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Variation in the temporal and spatial use of signals and its implications for multimodal communication

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Abstract The use of signals across multiple sensory modalities in communication is common in animals and plants. Determining the information that each signal component conveys has provided unique insights into why multimodal signals evolve. However, how these complex signals are assessed by receivers will also influence their evolution, a hypothesis that has received less attention. Here, we explore multimodal signal assessment in a closely related complex of island flycatchers that have diverged in visual and acoustic signals. Using field experiments that manipulated song and plumage colour, we tested if song, a possible long-range signal, is assessed before plumage colour in conspecific recognition. We find that divergent song and colour are assessed in sequence, and this pattern of sequential assessment is likely mediated by habitat structure and the extent of differences in signal characteristics. A broad survey of the literature suggests that many organisms from a wide range of taxa sequentially assess multimodal signals, with long-range signals attracting conspecifics for further assessment of close-range signals. Our results highlight the need to consider how signals are assessed when understanding multimodal signal evolution. Finally, given the results of our field experiments indicating sequential assessment of divergent song and colour in the recognition of conspecifics, we discuss the consequences of multimodal signal divergence for the origin of species, as changes in signals across different sensory modalities may influence the evolution of premating reproductive isolation.

Keywords Multimodal signals · Sequential assessment · Sexual selection · *Monarcha castaneiventris* · Premating reproductive isolation

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Introduction

Many organisms use a suite of signals, often of different sensory modalities, in communication (reviewed in Guilford and Dawkins 1991; Candolin 2003; Hebets and Papaj 2005; Partan and Marler 2005). For instance, most songbirds use colourful plumage and elaborate songs to attract and compete for mates (Ratti 1979; Lampe and Saetre 1995; Patricelli et al. 2003; Partan et al. 2005). Similarly, plants can use colourful and fragrant flowers to attract their pollinators (e.g. Kulahci et al. 2008; Goyret et al. 2009; Balkenius and Dacke 2010; Kaczorowski et al. 2012). In attempts to understand the evolution of these multimodal signals, much attention has been given to determining what information each signal component conveys. These studies suggest that multimodal signals are favoured either because (1) they are redundant, such that multiple signals can serve as backups in case one sensory modality becomes less perceptible or informative (e.g. Birkhead et al. 1998; Gibson and Uetz 2008; Kaczorowski et al. 2012) or (2) they are independent, with each signal conveying unique information about the sender and so facilitating decision making (e.g. Partan et al. 2005; Uetz et al. 2009; Leonard and Hedrick 2010). However, how multimodal signals are assessed by receivers, independent of signal content, should also influence the signals' utility and thus their evolution (Candolin 2003; Hebets and Papaj 2005). For example, different signal modalities may transmit differently through the environment, suggesting variation in the temporal and

spatial scales in which they can be used. In contrast to signal content, less is known about how multimodal signals are assessed.

The signalling environment, which includes an interaction of the physical habitat in which signals are transmitted and received, and the sensory physiology of receivers will dictate the efficacy of signal transmission, reception and detection (Morton 1975; Endler 1992; Wilkins et al. 2012). Signal efficacy, in turn, can influence how multimodal signals are assessed in at least two ways (Candolin 2003; Hebets and Papaj 2005). First, a variable environment may favour communicating in multiple sensory modalities, in case one modality is less useful in certain conditions (Bro-Jørgensen 2009). In this scenario, signals can be redundant or independent, and the presence of multimodal signals insures that information is effectively transmitted to the intended receiver across a wide range of conditions (Hebets and Papaj 2005; Bro-Jørgensen 2009). An example of this occurs in Bornean rock frogs *Staurios parvus*, where males chorus near rivers and have therefore modified their calls and evolved visual signals to compensate for the loud background noise of fast-flowing water (Grafe et al. 2012).

