

# Male and female golden whistlers respond differently to static and dynamic signals of male intruders

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Bird displays vary widely in their sensitivity to changes in signaler condition. Plumage ornaments are generally static and undergo minimal change. Behavioral ornaments, by contrast, are dynamic and may track signaler condition or motivation more closely. The relative importance of each trait type in signaling individual quality has been examined during female choice, but rarely in territorial defense. Male golden whistlers (*Pachycephala pectoralis*) display both a static plumage signal (throat patch) and a dynamic signal (song) during territorial disputes. We examined sex differences in the responses of territorial pairs to these traits during simulated territory intrusions by decoy males that had either normal or experimentally reduced throat patch sizes, in combination with low or high singing rates. Males paid attention to both categories of signals when estimating rival threat, responding for longer toward males with normal throat patches, and spending more time close to the intruder in high song rate trials. In contrast, females responded differentially only to dynamic signals. Patch size may reflect a male's long-term viability and status, whereas singing rates may correlate with willingness to escalate contests. As females participate in joint territorial defense and interactions between neighbors are sex specific, the song rates of intruding males may provide clues to their partners' motivation to escalate contests. By contrast, knowledge of an intruding male's intrasexual competitive abilities (signaled via patch size) may be unimportant to females. Differences in the signaling properties of static and dynamic signals may maintain the existence of multiple antagonistic signals in this species. *Key words:* dynamic signals, golden whistlers, multiple ornamentation, simulated territory intrusions, static signals, territorial disputes. [*Behav Ecol*]

Birds display a wide range of conspicuous sexual displays that convey information about the signaler's phenotypic or genetic quality during mate choice and male competition (Andersson 1994). These display ornaments vary considerably in the degree to which they can be modified by the bearer and the temporal precision with which they indicate male condition. Certain signals, such as elaborate plumage traits, are relatively static because they are generally modified only once per year (at the time of molt). Hence, there may be a significant temporal lag between a change in signaler condition and the reflection of this change in terms of trait expression (e.g., Hill 2000; McGraw and Hill 2000; Fitze and Richner 2002). Other, more dynamic signals such as song rates are highly plastic and therefore much more responsive to short-term variation in signaler condition or motivation (e.g., Birkhead et al. 1998; Mennill and Ratcliffe 2004; Naguib 2005).

Although dynamic signals would appear to provide reliable cues to the current condition of their bearer, they are also sensitive to short-term or motivational influences, and this may reduce their value to conspecifics. For instance, if the signal is vulnerable to cheating by inferior individuals (because they can temporarily express an ornament of apparently high quality), this will reduce its reliability (Scheuber et al. 2004). In contrast, static traits may be more reliable indicators of inherent "genetic" quality (or early nutritional stress, e.g., Naguib and Nemitz 2007) because they are less sensitive to short-term conditional or motivational influences on signal expression.

If dynamic signals are better indicators of current condition or motivation, whereas static signals better reflect genetic quality or long-term viability, male and female conspecifics are predicted to differ in the degree to which they pay attention to these 2 forms of signals when they are displayed by males (Fawcett and Johnstone 2003). In intrasexual competition during territorial disputes, for example, both static and dynamic signals could be predictors of a male's competitive ability. Static signals may correlate with male size or other traits that influence the outcome of contests (e.g., Hagelin 2002; Ferns and Hinsley 2004; Garamszegi et al. 2006). In many species, individuals are more likely to engage in contests with rivals with similar-sized plumage status signals (e.g., Pryke et al. 2002; Whiting et al. 2003; Tibbetts and Dale 2004). By assessing reliable predictors of rival male dominance, costly physical contests between highly mismatched rivals may be prevented (Maynard Smith and Harper 1988; Whiting et al. 2003). On the other hand, if males are able to temporally increase song output independent of actual viability (e.g., Scheuber et al. 2004), dynamic signals may be less reliable in predicting long-term male competitive ability. Instead, they may be more closely linked to current signaler condition or motivation-related attributes (Naguib 2005). For example, in nightingales (*Luscinia megarhynchos*), unpaired males have higher singing rates during simulated male intrusions compared with paired males, probably due to motivational differences in attracting females (Kunc et al. 2007), whereas male European robins (*Erithacus rubecula*) increase singing rates after temporary experimental removal from their territory due to a heightened need to reaffirm territory ownership to neighboring males (Tobias and Seddon 2000).

For females, interest in a male's static or dynamic ornaments may depend on whether the intruding male is being assessed as a potential extrapair mate or as a rival. In the former case, static signals may provide females seeking fertilizations with more

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reliable information about a male's genetic quality than dynamic signals (e.g., Møller et al. 1998). By contrast, if females cooperate with their mates in joint territorial defense, the competitive abilities of intruding males, as advertised by male plumage badges, may be unimportant to females, as territorial contests are typically sex specific (Langmore 1998). Nevertheless, females may still pay attention to dynamic traits if the willingness of both individuals to escalate encounters is correlated, such that the singing rates of intruding males also provide a cue to the motivation of their partners to engage in territorial contests.

Studies investigating static and dynamic ornaments concurrently have focused on male displays used to attract females, and these studies have produced conflicting results. Some studies have suggested that individual females may pay attention to different ornaments expressed by male conspecifics. For example, during mate choice, some female dark-eyed juncos (*Junco hyemalis*) were more influenced by a static plumage ornament than dynamic courtship displays, whereas other individuals used the opposite weighting (Hill et al. 1999). Other studies have found that females may base mate choice on multiple criteria. For instance, in barn swallows (*Hirundo rustica*), both singing rates and tail streamer length are important determinants of male extrapair reproductive success (Møller et al. 1998). Finally, females may pay differential attention to static and dynamic ornaments depending on the relative expression of those traits. In mate choice trials in which male color (presence vs. absence of carotenoid pigments) and display rate (high vs. low) were manipulated, female guppies (*Poecilia reticulata*) preferred high display rates when both males displayed color, but not when both males lacked color. Additionally, females used color as a criterion during low display rate trials, but not high display rate trials (Kodric-Brown and Nicoletto 2001). Unfortunately, few studies have focused on variation in male responses to both categories of traits during antagonistic contests (e.g., Hagelin 2002). Thus, our knowledge of the relative importance of static and dynamic traits during territorial competition remains limited.

