A test of the dear enemy hypothesis in female New Zealand bellbirds (*Anthornis melanura*): female neighbors as threats

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The "dear enemy" hypothesis proposes that the level of territorial aggression toward conspecific neighbors is lower than that shown toward strangers primarily because of differences in "threat." Individual recognition is considered to be an important component of this hypothesis. Among songbirds, recognition is often based on vocalizations and male song playbacks have been used to test this dear enemy hypothesis. However, territorial song is not an exclusively male activity and female song is more widespread than previously thought, although the functions are not well understood. The vocalizations of the endemic New Zealand bellbird (*Anthornis melanura*), a species in which both sexes sing prolifically, have recently been quantified, and bellbirds provide an exciting model for examining the function of female song. We experimentally tested the dear enemy hypothesis for territorial females using female neighbor–stranger playback. We found clear evidence that individual females discriminate between conspecific female neighbor and stranger song. Aggressive responses were strongest during the courtship and chick-rearing stages and involved rapid countersinging responses and movement toward the speaker. Most importantly, females were more aggressive toward the songs of neighboring females. This result is opposite to the dear enemy phenomenon and suggests that neighboring females pose a greater threat than strangers. A higher female neighbor threat may be linked to either competition for food resources or paternal care. We predict that these higher levels of aggression may play a role in sexual selection and polygny prevention and that neighboring females are the greatest threat to the loss of a mate. *Key words: Anthornis melanura*, bellbirds, countersinging, dear enemy hypothesis, female song, neighbor–stranger, playback experiment. *[Behav Ecol 19:791–798 (2008)]*

T he "dear enemy" hypothesis proposes that the level of territorial aggression toward conspecific neighbors (i.e., familiar individuals) should be lower than that shown toward strangers (Fisher 1954). Although exceptions have been found (reviewed in Temeles 1994; e.g., Dunn and Messier 1999), the dear enemy hypothesis has general support across a wide range of taxa. Temeles (1994) refined this hypothesis and proposed that the responses observed from territorial males are dependent not only on the familiarity of the intruder but also on the relative threats of familiar versus unfamiliar conspecifics. In view of this, the levels of relative aggression toward neighbors and strangers may vary with time of year, breeding activity (e.g., Hyman 2005), and resource availability (e.g., Jaeger 1981). Temeles (1994) found that the dear enemy phenomenon occurred primarily in species with multipurpose/breeding territories. Indeed, even very small defended nest sites such as in the Audubon shearwater (*Puffinus l. lherminieri*) have been found to exhibit neighbor–stranger discrimination (e.g., Mackin 2005).

The costs of territorial defense can be substantial (e.g., Jaeger 1981), and fitness benefits can be gained by using an appropriate level of defense thus minimizing wasted time, energy, and risk. Established neighbors are in many cases a "known" threat; in particular, neighbors already hold a territory and may be less likely to usurp the territory of their neighbor (e.g., Eason and Hannon 1994). In contrast, a stranger or

unfamiliar conspecific will have an unknown territorial status and should represent a greater threat. For this reason, neighbor recognition has been established as important in enabling optimal defense responses toward intruders. The mechanism by which neighbor recognition is facilitated will vary between species, but among songbirds, recognition is often based on vocalizations (e.g., Brooks and Falls 1975; Stoddard 1991, 1996; Stoddard et al. 1991; Naguib and Todt 1998; Molles and Vehrencamp 2001; Leader et al. 2002). Neighbor–stranger discrimination using song playbacks was nicely demonstrated in territorial white-throated sparrows by Brooks and Falls (1975). In these playback experiments, territorial males did not only respond more aggressively (by singing) toward strangers compared with neighbors but also maintained a significantly higher singing rate for a considerable time after the playback was completed. Experimental song playbacks have been used to test the dear enemy hypothesis for territorial males of many species of birds (reviewed in Temeles 1994; e.g., Lovell and Lein 2004; Mackin 2005; Hardouin et al. 2006). In contrast, female responses to female song playbacks have been largely neglected. However, one such experiment, conducted by Beletsky (1983) using territorial female red-winged blackbirds, found that neighbor and non-neighbor playbacks elicited equally aggressive responses by territorial females.

Although territorial song is not an exclusively male activity (reviewed in Nice 1943; e.g., Cooney and Cockburn 1995; Brunton and Li 2006), for most temperate northern hemisphere passerines, song has been seen as a male activity, functioning in territoriality, and mate attraction (e.g., Catchpole 1982; Searcy and Andersson 1986; Kroodsma and Byers 1991). Some time ago, Ritchison (1983) reviewed the occurrence of female bird song and found at least 40 species where female

song was common. As the number of worldwide studies of songbirds increases, the phenomenon of complex, territorial female song has been found to be more widespread than first thought. In particular, female singing can be a normal feature of female behavior, for example, female superb fairy wrens (*Malurus cyaneus*) (e.g., Cooney and Cockburn 1995), in Australia, are prolific solo singers throughout the year. Specifically, the context of female singing and the frequency of its use are extremely varied between geographic districts and species. In contrast to male song, the functions of female song are not well understood, but they are likely to parallel those associated with male song and may include territorial and resource defense, mate attraction, and intrasexual competition (e.g., Langmore 1998). Indeed, attention has recently been drawn to the lack of our understanding of sexual selection in females (e.g., Clutton-Brock 2007). The intensity of female competition for breeding opportunities is high in many species (e.g., Clutton-Brock 2007).