Second, each sensory modality has unique properties that make them more detectible at different distances or conditions (Candolin 2003; Hebets and Papaj 2005). Although signals in each modality can evolve ways to be more conspicuous for a given distance (e.g. larger colour patches, higher amplitude songs), each modality, in general, has properties that make them more suitable for specific spatial scales of communication (Endler 1992; Bradbury and Vehrencamp 1998). For instance, visual signals, which are easily obstructed by vegetation, work well in middle- to close-range communication, while acoustic signals, which can travel around obstructions and have reduced attenuation as they transmit through air and water, can be effective in long-range communication (Bradbury and Vehrencamp 1998). These long-distance signals—though still effective in closer ranges—may be adaptive if the costs of searching for conspecifics are significant. Therefore, multimodal communication may be favoured if there are advantages in assessing signals in a specific temporal and spatial sequence, and this can be independent of signal content (Candolin 2003; Hebets and Papaj 2005).

Here, we explore the evolution of multimodal signals by determining how each element of a suite of multimodal signals is assessed using data from field experiments and a survey of published work. First, we test if multimodal signals are assessed in sequence or simultaneously using two pairs of incipient flycatcher species that have diverged in plumage colour (i.e. visual) and song (i.e. acoustic) (Uy et al. 2009a, b). Through song playback and mount presentations, we experimentally test how each signal is assessed during conspecific recognition under natural conditions. Because song can travel further and is less obstructed in forests than visual signals, we predict that song will be assessed first at a distance, then plumage colour at closer range. Second, we review the literature to see how components of multimodal signals are assessed across a wide range of taxa and sensory modalities, focusing on studies that explore how signals influence receiver behaviour. Our field experiments suggest that song is assessed first at a distance then plumage colour at closer range. However, this pattern of sequential assessment of acoustic then visual signals depends on the extent of divergence in signal characteristics and aspects of the signalling environment. Our survey of the literature likewise suggests that multimodal signals are often assessed in sequence, with long-range signals attracting conspecifics for further assessment of close-range signals. We conclude by discussing the consequences of multimodal signal divergence in speciation, as divergence across multiple sensory modalities may accelerate the evolution of premating reproductive isolation.

Materials and methods

The *Monarcha* flycatcher complex

In his seminal work on speciation, Mayr (1942) presented the chestnut-bellied flycatcher *Monarcha castaneiventris* complex of the Solomon Islands as a putative case of incipient speciation. Allopatric populations of this complex have diverged in plumage colour and song (see Fig. 1; Diamond 2002; Filardi and Smith 2005; Uy et al. 2009a, b). The plumage colour variation ranges from an entirely iridescent blue–black form (e.g. melanic) to a chestnut-bellied and white-capped form, while variation in song structure ranges from a simple descending whistle note to a more complex up-slurred then down-slurred double whistle note (Figs. 1 and 2). In this study, we focus on two sister taxa pairs within the *M. castaneiventris* clade (see Uy et al. 2009a for the molecular phylogeny of this complex).