Here we report on a set of field experiments on an Australian passerine, the golden whistler (*Pachycephala pectoralis*), in which we simultaneously manipulated static and dynamic signals of decoy males, with the aim of determining their relative importance to male and female conspecifics. Male golden whistlers possess complex multicomponent displays incorporating both static and dynamic antagonistic traits. The throat patch is a static signal that can only undergo significant change once per year, at the time of molt. Males possessing larger throat patches defend larger territories and direct more aggression toward intruders with large patches. Females appear to ignore this signal during these aggressive disputes (van Dongen and Mulder 2007). In contrast, singing rates are highly dynamic and may vary with the motivation of the signaler to continue with a territorial dispute. In this species, both sexes cooperate in the defense of territories. Although partners regularly intrude into neighboring territories together during territorial disputes, individuals only engage in contests with same-sex rivals and females do not typically display any overt aggressiveness toward males (van Dongen and Yocom 2005). Here we present data on simulated territorial intrusions (STIs) in which caged males with experimentally altered throat patches and song rates were presented to both resident males and females. By comparing male and female responses to our manipulations, we assessed 1) which traits were emphasized by conspecifics during territorial disputes and 2) whether sex-specific differences existed in the perceived importance of variation in static and dynamic ornaments. In particular, if male singing rates reflect current motivation of intruding pairs to engage in territorial disputes, we expected both sexes

to respond more strongly to simulated intrusions broadcasting song at high rates. In contrast, if throat patch size signals male long-term competitive ability, we predicted that only males would respond differentially to variation in patch size due to the sex-specific nature of territorial contests.

## MATERIALS AND METHODS

### Song components and territory size

#### *Study species and site*

The golden whistler is a socially monogamous, sexually dichromatic passerine. Males display bright yellow breast plumage, a black crown and chin stripe, and a white throat patch, which is developed in their third year. Before developing into this full adult plumage, males are considered as subadult and possess a female-like gray-brown plumage. Throat patch size does not appear to be related to age (van Dongen and Mulder 2007). The throat patch begins at the base of the beak and extends down the throat (mean length =  $30.0 \pm 2.9$  mm standard deviation [SD] [range = 23.7–37.7 mm]; mean width =  $24.7 \pm 2.2$  mm SD [range = 20.6–31.6 mm]; mean area =  $579.7 \pm 66.4$  mm<sup>2</sup> SD [range = 420.9–755.5 mm<sup>2</sup>]; all  $n = 35$ ). Black plumage totally surrounds this throat patch, including the narrow black chin stripe, which separates the white throat patch from the yellow breast plumage.

The observational component of this study was carried out between September 2001 and February 2003 and the simulated intrusions between November and December 2003 at Toolangi State Forest, Victoria, Australia (37°31' S, 145°32' E). The study area initially covered 80 ha from a continuous stretch of forest covering approximately 38 000 ha (2001), but we expanded this to 106 ha in September 2002. The predominant vegetation is a mountain ash (*Eucalyptus regnans*) canopy with a variable understory dependent on local topography (van Dongen and Yocom 2005).

#### *Bird capture and daily population census*

Individuals were captured and individually marked with a unique combination of three color bands. We made standard measurements including head-bill length (distance from the tip of the beak to the back of the head, to the nearest 0.1 mm, using dial calipers), tarsus length (nearest 0.1 mm, calipers), and body mass (nearest 0.1 g, spring balance). The length and width (in millimeters) of the elliptical throat patch was measured using dial calipers ensuring that the male's head was fully outstretched to minimize variation in patch size due to the angle of the head relative to the body. Throat patch area was then calculated using the following equation: throat patch area =  $\pi \left(\frac{\text{width}}{2}\right) \left(\frac{\text{length}}{2}\right)$ .

The population was monitored via daily censuses throughout the breeding season. We monitored 25 pairs in 2001, 27 in 2002, and 24 in 2003. Although pair fidelity is high in this species and some pairs remained together for the entire 3-year study period, the composition of most pair-bonds varied considerably, depending largely on whether both members of a pair were present in a particular year (van Dongen and Yocom 2005). After locating an individual, we noted its position in relation to a set of fixed reference points spread throughout the study site (97 reference points covering an area of 106 ha). Male territories were mapped using the geographic information system software package ArcView GIS 3.2 (Environmental Systems Research Institute 1999). We mapped territories for males in 2001 and 2002. Territory sizes were calculated where we had a minimum of 8 fixes per male from different days (mean number of fixes per male—2001:  $11.1 \pm 3.0$  SD,  $n = 18$ ; 2002:  $12.4 \pm 4.0$ ,  $n = 20$ ). Using ArcView, we implemented minimum convex polygons to delineate the

boundaries of territories by outlining the outermost territory fixes for each individual (Southwood 1966).

#### *Behavioral observations*

In 2001, recordings were made using a Sony TCD-D8 Digital Audio Tape recorder and Sennheiser ME67 unidirectional microphone. We opportunistically recorded song time budgets (i.e., when a male was successfully located within his territory) throughout the breeding season between 0630 and 1100 h Australian Eastern Standard Time, the peak singing period for this species (van Dongen W, personal observation; mean song time budget duration: 21 min 19 s  $\pm$  11 min 34 s SD). In 2002, we documented individual variation in singing rates by following an individual for a 30-min period and counting all songs sung. We performed these counts once per male, wherever possible, during 4 stages of the breeding season: prebreeding (commencing when males first arrived at the site and ending when nest building was first observed for that pair), nest building (commencing when the female was first seen collecting nesting material for a nest and ending when the penultimate egg was laid), incubation (commencing after the final egg was laid in a clutch until egg hatching), and postbreeding (after all breeding activities had ceased, including the feeding of fledglings, and before individuals departed the study site). We made recordings using a Sony TC-D5 Pro-Stereo Cassette Recorder and Sennheiser ME67 microphone. We were thus able to estimate male singing rates in 2001 and 2002 and male repertoire sizes in 2001. Male song repertoires were determined by calculating the total number of different song types sung by an individual male for all recordings in a given year (for details on how different song types were identified, refer to van Dongen 2006). Repertoire exhaustion curves were constructed to ensure that the majority of song types were logged for each male (van Dongen 2006).