The vocalizations of the endemic New Zealand bellbird (*Anthornis melanura*), a species in which both sexes sing prolifically, have only recently been quantified (Brunton and Li 2006). Female singing in this species is particularly well developed, and female bellbirds may provide an exciting model for examining the selective advantages of female song. Bellbirds exhibit social monogamy, and both males and females display territorial and/or resource defense throughout the year (e.g., Craig and Douglas 1986; Kendrick 1994). Female singing behavior is most common early in the breeding season when territorial defense, mating, and nest site selection are predominant behaviors (e.g., Li 2002). Singing and countersinging by females continues to occur frequently throughout the breeding attempt, and females often sing on leaving the nest after an incubation bout (e.g., Li 2002). We used behavioral observations to examine the social context of countersinging behavior of bellbirds and experimentally tested, for the first time, the hypothesis that territorial female bellbirds

display the dear enemy phenomenon within Temeles' (1994) theoretical framework. This approach assumes that the relative threats of intruding female neighbors and strangers will differ. Our null hypothesis was that territorial females would not discriminate between songs of female neighbors and strangers. Furthermore, if female bellbirds can discriminate between these categories, then a more aggressive response toward strangers is predicted because stranger females are likely to be a greater risk to territorial females as territorial status is unknown. To test this hypothesis, we conducted female neighbor–stranger playback experiments within bellbird breeding territories of known reproductive stage and quantified the responses of the male and female territory owners.

MATERIALS AND METHODS

Study area and species background

This study was conducted on Tiritiri Matangi Island (Tiri), a 220 ha island in the Hauraki Gulf, 3.5 km off the end of the Whangaparoa Peninsula, and 28 km north of Auckland (Latitude 36°45′S, Figure 1). The bellbird population on Tiri is large (1000–1500 individuals; Brunton DH, unpublished data) and has existed on the island for at least 100 years (Lovegrove T, personal communication). Tiri is a wildlife sanctuary with open access to the public and currently has no introduced mammalian predators. The island has been extensively replanted over the last 20 years, and a series of avian and reptilian species have been reintroduced for conservation reasons (reviewed in Rimmer 2004).

Female bellbirds are easily distinguished in the field from males by plumage and morphological differences: females have a white cheek stripe, are paler gray-green, and approximately 20% smaller than males. Bellbirds are highly territorial during the breeding season (austral spring/summer) but outside of this period occasionally form small foraging flocks of either adult females and juveniles or adult males. Both sexes are observed singing on their territories year round (e.g.,
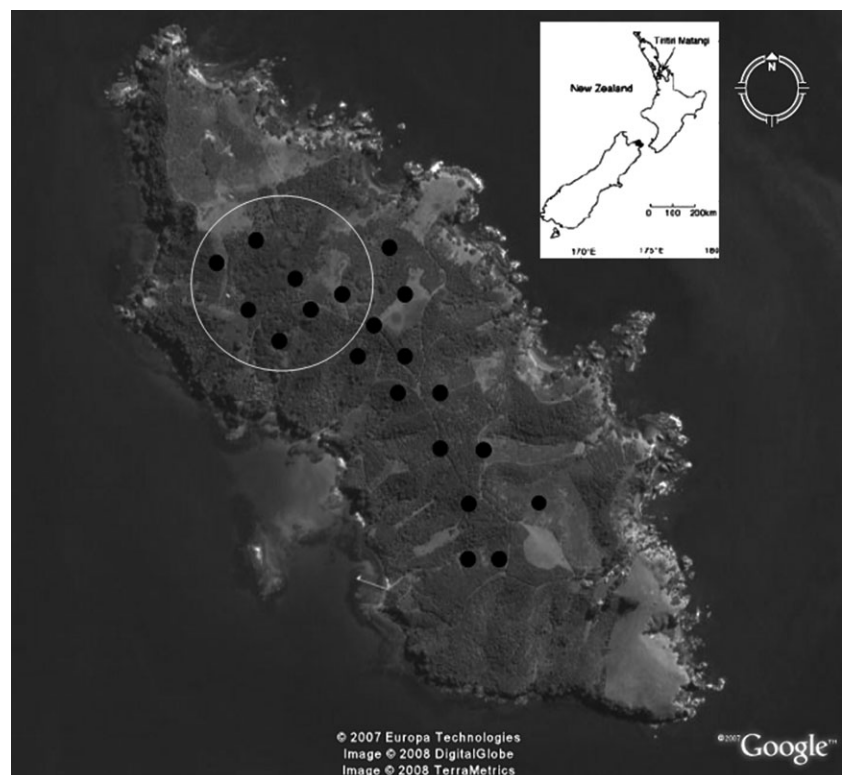
Figure 1
Map of Tiri. Black circles indicate the location of the listening posts within the study area, whereas the circled area indicates the neighborhoods in which the female playback experiments were conducted.