The first sister taxa comparison is between the nominate chestnut-bellied *M. c. castaneiventris* and the white-capped *M. c. richardsii* forms (orange and red islands in Fig. 1, respectively). The chestnut-bellied form is sexually monochromatic, with a chestnut belly and blue–black upper parts. In contrast, the white-capped form is dichromatic, with males having chestnut bellies, blue–black upper parts and white caps, and females having chestnut bellies and grey upper parts (Fig. 1 and Table 1). Both colour forms sing a simple descending, single whistle note, with the white-capped form's whistle significantly shorter in duration than the chestnut-bellied form (Fig. 1, Uy et al. 2009a). The white-capped form is restricted to the Western Province,
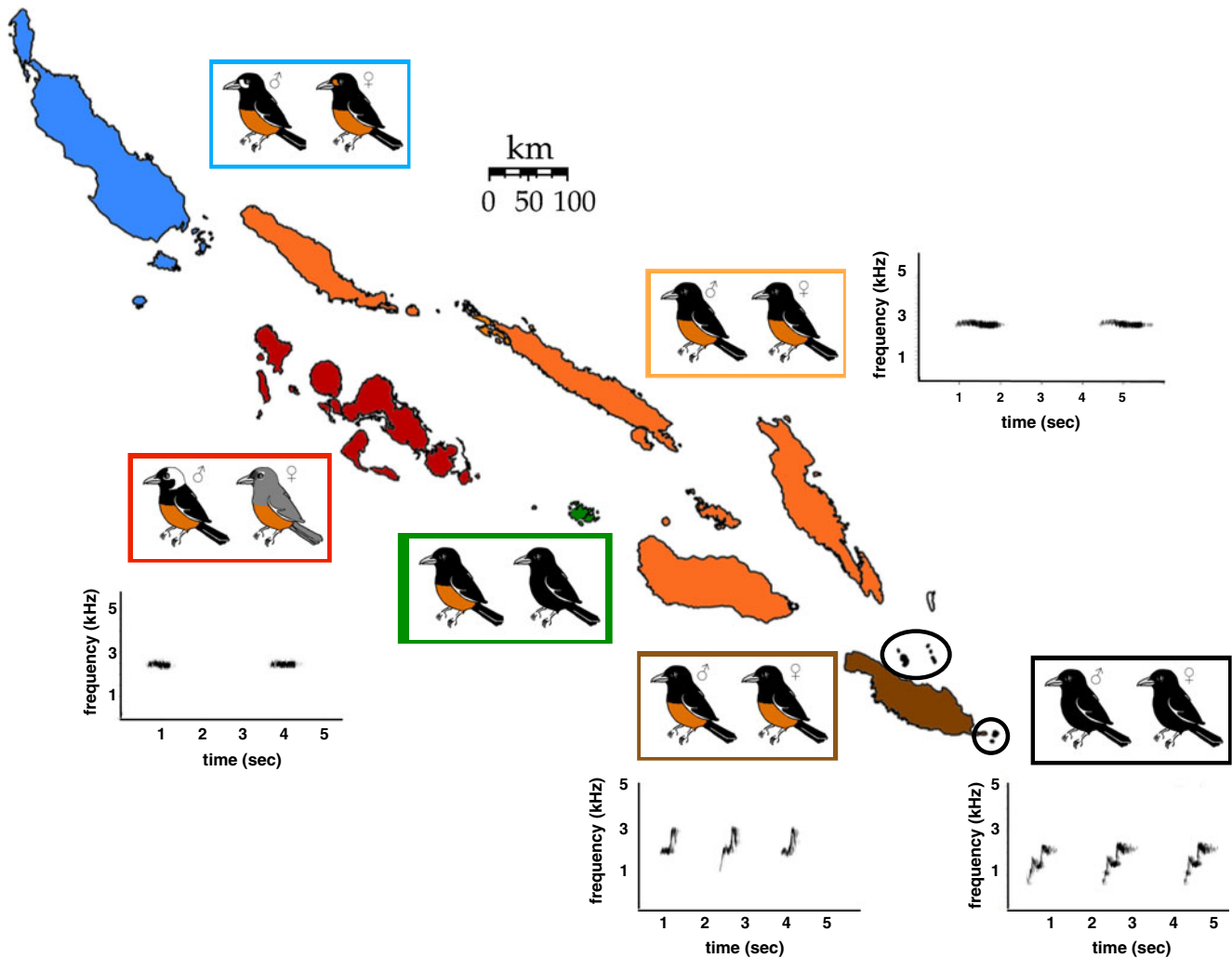
Fig. 1 Geographic variation in plumage colour and song among populations of the *M. castaneiventris* flycatcher of the Solomon Islands. Six subspecies are shown, but for this work, we focus on four subspecies that represent two sister taxa pairs. The first sister taxon is the nominate chestnut-bellied and white-capped forms. The nominate chestnut-bellied form *M. c. castaneiventris* (*orange box*) is sexually monochromatic, sings a simple, descending whistle note, and is found in several islands across the archipelago (*orange islands*). The white-capped form *M. c. richardsii* (*red box*) is sexually dichromatic, sings a simple, descending whistle note, and is found in the Western Province of the Solomon Islands (*red islands*). The second sister taxon is the Makira chestnut-bellied and melanic forms. The Makira chestnut-bellied form (*brown box*) is sexually monochromatic, sings a more complex ascending then descending whistle note and is endemic to the island of Makira (*brown island*). The melanic form *M. c. ugiensis* (*black box*) is sexually monochromatic, sings an ascending then descending whistle note, and is found on satellite islands 8 km off Makira (*black islands*; Ugi and Three sisters to the north, and Santa Ana and Santa Catalina to the southeast of Makira). Finally, the Russell Island *M. c obscurior* form (*green box/islands*), a polymorphic taxon, and the Bougainville *M. c. erythrostictus* form (*blue box/islands*) are shown but were not used in this study