#### **STI experiments**

##### *Decoy male capture and manipulation*

Males used as live decoys were captured within the same forest but outside the study area. When not used in experiments, males were housed in cages measuring 18  $\times$  18  $\times$  36 cm and provided with meal worms ad libitum by placing a small feeding tray containing meal worms at the base of the cage. Males were not fed during experimental trials (which lasted 10 min). The cage was covered by a cloth to minimize stress and transported to housing aviaries measuring 120  $\times$  60  $\times$  60 cm. Aviaries were located outdoors in a sheltered area, and birds were provided with meal worms ad libitum. Eight males were captured for use as decoys in total, and each was used in an average of 12.1  $\pm$  5.1 SD trials (range: 4–17 trials). Males were housed for a maximum of 11 days (average duration: 4.9  $\pm$  3.3 SD trials [range: 1–11 days]), after which they were released at the site of capture. Release weight of individuals was not different from capture weight (capture weight: 28.6  $\pm$  3.5 g SD, release weight: 27.0  $\pm$  2.3 g SD; paired *t*-test:  $t_6 = 1.182$ ,  $P = 0.290$ ).

We randomly assigned males to 1 of 2 groups—4 “reduced throat patch” males and 4 “control” males. Males assigned to each group did not differ in tarsus length (control: 22.43  $\pm$  0.40 mm<sup>2</sup> SD; reduced: 22.01  $\pm$  0.25 mm<sup>2</sup> SD;  $F_{1,7} = 2.861$ ,  $P = 0.134$ ), head-bill length (control: 38.29  $\pm$  0.64 mm<sup>2</sup> SD; reduced: 38.12  $\pm$  0.31 mm<sup>2</sup> SD;  $F_{1,7} = 0.740$ ,  $P = 0.516$ ), body mass (control: 27.2  $\pm$  3.4 mm<sup>2</sup> SD; reduced: 28.9  $\pm$  3.5 mm<sup>2</sup> SD;  $F_{1,7} = 0.619$ ,  $P = 0.570$ ), or original throat patch area (i.e., before manipulation; control: 643  $\pm$  84 mm<sup>2</sup> SD; reduced: 634  $\pm$  42 mm<sup>2</sup> SD;  $F_{1,7} = 4.203$ ,  $P = 0.085$ ). Throat patch sizes were reduced by using black nontoxic “Sharpie” markers (Sanford, Bellwood, IL) to blacken the outer edges of the white throat patch to resemble the surrounding black plum-

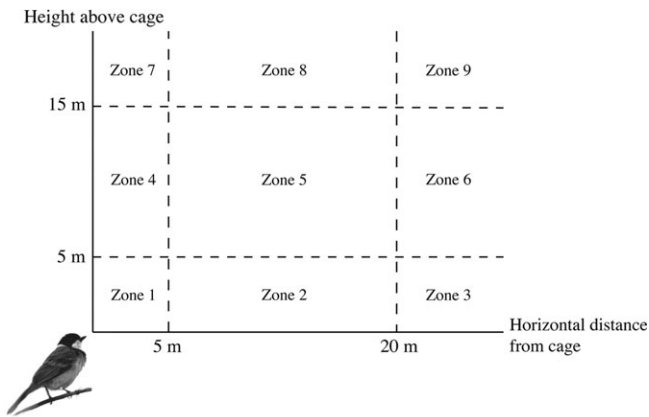
age. We reduced patch sizes to the minimum limit of natural variation (ca., 420 mm<sup>2</sup>). The length and width of the throat patch of “reduced” males were reduced by an average of 78.0  $\pm$  11.3% (range: 63.3–88.9%) and 92.9  $\pm$  4.2% (range: 88.2–97.3%) of the original size, respectively. Control males were subjected to similar treatment, but here we applied transparent nontoxic “Setasilk” dye thinner (Pèbèò, Gémenos Cedex, France) to the outer edges of the white throat patch, so that the size of the throat patch remained the same. After our manipulation, the mean throat patch size of the reduced group was significantly smaller than that of the control group (control: 623.5  $\pm$  52.5 mm<sup>2</sup> SD; reduced: 495.1  $\pm$  81.1 mm<sup>2</sup> SD;  $F_{1,8} = 15.65$ ,  $P = 0.003$  [individual throat patches sizes—control males: 570.5, 587.10, 659.2, and 677.0 mm<sup>2</sup>; reduced males: 433.4, 440.2, 496.7, and 610.1 mm<sup>2</sup>]). The blackened white throat patch feathers of reduced males closely matched the reflectance of the naturally black chin stripe feathers of control males (chin stripe spectral brightness—control: 180  $\pm$  45, reduced: 216  $\pm$  46; analysis of variance [ANOVA]:  $F_{1,8} = 7.50$ ,  $P = 0.412$ ). Applying the dye thinner did not cause any change in overall brightness of the throat patch (overall throat patch spectral brightness—with dye thinner: 4260  $\pm$  1769 SD, without dye thinner: 4073  $\pm$  634; ANOVA:  $F_{1,6} = 0.039$ ,  $P = 0.849$ ) nor UV reflectance (UV throat patch spectral brightness—with dye thinner: 780  $\pm$  259 SD, without dye thinner: 700  $\pm$  106; ANOVA:  $F_{1,6} = 0.321$ ,  $P = 0.592$ ). Our plumage manipulations did not include a treatment increasing signal size because we were unable to obtain a white paint or dye that convincingly matched the spectral coloration of the throat patch. However, studies in which signal sizes are manipulated in only one direction are common and have been able to convincingly show that individuals perceive and change their behavior relative to variation in the trait of interest (Hagelin 2002; Ferns and Hinsley 2004; Senar et al. 2005; Torres and Velando 2005).