Li 2002), but the extent to which individuals stay close by their breeding territories is unknown, although banded male and female birds are frequently observed year round at sugar-water feeder stations near or on their territories. Tiri is typical of most northern New Zealand forest ecosystems where year-round fruiting and flowering of plant species provide a "movable" feast of food resources. Consequently, the social behavior and breeding chronology of the avian species and particularly honeyeater species are closely linked to the spatial and temporal patterns of plant breeding phenology.

The breeding cycle of bellbirds begins in late August and extends until January (Anderson and Craig 2003). Several clutches are laid each season. Nest-building activities (2–3 weeks) and incubation (2 weeks) are solely by females, whereas nest-based chick rearing is by both sexes and lasts until chicks fledge at 14–20 days of age. Chick provisioning by both parents can extend past fledging from the nest (Anderson and Craig 2003).

The data presented in this paper were collected over the period 2002–2007. A playback pilot study was conducted in 2002, and countersinging observations were made from 2003 to 2004. In 2004, a large banding program was begun and more than 300 bellbirds have been individually color banded since then. Finally, female song playbacks and observations of territorial behaviors were conducted in 2005 and 2007.

Observations

Countersinging
Observations of singing behavior by male and female bellbirds were made throughout the period of June 2003 to December 2004 during regular trips (1–3 days long) to the island. Twenty observer listening posts at the top of gullies with good visibility were randomly chosen from more than 50 possible sites (Figure 1). Each listening session was 30 min long and was conducted by a trained observer capable of recognizing male and female songs; all singing behavior in the vicinity was recorded on a data sheet, and a stopwatch was used to record time intervals between singing bouts. Repeated songs initiated by the same individual (identified by location or band combination) were not included in the analyses. A nearby conspecific was categorized as countersinging if it sung within 3 s of another bird. A countersinging initiation was defined as a single singing event occurring after a minimum of 3 min silence. The sex of the initiating bird was noted. Each listening post was randomly sampled at least 3 times from June 2003 to December 2004. During these sampling periods, the sex of the singers, date, time, site, and any observable behavioral interactions were also recorded.

Chi-squared tests were used to compare the types of countersinging responses (same sex, opposite sex, or no response) to male and female song and the number of countersinging events in a bout ($\alpha = 0.05$).

Territory intrusions
During the 2005 breeding season, 1-h-long observation periods of bellbird interactions were conducted on bellbird territories where both the male and the female were color banded. Intrusions were defined as movements (flight, perching, or foraging) of bellbirds other than the territorial owner within the focal territory. The frequency of these intrusions was recorded along with the sex and band combination of the intruders. Territories had been previously mapped using bellbird sighting and chasing behavior (Cope 2008).

Spearman rank correlations were used to measure the association between the number of intrusions and the number of adjoining neighbors ($\alpha = 0.05$). Male and female intrusions were analyzed separately.

Playback experiments

Playback experiments were conducted during the breeding seasons of 2005 (incubation and first clutch periods) and 2007 (courtship, incubation, and first clutch periods). Nests were located by observing bellbird behavior (foraging and nest building) and movements within mapped territories. Only pairs where both males and females were color banded were used for playbacks, and all suitable territories were located in bush patches at the northern end of the island (Figure 1). Female stranger recordings were collected during 2002 from the nearby bellbird population on Little Barrier Island (20 km away), easily within dispersal distance for this species. During a pilot study on Tiri in 2002 (Li 2002), bellbird calls from Little Barrier Island and calls from the southern end of Tiri were played on 10 territories at the northern end of the island. Although these birds were unbanded, they did have nests, and no significant differences in responses by territorial females to these 2 types of playbacks were detected; therefore, a random selection of 5 Little Barrier Island female calls were used as stranger playbacks in the current study. Recordings used as neighbors were randomly chosen from a number of females with a territory adjacent to the focal female and collected during the start of the 2005 breeding season (July–August 2005). Although individual female bellbirds typically sing up to 3 song types, there is considerable syllable sharing between song types and all songs are used in the context of territorial defense (e.g., Brunton and Li 2006). For the purposes of these playback experiments, we chose the most frequently used song type of a female on her territory. Matching of song types was done by visually comparing spectrograms using Raven 1.2 (Cornell Laboratory of Ornithology Bioacoustics Research Program).

Recordings used for playbacks were made using a Sony HiMD and Sennheiser ME66 K6 microphone and standardized for amplitude using a DSE Digital Sound Level Meter (from Dick Smith Electronics, Auckland, New Zealand). The playback speaker was a Remote Audio Speak Easy v2 (powered by a 9-V battery), and the speaker amplitude was determined by adjusting volume levels of our field speaker so that it matched female song amplitude levels at a distance of 10 m. All playbacks using the speaker were fixed at this standard volume.