while the chestnut-bellied form is found in many large islands across the Solomon Archipelago (Fig. 1). The two forms are allopatric throughout their range, with no zone of contact (Fig. 1). Molecular phylogenetic analyses suggest that the two taxa shared a common ancestor ca. 300,000 years ago (Uy et al. 2009a).

The second sister taxa comparison is between a melanic form that lost the chestnut belly and is instead entirely blue–black (*M. c. ugiensis*), and a chestnut-bellied form (*M. c. megarhynchus*) similar to the nominate subspecies in plumage, but larger in body size and bill morphology (black and brown islands in Fig. 1, respectively). Unlike all of the other *M. castaneiventris* subspecies that sing a single down-slurred whistle note, *M. c ugiensis* and *M. c. megarhynchus* sing a more complex up-slurred, then down-slurred whistle note (Diamond 2002; Uy et al. 2009b). The chestnut-bellied *M. c. megarhynchus* form is endemic to the large island of Makira, while the melanic form is found exclusively in small, satellite islands ca. 8 km to the north and southeast of Makira (Fig. 1). Our previous work in these sister taxa identified mutations in the melanocortin-1 complex mediating the difference in
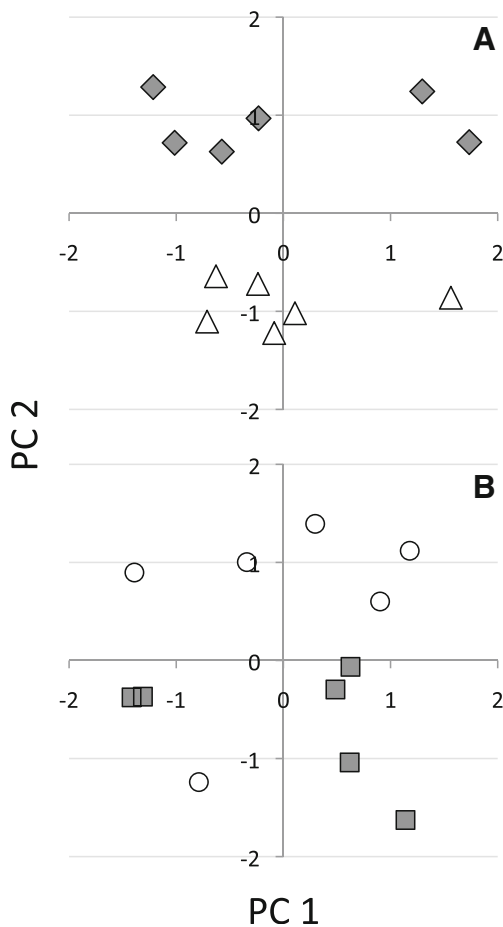
Fig. 2 Comparison of song structure (i.e. PC1 and PC2) of *Monarcha* whistles between **a** the white-capped (*open triangles*) and nominate chestnut-bellied (*grey diamonds*) forms, and **b** the melanic (*grey squares*) and Makira chestnut-bellied (*open circles*) forms. PC1 generally describes frequency characteristics (e.g. peak frequency, maximum frequency) and PC2 describes temporal characteristics (e.g. note duration) of *Monarcha* whistle songs

plumage colour (Uy et al. 2009b). Molecular phylogenetic and population genetics analyses indicate that the two taxa, despite having fixed differences in plumage colour, do not form reciprocally monophyletic clades, likely due to

Table 1 Distribution of nape (white vs. black/iridescent blue) and belly (chestnut vs. black/iridescent blue) colours across the four *M. castaneiventris* subspecies in the study. Values indicate the observed numbers of territory owners (likely males) in our field experiments, with the observed, specific plumage colour for each subspecies

| | Nape colour | | Belly colour | |
	White	Black	Chestnut	Black
M. c. richardsii	60	0	60	0
M. c. castaneiventris	0	60	60	0
M. c. megarhynchus	0	55	55	0
M. c. ugiensis	0	60	0	60

contemporary gene flow or incomplete lineage sorting (Uy et al. 2009b).