##### *Playback tracks*

We recorded songs from 8 singing males about 15 km from the study site to prevent variation in responses due to familiarity with songs. Eight separate 5-min playback tracks were made, consisting of 4 different tracks per song rate treatment (i.e., high and low song rates; see below). Each track incorporated 4 song types recorded from a single male in a continuous loop. The low song rate tracks broadcasted songs at 4 songs per minute and the high song rate tracks at 8 songs per minute. We randomized the tracks used in each experiment.

##### *Experimental setup*

We performed STI experiments by introducing caged males into the territories of resident pairs. Each trial consisted of introducing a decoy male with either a control or a reduced throat patch (the static trait) and song broadcast at a high or low rate (the dynamic trait). Four different treatment combinations were therefore possible. All STI trials were conducted during the nest-building stage for each subject pair and between 0730 and 1130 h Australian Eastern Standard Time (the peak singing period for this species; van Dongen W, personal observation). A trial commenced with a 5-min preplayback period, during which all vocalizations made by the focal individual were recorded. A wire cage (18  $\times$  18  $\times$  36 cm) containing the live decoy male was then placed on a stand (height: 1.2 m) within 55 m of the focal individual (mean distance from focal individual: 21.8  $\pm$  10.3 m SD). As pairs were often together at the commencement of trials, we frequently conducted intrusion experiments to both members of a pair simultaneously. In these cases, we estimated initial distance from the decoy male separately for each member. The first treatment was chosen randomly for each simulated intrusion trial, after which the remaining were



**Figure 1**  
The 3-dimensional zoning system used during STIs to describe the position of focal golden whistlers relative to a cage containing the decoy male. For example, individuals were in zone 4 when within 5 m of the cage horizontally and between 5 and 15 m above the cage. Changes in the location of individuals within the zones were dictated onto a cassette recorder throughout the trial. The focal individual's average distance from the cage during the trial was later estimated via the proportion of time spent within each zone.

alternated systemically. The playback track was broadcast from a Sony CDX-L460X portable car stereo with Realistic 30-W speakers placed adjacent to the cage. Songs were broadcast at a volume approximating the natural intensity of golden whistler song (50 dB at 10 m, Lutron SL-4001 sound level meter). The decoy male neither sang during the trials nor responded to the playback in any noticeable way. Therefore, it is unlikely that the behavior of the focal individuals was affected by the response of the decoy male to the playback. During the 5-min playback period, 2 observers were present, hidden from view. One observer described the subjects' behavior while the other observer transcribed this information. We recorded the following response attributes: 1) latency (seconds; the time elapsed before the focal individual displayed an obvious response to the STI, such as movement toward the cage); 2) number of songs sung; 3) distance of closest approach to the cage (meters); and 4) the total duration of the response (seconds; time elapsed between the first observed obvious response to the playback stimulus, as outlined above, and the point when the individual appeared to lose interest in the caged male by moving away from stimulus—this was easily quantified as we recorded the timing of any changes in the individual's position relative to the cage onto a cassette recorder).

We also estimated the focal bird's distance from the cage during the trial using a 3-dimensional zoning system. Nine dif-

ferent zones were identified (in a  $3 \times 3$  design) from zone 1 (within 5 m from the cage, both horizontally and vertically) to zone 9 (farther than 20 m from the cage horizontally and higher than 15 m above the cage; Figure 1). Changes in the location of individuals within the zones throughout the trial were dictated onto a cassette recorder. Individual distance from cage was later estimated by calculating the length of the vector spanning the top of the cage to the middle of each zone (i.e., distance from cage =  $\sqrt{d^2+h^2}$ , where  $d$  = the zone's horizontal distance from cage and  $h$  = the zone's height above cage). The mean horizontal distance of birds in zones 3, 6, and 9 was estimated to be 30 m, whereas the mean height above the cage in zones 7, 8, and 9 was estimated to be 20 m. We then estimated average distance of the individual from the cage throughout the trial by calculating the proportion of time spent within each zone, that is, average distance = (proportion of time in zone 1)  $\times$  (mean distance of zone 1 from cage [3.5 m]) +  $\dots$  + (proportion of time in zone 9)  $\times$  (mean distance of zone 9 from cage [36.1 m]). A 5-min postplayback period followed the playback period in which all male vocalizations were recorded.

#### Statistical analysis

Many of our measures of response to the simulated intrusions were intercorrelated for both males and females (Table 1). A standard measure to reduce such highly correlated data into 1 or 2 explanatory variables is the use of principal components analysis. However, as this study focuses on fine-scale variation in individual responses to signal manipulation (i.e., whether our manipulations affect differently the focal individuals' temporal and spatial responses), we used the raw data in all analyses. In order to reduce the chance of Type I error, we condensed the number of variables measured into 2 spatial responses, 2 temporal responses, and singing rates. We refrained from using Bonferroni corrections due to the high likelihood that, with low sample sizes in each treatment, biologically meaningful relationships would be lost. As we have distinct predictions as to how responses should vary with our manipulations, including data from previous STI experiments in which only throat patch size of decoy males was manipulated (van Dongen and Mulder 2007), our statistical analyses without Bonferroni corrections are, in this case, more appropriate (Nakagawa 2004).