Playback experiments were conducted 2 weeks apart during incubation and chick-rearing stages in 2005 and during a single session in 2007. Playback sessions included 2 controls (control 1 = silence and control 2 = whitehead; Mohoua albicilla song, a sympatric species), a stranger female, and a neighbor female. Each territorial female was subjected to 3 playback sessions (control 1 and control 2, control 1 and stranger, and control 1 and neighbor). Each session consisted of three 1-min recordings separated by 2 min of silence. The playback order was randomized, and a minimum of 3 h was allowed between playbacks on a territory. In addition, no playbacks were conducted on any nearby territory within 3 h. Three observers were present on the territory during all playbacks in 2005; 1 observer controlled the playbacks, and 2 recorded the behavior of the focal bird from separate vantage points approximately 10 m from the nest. In 2007, a single observer conducted playbacks using an audio remote control. Playbacks commenced when the female was observed on her territory, on the nest during incubation, or had returned to the nest to feed chicks. In 2005, the speaker was placed 1.5 to 2 m above the ground in the fork of a tree and 8–10 m from the nest. The same territories were occupied by the banded birds in 2007, and speakers were placed in the center of these mapped territories. All sessions were continuously recorded using a Sony HiMD and a Sennheisser microphone to allow precise measurement of responses (timing and song type).

The following responses by the focal bird (and its mate when present) were measured: frequency of approach and countersinging, minimum distance to the speaker (meters), and latency to approach the speaker (seconds).

To avoid pseudoreplication due to the same individual being tested more than once, pairwise statistical comparisons of the responses of bellbird females and males to stranger and neighbor playbacks were conducted. These included McNemar tests for paired samples to compare the frequency of approaches and countersinging responses and paired t-tests to compare the differences in minimum approach distance to the speaker and latency to respond. Territorial males and females were tested separately. A significance level of $\alpha = 0.05$ was used for all tests.

RESULTS

Countersinging

Three hundred and thirty countersinging events ($n = 143$ initiated by females and $n = 187$ initiated by males of which 12 were by banded birds) were observed during 72 listening sessions over 18 months. During each listening session, the median numbers of countersinging events were 2 for females and 3 for males; countersinging was observed throughout the year. Although both sexes respond more frequently to same sex songs, the overall patterns of vocal responses to male and female singing were significantly different ($\chi^2_2 = 34.6$, $P < 0.0001$). In particular, nearly 60% of female songs elicited a response by females, whereas almost 90% of male songs elicited a response by males (Figure 2). Females were never observed to countersing in response to a male song, but occasionally males countersung to females (Figure 2). In addition, the number of countersinging responses varied significantly between males and females ($\chi^2_5 = 229$, $P < 0.0001$). Usually, only a single female responded to a female song, but up to 4 females did sing in sequence. For males, the mode was 3 while up to 8 males were observed in a sequence.
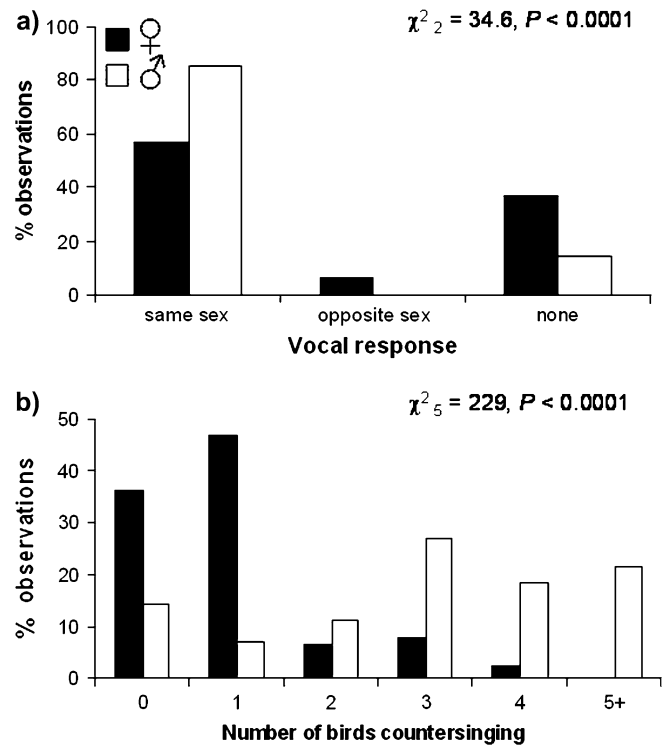
Countersinging observations were made during the period when only a small number of bellbirds in the population were banded (11 out of an estimated population size of more than 1500, Brunton DH, unpublished data). Hence, there was potential for the same individuals to be sampled more than once. However, this pseudoreplication was thought to be minimal as 10 out of 11 banded birds (all males) were observed to initiate countersinging bouts only once during the 18-month period, but all 11 were resighted multiple times during this period. In addition, each listening post was sampled only 3 times over the 18-month period.