Mount presentation and song playback experiments

Monarcha flycatchers are insectivorous, leaf-gleaners found primarily in the middle and lower strata of forests (Filardi 2003; Filardi and Smith 2008). They are socially monogamous and pairs defend breeding or nesting territories from other breeding pairs (Uy et al. 2009a). Therefore, to simulate secondary contact and experimentally test how divergent multimodal signals are assessed and mediate conspecific recognition, we observed the response of territory owners to different combinations of taxidermic mounts and song recordings.

For the visual signal test stimuli, two adult males were caught and prepared for taxidermic mounts for each taxon. For song playbacks, we recorded long-range advertisement songs ("whistles") from six different individuals for each taxon with a Marantz (Mahwah, NJ) PMD670 digital recorder set at 16-bit PCM, 48 kHz sampling rate, and fitted with a Sennheiser (Old Lyme, CT) shotgun microphone. From the recordings used in the experiment, the following song characteristics were measured through visual inspection of sonograms in Raven Pro (Cornell Lab of Ornithology, Ithaca, NY): duration (second), minimum and maximum frequency, and peak frequency (kilohertz) of whistle notes. We searched for territory owners by walking along trails and finding calling pairs, and at each territory, we randomly chose one of five treatment groups: (1) homotypic mount and song, (2) homotypic mount with heterotypic *M. castaneiventris* ssp. song, (3) heterotypic *M. castaneiventris* ssp. mount with homotypic song and (4) heterotypic *M. castaneiventris* ssp. mount and song. Because territory owners may also aggressively respond to ecological competitors (e.g. other species that use the same food resources), we included a fifth treatment of a heterospecific mount and song as a control. For the heterospecific control, we chose a sympatric and distantly related species that shares a similar ecological niche to *M. castaneiventris* ssp., the golden whistler *Pachycephala pectoralis* ssp. Mounts were perched on a locally collected sapling ca. 2 m tall and placed adjacent to vegetation suitable for perching by territorial birds. Beneath the mount's perch, we mounted a small speaker (Mini-Amplifier; RadioShack Corp., ForthWorth, TX) and a digital player (iPod Shuffle; Apple, Inc., Seattle, WA), concealed by leaves. The digital player played 3 min of silence at the start the experiment, followed by whistle songs for 3.5 min (210 s). Amplitude of song playbacks was measured in the lab with a sound level meter (Extech 407330, Extech Instruments, Nashua, NH) 1 m from the speaker. The amplitude of the song playback based on a

fixed speaker volume and iPod setting ranged from 77 to 85 dB.

We noted several behavioural responses during the experiment. In two previous studies, we used principal component analysis to collapse these variables into a single, orthogonal index of conspecific recognition (Uy et al. 2009a, b). In this study, however, we wished to explore the sequential assessment of acoustic and visual signals, and so we focused on two specific behaviours: the latency of response and the latency to approach the test stimuli. Latency of response was the time it took for a territory owner to respond, either by singing back or starting to approach the test stimuli. We use the latency of response to the test stimuli as a reaction to a long-distance signal because long-range signals will catch the attention of territory owners in the canopy. Latency of approach was the time it took for the territory owner to be within 2 m of the taxidermic mount. We used latency to approach as a response to a close-range signal because close-range signals should be assessed after the long-range signal has been evaluated. Observations were conducted 15–20 m away from the mount by JACU and local field assistants, who were concealed in thick vegetation. Observations were spoken into a digital recorder (Marantz PMD670 digital recorder and built-in microphone) for later transcription. All trials were conducted between 0630 to 1100 hours and 1500 to 1730 hours, the time periods in which individuals were observed to sing most often from territories. Global positioning system coordinates at each territory was taken to ensure that we did not return to the same pair for subsequent experiments.