Due to the large number of trials conducted ( $n = 96$ ), individuals were subjected to multiple trials throughout the sampling period (mean number of trials per individual:  $2.6 \pm 0.7$  SD trials; range: 1–3). We attempted to conduct trials at least 3 days apart for each individual, but because this species is single brooded and we conducted all trials during the nest-building stage, the window of opportunity was often small. Therefore, we conducted trials on some individuals on subsequent

**Table 1**  
Pearson correlation matrix for male and female golden whistler responses to decoy males during STIs

	Males				Females			
	Latency	Response duration	Closest approach	Average distance	Latency	Response duration	Closest approach	Average distance
Response duration	-0.806***				-0.870***			
Closest approach	0.677***	-0.590***			0.658***	-0.502***		
Average distance	0.556***	-0.704***	0.685***		0.553***	-0.555***	0.658***	
Song rate	-0.148	0.201	0.004	-0.267	-0.020	0.101	-0.214	-0.020

Values are Pearson correlation values ( $R$ ), and asterisks denote significance at the 0.001 (\*\*\*) levels (Bonferroni-corrected critical alpha value for 10 correlations is  $P = 0.01$ ; note that the initial critical value was increased to  $P = 0.10$  for these tests only to avoid the risk of a Type II error; Wright 1992; Chandler 1995). Sample sizes for male and female trials are  $n = 51$  and  $n = 46$ , respectively.

days (mean number of days elapsed between each trail for an individual:  $7.5 \pm 9.8$  SD days; range: 1–44 days). Because this species renests after nest failure (van Dongen and Yocom 2005), we occasionally had additional opportunities during which to conduct trials. As such, some trials were conducted up to 44 days apart.

To allow for the nonindependent nature of the data, we used generalized linear mixed models (GLMMs) incorporating individual identity as a random factor. This controlled for differences in responses between individuals. In addition, because a small number of decoy males were used a large number of times, variation in responses may have been influenced by decoy male identity. In order to control for decoy identity effects, we included male decoy identity as a random factor in all models. In all cases, the response variables followed either a normal or a Poisson distribution and the models calculated using normal (with identity link) or Poisson (logarithm link) error variances.

When analyzing the song output data, we incorporated singing rates during the preplayback period as a covariate to control for differences in baseline vocal activities before the trials (Hall 2000). For males, mean baseline singing levels were  $5.15 \pm 2.86$  SD songs per minute (minimum = 0.00 songs per minute, maximum = 11.33 songs per minute) and approximated a normal distribution (skewness =  $-0.069 \pm 0.333$ ). For females, mean baseline singing levels were  $0.17 \pm 0.50$  SD songs per minute (minimum = 0.00 songs per minute, maximum = 3.00 songs per minute). However, these data were highly skewed (skewness =  $4.281 \pm 0.350$  SD), which could not be improved via transformation. However, the results of analyses of song rate differences between treatments for both sexes did not qualitatively differ with and without baseline singing levels as a covariate. Therefore, for purposes of clarity, only the analyses using baseline singing levels as a covariate are given here.

An inadvertent consequence of throat patch reduction was the concurrent enhancement of chin stripe width. Due to our manipulations, the chin stripe width of males with reduced patches was larger than control males (chin stripe width—reduced:  $11.2 \pm 2.4$  mm SD [range: 8.3–14.0 mm], control:  $6.9 \pm 1.0$  mm SD [range: 5.7–8.3 mm];  $F_{1,8} = 16.29$ ,  $P = 0.004$ ) but remained within the natural range of variation ( $8.6 \pm 2.3$  mm SD, range: 5.0–17.7 mm,  $n = 58$ ). Associations between the focal individual's behavior and treatment may therefore be due to variation in chin stripe width and not throat patch size. To separate these effects, we conducted a GLMM, incorporating chin stripe width within the fixed model and resident responses as the response variable. Both test male and subject identities were included as random factors. In all cases, the chin stripe width of the caged male was unrelated to resident male and female response during the simulated intrusions (males: all  $P > 0.126$ ; females: all  $P > 0.137$ ). In addition, observational data show that chin stripe width is related neither to any aspect of any ecological variable such as territory size (van Dongen and Mulder 2007) nor to male genetic reproductive success (van Dongen WFD, Mulder RA, unpublished data). Hence, it is unlikely that males or females are responding to this trait instead of variation in throat patch size.

All generalized linear models were analyzed using SPSS 12.0 (SPSS Inc., Chicago, IL) and all GLMMs using Genstat 7.0 (Lawes Agricultural Trust 2003). Data are reported as means and standard errors unless otherwise stated.

## RESULTS

### Song components and territory size

Male song rate tended to positively correlate with territory size (mean song rate across all 4 breeding stages:  $r^2 = 0.30$ ,

$F_{1,12} = 4.69$ ,  $P = 0.053$ ; mean song rate during nest building and incubation:  $r^2 = 0.33$ ,  $F_{1,12} = 5.34$ ,  $P = 0.041$ ). We also found interactive effects between song rate and throat patch size, with the effect of singing rates on territory size being greatest for males with large throat patches (overall model:  $F_{3,5} = 24.02$ ,  $P = 0.002$ ; throat patch size:  $F_{1,5} = 4.44$ ,  $P = 0.089$ ; song rate:  $F_{1,5} = 9.09$ ,  $P = 0.030$ ; throat patch  $\times$  song rate interaction:  $F_{1,5} = 10.43$ ,  $P = 0.023$ ). Song repertoire size was unrelated to territory size ( $r^2 = 0.12$ ,  $F_{1,9} = 1.234$ ,  $P = 0.296$ ).

### STI experiments

Focal individuals typically did not respond to the simulated intrusions alone. In 93% of all trials involving female subjects (43/46), the male partner also responded. In addition, female partners responded in 64% of trials targeting male subjects ( $n = 60$ ). Male behavior (e.g., latency to first response, average distance to caged decoy during trial, etc.) did not vary relative to the absence or presence of female partners (all  $P > 0.943$ ). We could not conduct a similar analysis for females as males were present during the majority of trials.

