season: breeding	-6.97	-73.43	59.00	55890	0.84
Subsequent behavior – Immediate behavior	All roles	Hop/Look up: Sex: male – Season: breeding	-1.63	-3.77	0.54	1587.2	0.14
		Perch: Sex: male – Season: breeding	-0.21	-1.14	0.71	9540.3	0.66
Subsequent behavior – Reaction direction to mate	All roles	No change: Role: initiator – Season: breeding	-0.03	-1.66	1.58	2365	0.97
		Toward mate: Role: initiator – Season: breeding	0.03	-1.48	1.54	2418	0.96
		No change: Role: soloist – Season: breeding	0.93	-0.57	2.43	2476	0.22
		Toward mate: Role: soloist – Season: breeding	-0.43	-1.85	0.95	2614	0.55
		No change: Role: non-answerer – Season: breeding	0.85	-0.73	2.45	2510	0.29
		Toward mate: Role: non-answerer: Season: breeding	-0.68	-2.18	0.79	2565	0.37