Some experiments started with territory owners already singing in the canopy at their territories. Because we were interested in exploring the factors that predict the latency to respond to various combinations of plumage colour and song playback, we only included experiments in which territory owners were quiet at the start of the experiment (i.e. before and at the start of the song playback). For the nominate chestnut-bellied form, we tested 60 territories in Mt. Austen, Guadalcanal Island (9°28.035′S, 159°58.452′E) from July 6 to July 12, 2007, and May 22 to May 26, 2008. Five of these 60 trials involved territory owners already singing at the start of the experiment and were excluded from this study. Guadalcanal is one of the largest islands in the Solomon Archipelago (Fig. 1), and the habitats in Mt. Austen, where experiments were conducted, were in a combination of intact rainforests and mature secondary growth adjacent to villages. For the white-capped form, we tested 60 territories on Tetepare Island (9°29.218′S, 159°59.230′E) from June 24 to June 30, 2007 and May 15 to May 20, 2008. Twenty-three of these 60 trials involved territory owners already singing at the start of the experiment and were excluded from this study.

Tetepare Island is the largest uninhabited island in the South Pacific and is managed as a nature reserve (Read 2011). Although secondary forests are found in tree gaps and mangroves, most of the experiments were carried out in territories within forests with full canopies. For the melanic form, we tested 60 territories in Santa Ana Island (10° 50.316′S, 162°27.452′E) from June 11 to June 19, 2007, and May 4 to May 9, 2008. Seven of these 60 trials involved territory owners already singing at the start of the experiment and were excluded from this study. Santa Ana Island is the easternmost island of the Solomon Archipelago (Fig. 1) and is thus exposed to cyclones. The experiments were carried out in immature, secondary forest adjacent to villages and farmed plots. Finally, for the Makira chestnut-bellied form, we tested 55 territories in Star Harbor, Makira Island (10°49.120′S, 162°17.139′E), which is the easternmost tip of Makira and ca. 12 km from Santa Ana. The experiments were conducted in immature, secondary forests on ridges and adjacent to villages and farmed plots. Mount presentation and playback experiments were carried out from May 28 to June 10, 2007, and April 30 to May 3, 2008. Nine of these 55 trials involved territory owners already singing at the start of the experiment and were excluded from this study.

Because territory owners did not respond (e.g. stayed quiet in the canopy) to the golden whistler taxidermic mount and song playbacks, the inclusion of the heterospecific control artificially enhanced the effects of heterotypic song and plumage colour (Uy et al. 2009a, b). We therefore did not include the heterospecific controls in our analyses (Tables 2 and 3). For reference, however, we include the mean (±S.E.) latency to respond and latency to approach for the heterospecific control treatment in Figs. 3 and 4 to provide a benchmark for how territory owners responded to a distantly related, sympatric species that is an ecological competitor.

The use of the same mount and same recording across multiple replicates constitutes pseudoreplication (McGregor et al. 1992; Kroodsma et al. 2001). To avoid pseudoreplication, we used a nested mixed-model ANOVA to explore the roles of song and plumage colour in conspecific recognition, with specific mount nested within plumage type and specific recording nested within song type (as suggested by Kroodsma et al. 2001). In the model, plumage colour (fixed between sister taxa) and song type were predictors, and we tested for an interaction between the two, as well as any taxon effects. All tests of hypotheses were two-tailed. In previous analyses of similar data sets, we found that the use of parametric and randomization tests yielded near-identical results (Uy et al. 2009a, b). We therefore present results from parametric tests in this study.