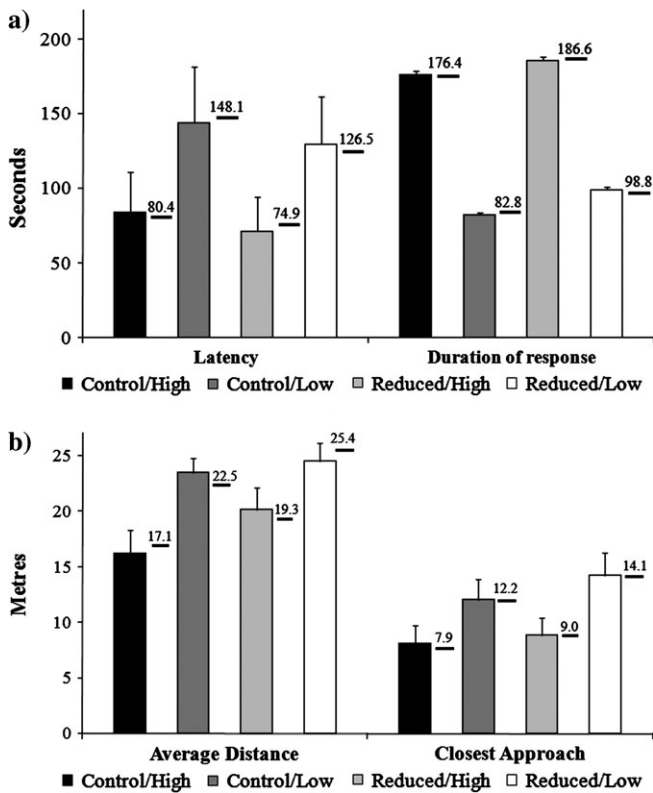
#### Female responses

Females typically responded to the intrusion trials by slowly and quietly approaching the stimulus, although occasionally their responses were more aggressive (e.g., singing in close proximity to the cage). Females showed some evidence of habituation to the trials. Females that had been subjected to a previous trial did not approach the cage as closely (closest approach: first trial =  $8.2 \pm 5.1$  m, second =  $11.3 \pm 6.0$  m, third =  $14.6 \pm 7.2$  m; Wald = 6.58, degrees of freedom [df] = 2,  $P = 0.038$ ) and tended to sing less (song rate during playback: first trial =  $1.0 \pm 1.5$  songs per minute, second =  $0.8 \pm 1.7$  songs per minute, third =  $0.2 \pm 0.4$  songs; Wald = 5.82, df = 2,  $P = 0.054$ ). We therefore included trial number as a covariate in all female analyses involving these response measures. In contrast, we found no effect of time elapsed since last trial on any female responses to the male decoy (regression of time elapsed between trials against strength of response:  $P > 0.518$  for all response variables.).

Females showed more interest toward high song rate treatments. When songs were broadcast from the speakers at a high rate, females were faster to respond to the threat (song rate—Wald = 5.60, df = 1,  $P = 0.018$ ; throat patch—Wald = 0.02, df = 1,  $P = 0.881$ ; Figure 2a) and approached closer to the cage (song rate—Wald = 5.77, df = 1,  $P = 0.016$ ; throat patch—Wald = 0.72, df = 1,  $P = 0.395$ ; trial number—Wald = 3.84, df = 1,  $P = 0.021$ ; Figure 2b), while their average distance from the cage was also closer (song rate—Wald = 9.57, df = 1,  $P = 0.002$ ; throat patch—Wald = 1.72, df = 1,  $P = 0.190$ ; Figure 2b). The duration of their aggressive response was longer during high song rate trials (song rate—Wald = 12.61, df = 1,  $P < 0.001$ ; throat patch—Wald = 0.33, df = 1,  $P = 0.564$ ; Figure 2a). There was no difference in female song rates between the treatment groups (preplayback song rate—Wald = 12.41, df = 1,  $P < 0.001$ ; song rate—Wald = 1.28, df = 1,  $P = 0.258$ ; throat patch—Wald = 0.52, df = 1,  $P = 0.471$ ; trial number—Wald = 5.64, df = 1,  $P = 0.004$ ).

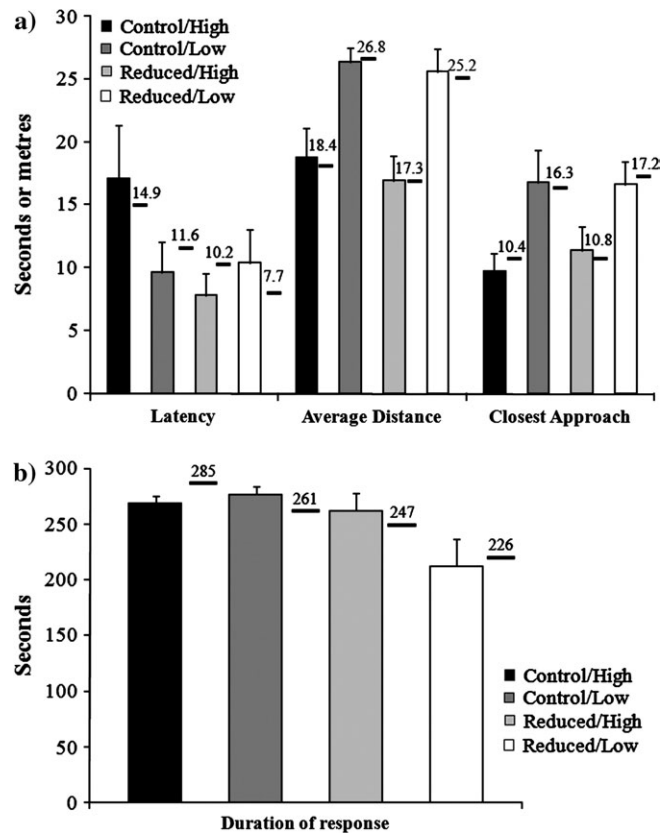
#### Male responses

Males did not appear to habituate to the playback trials. There was no effect of trial number (i.e., first, second, or third experimental trial on the same individual) on the strength of any male behavioral responses (all  $P > 0.332$ ) nor was there an effect of time elapsed since last trial on male aggression



**Figure 2**  
Behavioral responses of female golden whistlers to caged males during STIs, including (a) temporal responses and (b) spatial responses. Caged males possessed either a large (control) or a reduced throat patch, and song was broadcast from speakers at either high or low rates. Latency describes the time elapsed before the female responded to the trial, duration of response was the temporal difference between the first and last responses, average distance from the cage was calculated via continual estimations of distance throughout the trials, and closest approach was the closest distance to the cage attained by the female during the trials. The vertical bars represent means, and the horizontal bars and values indicate the fitted values derived from the GLMM model. Error bars represent standard error.