Territory intrusions

Eighteen nests were observed for a 1-h period during the chick-rearing stage. Territorial encroachments were frequent (30% of territories had female incursions, whereas 45% of territories had male incursions), and all resulted in chases. The number of female incursions per hour (maximum 2) correlated significantly with the number of abutting territories (maximum 5; $r_s = 0.57$, $P = 0.01$). In contrast, there was no significant correlation between the number of male incursions (maximum 3) and the number of abutting territories (maximum 5; $r_s = 0.07$, $P = 0.78$).

Playbacks

Eighteen bellbird territories were identified as suitable for playback experiments, and good quality recordings were collected from all these females in the 2 months prior to the playbacks. Playback experiments were conducted on 13 territories during
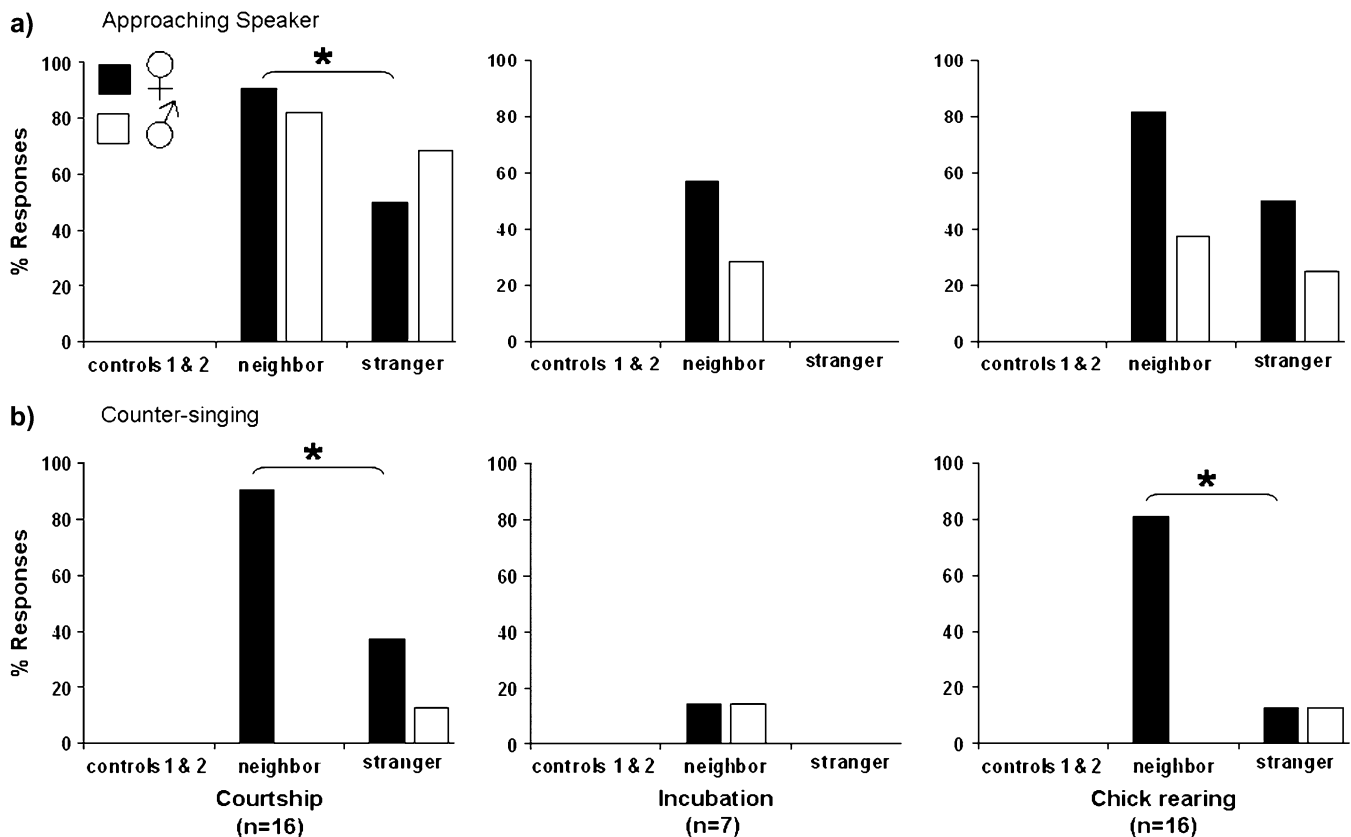

Figure 2
Countersinging observations in response to naturally occurring bellbird songs: (a) the frequency of same sex, opposite sex, and no responses to male and female singers and (b) the number of birds involved in countersinging activity in response to male and female song.

2005 (5 during incubation and 13 during chick rearing) and 16 territories during 2007 (13 during courtship, 2 during incubation, and 3 during chick rearing). Each set of playbacks was conducted on a given territory no more than once during each breeding stage. No bellbirds responded to any playbacks of either control at any breeding stage.