(all  $P > 0.447$ ). Both singing rate and throat patch size had significant effects on the behavior of the focal males. Males responded more slowly to trials in which caged males had large throat patches, but only when song was broadcast at high rates (song rate—Wald = 2.41,  $df = 1$ ,  $P = 0.121$ ; throat patch—Wald = 0.31,  $df = 1$ ,  $P = 0.578$ ; song rate  $\times$  throat patch interaction—Wald = 5.92,  $df = 1$ ,  $P = 0.015$ ; Figure 3a). The closest distance that males approached the cage during the trial was shorter during high song rate treatments (closest approach—song rate: Wald = 9.66,  $df = 1$ ,  $P = 0.002$ ; throat patch: Wald = 0.10,  $df = 1$ ,  $P = 0.757$ ; Figure 3a). The average distance of focal males throughout the entire trial was also closer during the high song rate treatments (song rate—Wald = 16.89,  $df = 1$ ,  $P < 0.001$ ; throat patch—Wald = 0.22,  $df = 1$ ,  $P = 0.635$ ; Figure 3a). Responses of males were longest during trials using males with large throat patches (song rate—Wald = 1.54,  $df = 1$ ,  $P = 0.215$ ; throat patch—Wald = 3.87,  $df = 1$ ,  $P = 0.049$ ; Figure 3b). We found no difference in male singing rates between treatments (pre-playback song rate—Wald = 19.58,  $df = 1$ ,  $P < 0.001$ ; song rate—Wald = 1.25,  $df = 1$ ,  $P = 0.264$ ; throat patch—Wald = 3.57,  $df = 1$ ,  $P = 0.059$ ).



**Figure 3**  
Behavioral responses of male golden whistlers to caged males during STIs, including (a) latency (the time elapsed before the male responded to the trial), average distance from the cage (calculated via continual estimations of distance throughout the trials), and closest approach to the cage and (b) the duration of male golden whistler responses during STIs. Caged males possessed either a large (control) or a reduced throat patch, and song was broadcast from speakers at either high or low rates. The vertical bars represent means, and the horizontal bars and values indicate the fitted values derived from the GLMM model. Error bars represent standard error.

## DISCUSSION

Male golden whistlers display a range of static and acoustic signals that appear to vary greatly in sensitivity to changes in signaler condition or motivation. The antagonistic displays of males incorporate both a static white throat patch and dynamic singing rates. Because both sexes participate in territorial defense, we were able to compare sex differences in response to each signal category in the context of territorial defense. Our manipulations of both signals in “decoy” males during STIs prompted strikingly different reactions from male and female subjects. Female golden whistlers reacted more strongly to high song rates and appeared to pay no attention to variation in the size of the throat patch of the introduced male. In contrast, resident males showed clear-cut responses to manipulations of both the throat patch and the singing rate of the introduced male and appeared to assess different aspects of the intruders display during various stages of the intrusion.

The information content of static and dynamic signals can differ dramatically, and their importance is often context specific. For example, annual variation in static traits is relatively small, and significant changes in trait expression typically occur infrequently (e.g., plumage in birds: Payne 1972). Therefore, in terms of mate choice, static traits may reflect

a “historical” state of signaler condition and may be a more reliable indicator of long-term male quality compared with dynamic signals (e.g., Collias 1979; Møller et al. 1998; Fawcett and Johnstone 2003; Scheuber et al. 2004; although exceptions occur—see, e.g., Ligon and Zwartzes 1995; Hagelin and Ligon 2001). Females may instead only use dynamic cues to assess males that simultaneously possess high-quality static cues (e.g., singing rates and tail streamer length in barn swallows, Møller et al. 1998) or initially base choice on dynamic signals if the assessment costs of these signals are lower and then switch to more reliable static cues to make a final choice of a subset of these males (e.g., nest invitation displays and nest construction quality in village weaverbirds, Collias 1979). In contrast, the relative importance of static and dynamic signals as indicators of male quality during territorial disputes remains poorly understood. Static antagonistic traits are typically reliable indicators of long-term male quality and fighting abilities (reviewed by Whiting et al. 2003) and may be assessed by opponents in decisions on whether to engage in costly physical contests (Bradbury and Vehrencamp 1998; Senar 1999). For example, in house sparrows (*Passer domesticus*), individuals expressing high levels of testosterone prior to the molting period typically develop high-quality status signals and also have superior competitive abilities (Evans et al. 2000; Gonzalez et al. 2001). In contrast, singing rates readily fluctuate with current motivation during a territorial dispute (Naguib 2005) but may be less reliable signals of long-term viability if inferior individuals are able to temporarily express a high-quality signal (Scheuber et al. 2004).

When individuals display both types of ornaments, conspecifics are expected to emphasize those signals that are most informative about aspects of signaler quality relevant to the receiver (Fawcett and Johnstone 2003). This can lead to sex-specific differences in ornament prioritization if the value of information extracted from signals differs between the sexes. For example, testosterone-dependent behavioral displays of male Gambel’s quails (*Callipepla gambelii*) are an important signal during both male competition and female choice because they are thought to accurately reflect male quality (Hagelin and Ligon 2001; Hagelin 2002). By contrast, head plume size is a poor indicator of male quality and is therefore not female selected but reliably predicts male dominance, thus playing a key role in determining the outcomes of male contests (Hagelin 2002).

Similarly, differences in the information content of antagonistic signals expressed by golden whistlers appeared to stimulate sex-specific differences in responses during the aggression trials. Female golden whistlers did not respond differentially to our manipulations in throat patch size and only reacted more strongly during high song rate trials. This result supports a previous experimental study in which males, but not females, displayed weaker territorial responses to intruding males with experimentally reduced throat patch sizes (van Dongen and Mulder 2007).

The emphasis by females on singing rates but not throat patch size during territorial encounters may arise for several reasons. First, females may assess the intruders as potential extrapair mates and preferentially focus on a dynamic signal because it more accurately reflects the current condition of the potential extrapair mate. However, paternity analyses reveal that male singing rates throughout the season are unrelated to male genetic reproductive success (van Dongen WFD, Mulder RA, unpublished data). An alternative explanation is that female approaches are aggressive and are related to joint territorial defense. Cooperative defense of territories may arise if joint defense is more effective at deterring intruders or if each member of the pair defends the territory against same-sex rivals (Langmore 1998). Golden whistler pairs typically intrude onto a neighboring territory together. However, fe-

male whistlers only actively chased other females and never engaged in aggressive contests with males (van Dongen and Yocom 2005), although the possibility that females cryptically assess male quality during such intrusions remains. This suggests that the relative fighting abilities of males, as advertised by the throat patch, may be relatively unimportant to females. Nevertheless, if territorial intrusions involve coordinated aggression by the members of a pair and the willingness of both individuals to escalate encounters is correlated, females could use the singing rates of intruding males to predict the motivation of his partner to engage in a territorial contest.

In contrast to females, both high singing rates and large throat patches induced aggressive responses from males. Surprisingly, ornament assessment did not occur in a linear additive manner. Thus, focal males were not most aggressive toward introduced males possessing both a large throat patch and high singing rates, suggesting that males pay attention to each trait separately and for different reasons. By assessing both traits, males may gain information on both the intruder’s long-term competitive abilities and current motivation. The use of 2 different ornaments by males to gain different types of information on intruders gives new insights into the evolution of multiple display signals in birds. This pattern is in accordance with the multiple message mechanism for multiple ornamentation proposed by Møller and Pomiankowski (1993), which proposes that individuals display multiple signals to advertise different aspects of their quality to conspecifics. Variation in the throat patch resulted in differences in response latency and duration, and males invested more time attempting to expel intruders with large patches. This suggests that patch size is a better indicator of the overall threat of the male. Conversely, variation in singing rates was related to response intensity or how closely the resident male approached the intruder, presumably because they reliably reflect intruder willingness to continue the contest.

Our experimental results, coupled with observational data, strongly suggest that males pay attention to both intruder throat patch size and singing rates during territorial responses, whereas females only pay attention to singing rates. However, the song rates broadcast during the “high song rate” trials were 100% higher than those during the low song rate trial (i.e., 4 songs per minute and 8 songs per minute, respectively) with no overlap between the groups. This difference of 4 songs per minute between the groups represented approximately 35% of the total range of natural variation in this signal (0–11.3 songs per minute). In contrast, the average size of throat patches in the control treatment was only 26% larger than that of the reduced group, with a slight overlap in throat patch sizes between the 2 groups. This difference between the 2 throat patch groups (128 mm<sup>2</sup>) represented 38% of the total range of variation in this signal (420–756 mm<sup>2</sup>). Thus, although our signal manipulations represented similar percentages of the total range in variation, they were not identical with respect to the difference in signal amplification in control versus reduced trials. It is therefore difficult to be certain about the relative importance of each ornament as an antagonistic signal because this could depend on the extent to which each signal was manipulated. It might, for example, provide an alternate explanation as to why females only responded to variation in singing rates—this signal was manipulated to a larger degree. Although possible, this possibility seems unlikely both because genetic data suggest that females do not use throat patch sizes during mate choice decisions (breast plumage quality and song repertoire sizes are emphasized during mate choice decisions; van Dongen WFD, Mulder RA, unpublished data), and similar results were obtained in a previous study in which differences between throat patch treatment groups were much larger (67%), with no overlap

between the groups (van Dongen and Mulder 2007). Finally, the issue of the relative importance of each signal does not apply to male responses, as signal manipulations influenced distinctly different response variables in males (i.e., temporal responses tended to vary with throat patch size, whereas spatial variation was related to intruder singing rates).

In one of the few studies concurrently investigating the relative importance of static and dynamic traits in male competition, Hagelin (2002) reported that both a plastic signal reflecting male motivation (an erectable head crest) and a static trait (body size) in Gambel's quail (*C. gambelii*) were important predictors of outcomes of male–male contests. Large males with enlarged, erect crests were more likely to dominate their competitors. Our study provides further insight into how static and dynamic traits are perceived by conspecifics, demonstrating that subtle variation may occur in male response effort and intensity to different combinations of manipulated traits. By focusing on different aspects of male–male encounters, instead of only on winners and losers, we have shown that males may assess different aspects of aggressive displays during different stages of elevated contests. Although multiphase assessment of conspecifics has been documented in studies of female mate choice (e.g., Andersson 1989), analogous studies targeting context-specific assessment of male antagonistic signals are lacking.

What prevents males with inferior competitive abilities from cheating in the expression of these signals? Inferior males may incur high physiological costs related to the immunosuppressive effects of testosterone (Folstad and Karter 1992; but for studies reporting negative results, see Roberts et al. 2004). Another possibility is that honesty in the signals is maintained by a form of social “policing,” in which individuals are regularly tested to identify discrepancies between actual and signaled competitive ability (Metz and Weatherhead 1992; Senar 1999). The costs of such frequent physical testing may be particularly high for low-quality males (e.g., Veiga 1995). Such a system could also apply to singing, which probably imposes only minimal physiological costs on the signaler (Oberweger and Goller 2001; Franz and Goller 2003; Ward et al. 2003).

We have shown experimentally that both throat patch size and singing rates are assessed by golden whistler conspecifics during elevated territorial disputes but that there are sex-specific differences in response to the manipulated traits. Females display increased aggression toward intruders singing at high rates but ignore variation in throat patch size. In contrast, both high song rate and large throat patches elicit strong responses from males, although these ornaments appear to be assessed for different purposes. These striking differences in responses appear to reflect alternate strategies adopted by each sex during the defense of territories. Our study highlights the value of simultaneously quantifying multiple antagonistic signals during STIs to explore the complexities of how multicomponent antagonistic displays are perceived by conspecifics. In addition, comprehensively quantifying aspects of the resident's behavioral response to the introduced male, instead of only documenting winners and losers of contests, provide useful insight into more subtle variation in the perception and use of each signal during different stages of aggressive encounters.

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