During both courtship and chick rearing, females countersung more frequently to playbacks of neighboring females compared with strangers (Figure 3; McNemar tests, $n = 16$, $P < 0.01$ and $P < 0.005$, respectively). They also approached the speaker more frequently during courtship to neighbor playbacks (Figure 3; McNemar test, $n = 16$, $P < 0.05$). The difference in approaches to neighbor compared with strangers during chick rearing was not statistically significant. However, when females responded to playbacks during both courtship and chick-rearing stages, the latency to respond were significantly less (courtship: paired t-test = 5.13, degrees of freedom [df] = 16, $P < 0.0005$; chick rearing: paired t-test = 4.30, df = 16, $P < 0.001$) for neighboring females (2.1 ± 1 and 7 ± 2 s, respectively) than for stranger females (12 ± 10 and 43 ± 8 s, respectively). The minimum distance that territorial females approached during playbacks was also significantly less for neighbors than strangers during both courtship and chick rearing (Figure 4; paired t-test = 4.32, df thinsp;= 16, $P < 0.01$; paired t-test = 8.98, df = 16, $P < 0.001$). During 2005, songs were recorded during chick-rearing playbacks and of the 11 females that countersung after neighbor playbacks 6 of these matched the song type of the playback. For the one female that countersung in response to a stranger, the song was not matched.

Although sample sizes during incubation were too small to do meaningful statistical analyses, we did find that incubating

Figure 3
The behavioral responses of territorial females (black bars) and males (white bars) to playbacks; control 1 (silence), control 2 (sympatric species), neighbor female song, and stranger female song. Responses include (a) approaching the speaker and (b) countersinging. The number of territories on which playback experiments were conducted varied with each breeding stage and is indicated on the graph. Due to small sample sizes, the responses to the neighbors versus strangers were not tested during the incubation stage. Significant differences (McNemars paired tests, $P < 0.05$) are indicated by asterisk.

females only responded to playbacks of neighboring females (4/7 approached, 1/7 countersung, latency to respond varied from 15 to 55 s, and the minimum approach distance varied from 3 to 8 m). Despite these small sample sizes, responses by females were generally less aggressive during incubation than during chick rearing.

Territorial males responded to female playbacks during all breeding stages (and not to controls), although generally not as strongly as their mates (Figures 3 and 4). Males did not approach the speaker or countersing significantly more for female neighbor versus female stranger playbacks during either courtship or chick rearing (Figures 3 and 4). There were also no significant differences in the minimum approach distances to either female playbacks (Figure 4) during these stages. It should be noted, however, that the number of males approaching the speaker during the courtship period was at least twice that of the chick-rearing period. In addition, males had less intense responses during the incubation period compared with the other stages (only 2/7 approached and 1/7 countersung, latency to respond was 15 s, and the minimum approach distance was less than 2 m).

DISCUSSION

The female bellbird countersinging behavior described in this study occurred year round and demonstrates that neighboring females have frequent vocal interactions. It is clearly advantageous to know the location of nearby conspecifics when defending resources whether these resources are food or

mates. Countersinging, in which individuals sing in response to the vocalizations of their neighbors, is common among territorial passerines (e.g., Brooks and Falls 1975; Hyman 2003; Mennill and Vehrencamp 2005). One result of these interactions is that singing behavior can be temporally related (e.g., Beecher et al. 2000; Vehrencamp 2001; Beecher and Brenowitz 2005), and all individuals within the acoustic network are able to garner information about the interactions. Eavesdropping, defined as extracting information from social interactions that cannot be obtained from signals alone, is one benefit of receiving signals within an acoustic network (e.g., McGregor and Peake 2000). Although female bellbirds do not respond vocally to male song (with the exception of quieter call responses to their mate), it is likely that they are capable of eavesdropping on the frequent male and female acoustic interactions and countersinging in their vicinity and therefore know both the location of their mate and other individuals and the outcome of aggressive interactions. Eavesdropping has been described in many avian species and is implicated in mate choice (e.g., Naguib et al. 2004; Peake 2005) and assessment of conspecific competitors (e.g., Poesel et al. 2007).

Our neighbor–stranger playback experiments were conducted during the first nesting attempts of the breeding season when females were strongly tied to their territories and breeding activities were highly synchronous. These experiments showed clear evidence that individual female bellbirds were able to discriminate between conspecific female neighbors and strangers on the basis of acoustic cues. Such acoustic discrimination has now been documented in a wide range

Minimum approach distance to speaker
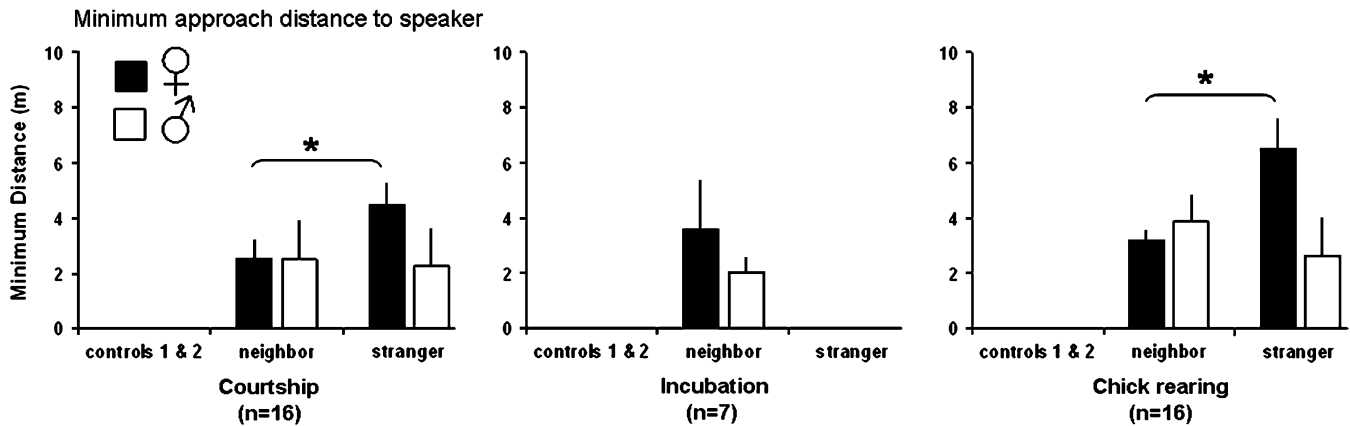
Figure 4
The minimum distance (meters) of territorial females (black bars) and males (white bars) to speaker after playbacks; control 1 (silence), control 2 (sympatric species), neighbor female song, and stranger female song. The number of territories on which playback experiments were conducted varied with each breeding stage and is indicated on the graph. Due to small sample sizes, the responses to the neighbors versus strangers were not tested during the incubation stage. Significant differences (paired *t*-tests, $P < 0.05$) are indicated by asterisk.

of avian species including suboscines (e.g., Lovell and Lein 2004), seabirds (e.g., Mackin 2005), and passerines (e.g., Brooks and Falls 1975; Falls 1982), but rarely between females. In one of the few previous female song playback studies, Beletsky (1983) failed to find support for differential recognition of neighbors and strangers by female red-winged blackbirds. However, Beletsky's classification of "neighbor" could have influenced this outcome; neighbors were defined based on male territories (which contain multiple female territories) rather than female territories so that neighbor playbacks were not necessarily songs of adjacent females.

Female bellbird aggressive responses to playbacks were strongest during the courtship and chick-rearing stages and frequently involved a countersinging response by the territorial female. Furthermore, females were significantly more aggressive toward playbacks of the songs of neighboring females, approaching the speaker more quickly and closer than for strangers. This result is opposite to the dear enemy phenomenon and suggests that neighboring female bellbirds pose a greater threat than stranger females. Other studies have demonstrated the opposite of dear enemy phenomenon and provide evidence that neighbors may represent a larger threat (e.g., Dunn and Messier 1999; Bard et al. 2002; Lachish and Goldizen 2004), but our study is the first to demonstrate this effect for territorial females. The similarity in strength of this response during both courtship and chick rearing suggests that neighboring females represent a prolonged and substantial threat during the breeding season.

We hypothesize that a greater female neighbor threat is due to competition for either food resources or paternal care, although these need not be mutually exclusive. The bellbird population on Tiri is among one of the densest in existence, with some of the smallest known territories ($<100 \, \text{m}^2$; Brunton DH, unpublished data) and is considered to be at carrying capacity. Tiri is also an island in the process of restoration with substantial areas of young forest (Rimmer 2004). This combination of factors would support the suggestion that food resources (invertebrates, nectar, and fruit) may be limited. Bellbirds are likely to be familiar with the food resources in the local area surrounding their territory, and hence, neighboring females may be a greater threat due to competition for food. As with many passerines, bellbird chicks are fed a high protein, almost exclusively invertebrate diet (Heather and Robertson 1996), although few detailed studies exist for this species. Foraging for invertebrates usually occurs on the ter-

ritory, and both parents visit and feed the chicks frequently (up to 10 times per hour, e.g., Cope 2008). We found that territories are actively defended by both sexes and incursions by conspecifics are frequent. Finally, stranger females are likely to be nonbreeding birds especially at the start of the breeding season when nesting is more synchronized (e.g., Anderson and Craig 2003) and so perhaps less likely to be foraging for invertebrates and therefore a lesser threat to the food resources needed for chick provisioning.

The second major threat that neighboring females may pose is to the security of paternal care. Cope (2008) observed one instance of male abandonment where the female attempted, unsuccessfully, to raise offspring alone. Although females do all of the incubating, both parents are needed to successfully rear chicks. It is tempting to speculate that the higher levels of aggression displayed toward neighboring females may play a role in polygyny prevention (e.g., Arcese et al. 1988; Cooney and Cockburn 1995; Langmore 1998) and in reducing the risk of abandonment. This contention would predict that deserting males would be more likely to pair with nearby females; the frequency of which is as yet unknown. As with the food competition hypothesis, the synchrony of breeding (particularly for first clutches) means that stranger females are likely to be nonbreeding and less likely to cause male abandonment. Eikenaar et al. (2007) found for Seychelles warblers (*Acrocephalus sechellensis*) that "floaters" have very low probabilities of breeding. Likewise, Olendorf et al. (2004) found that male red-winged blackbirds considered floaters to be less of a threat to territory holders than breeding neighbors. Temeles (1990) also found that Northern Harriers (*Circus cyaneus*) on feeding territories were more aggressive to their competing territorial neighbors than to floaters.

A potentially important aspect of the bellbird's parental care and mating system is the very high level of extrapair paternity, particularly by neighboring males (between 50% and 100% of each clutch, Cope 2008). The extent of mate guarding in this species is also unknown but clearly has limited success as clutches frequently have mixed paternity. Although this would suggest that neighboring males pose great threats to each other, it is unclear how extrapair paternity may influence female neighbor interactions unless extrapair copulations increase the likelihood of mate abandonment or if strong selection occurs for mating genetically comparable partners and multiple males (e.g., Jennions and Petrie 2000; Clutton-Brock 2007). During our experiments, males were almost

always present on the territory and responded equally to neighbor and stranger female playbacks. In addition, the majority of female playbacks during the courtship period resulted in an approach by the territorial male. Female incursions onto neighboring territories were frequent, correlated with the number of adjacent neighbors, and may provide males with an opportunity for extrapair copulations and paternity. Indeed, copulations with neighboring males may make it easier for females to forage on neighboring territories. However, the difference in territory intrusion rates between the sexes may simply reflect the fact that males are more likely to wander than females, and their greater frequency of incursions therefore reduces the relationship between intrusion rate and the number of adjacent territories.

Bellbird pairs communicate during nesting using acoustic cues, females usually sing or call immediately after leaving their nest between incubation bouts to feed, and their mate frequently replies (Li 2002). Eavesdropping on these interactions (e.g., McGregor 1993; Otter et al.1999; Mennill and Ratcliffe 2004) may add in undetected territory incursions by neighboring conspecifics. Clearly, as more of the bellbirds on Tiri are color banded, blood sampled, and monitored, it should be possible to test these predictions and assess the feasibility of these ideas.

The more aggressive responses exhibited by females during the courtship and chick-rearing stages are likely to reflect both her physiological state and the cost of territory intrusions. Although bellbirds are territorial year round, there is increased defense activity during the breeding season (e.g., Li 2002), and territorial boundaries appear to be constantly challenged by intruders. In contrast, incubating birds generally remain inconspicuous and quiet, presumably to reduce the likelihood of attracting predators (e.g., Tweed et al. 2006). Physiological responses to incubation also include less activity and less frequent feeding bouts. Once chicks have hatched and are past the brooding stage, females spend considerable amounts of time foraging and feeding chicks and make many short trips to the nest. It is also during the chick-rearing period that females will be preparing to lay additional clutches if there is still sufficient time left in the breeding season. Bellbirds on Tiri usually have 2 clutches per year, and second clutches are less successful (e.g., Anderson and Craig 2003; Cope 2008). Although it has not been examined for bellbirds, it is likely that paternal care during second clutches correlates strongly with breeding success. This places selective pressure on females to breed early and to reduce the time between successive clutches. During the relatively short chick-rearing period of the first clutch, the body condition of the territorial female will be crucial in determining how quickly she can renest. Our playback experiments were done only during first clutches when this pressure to renest, and arguably the threat by neighboring females, was highest.

Male bellbirds are also aggressive toward conspecifics, sing prolifically year round (e.g., Brunton and Li 2006), and respond preferentially to male playbacks. Males clearly have an interest in preventing other males from intruding and may loose both reproductive success and potentially their territory (e.g., Arnqvist and Kirkpatrick 2005). Furthermore, given the occurrence of apparently nonrandom extrapair paternity (Cope 2008), it seems likely that neighboring males may also be a greater threat to territorial males that stranger males. The dear enemy phenomenon is yet to be tested on male bellbirds but is planned for the near future.

In conclusion, the singing behavior of female bellbirds clearly plays an important role in female–female aggressive interactions, spatial awareness of competitors, and defense of resources (mates and/or food). Certainly, intrasexual competition between female bellbird has potential implications for understanding sexual selection in females, an aspect that has received relatively little attention to date (e.g., Clutton-Brock 2007). The opposite of the dear enemy hypothesis has been demonstrated for female bellbirds, and female neighbors are predicted to be a direct threat to the female territory holder. We suggest that both the importance of biparental care in the nesting success of this species and the likely food limitations in such a dense population provide 2 explanations for the differential threat of female neighbors and strangers to territorial females.

Further research is required to determine more precisely the nature of the threat that neighbors represent and to test whether male bellbirds exhibit the dear enemy hypothesis or its opposite. Playback experiments using songs from female territories at varying distances to the focal bird and at different times of the year would permit us to further explore the nature of female threat in this species.

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