Additionally, to test for quantitative differences in song structure between sister taxa pairs, we quantified the duration (second), minimum and maximum frequency, and

Table 2 Mixed-model nested ANOVA of latency (second) to respond to and approach the taxidermic mount and call playbacks by territory owners for the white-capped and chestnut-bellied sister taxa. This analysis excluded the heterospecific golden whistler control

Factor	df	Type III SS	F	p
Latency to respond				
Plumage type	1, 2	134	0.08	0.79
Mount	2, 56	8452	2.36	0.11
Song type	1, 10	20790	11.61	0.001
Recording	10, 56	10842	0.61	0.80
Taxon	1, 56	642	0.36	0.55
Plumage × call	1, 56	636	0.36	0.55
Residuals	56			
Latency to approach				
Plumage type	1, 2	86405	30.58	<0.001
Mount	2, 56	4514	0.79	0.46
Song type	1, 10	39712	14.06	<0.001
Recording	10, 56	28702	1.02	0.44
Taxon	1, 56	24131	8.54	0.01
Plumage × call	1, 56	23663	8.38	0.01
Residuals	56	158232		

frequency of maximum amplitude of whistle calls for the six recordings for each taxon ($n=4$ taxa, 24 recordings/individuals). We then used a principal component analysis (PCA) to collapse these non-orthogonal song measurements into orthogonal indexes of song structure. A one-way ANOVA was used to test for differences in song structure (e.g.

Table 3 Mixed-model nested ANOVA of latency (second) to respond to and approach the taxidermic mount and song playbacks by territory owners for the melanic and Makira chestnut-bellied sister taxa. This analysis excluded the heterospecific golden whistler control

Factor	df	Type III SS	F	p
Latency to respond				
Plumage type	1, 2	6298	4.96	0.03
Mount	2, 67	694	0.55	0.58
Song type	1, 10	1351	1.07	0.31
Recording	10, 67	2785	0.22	0.99
Taxon	1, 67	179	0.14	0.71
Plumage × call	1, 67	49	0.04	0.84
Residuals	67	85065		
Latency to approach				
Plumage type	1, 2	54778	11.25	0.001
Mount	2, 67	1015	0.10	0.90
Song type	1, 10	12454	2.56	0.11
Recording	10, 67	24231	0.50	0.89
Taxon	1, 67	4806	0.99	0.32
Plumage × call	1, 67	1595	0.33	0.57
Residuals	67	325990		
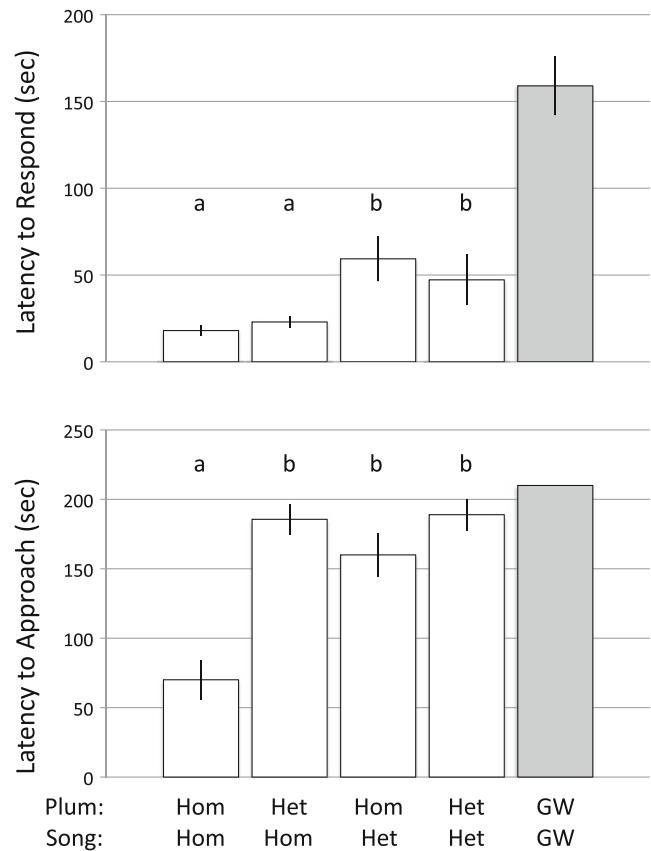
Fig. 3 Latency (second) to respond to (*top*) and approach (*bottom*) the test stimuli for white-capped and nominate chestnut-bellied territory owners

principal component scores) between sister taxa pairs. Plumage variation is fixed between sister taxa pairs (e.g. presence or absence of white cap; presence or absence of chestnut belly); hence, we compare and present the plumage colour data in a contingency table to show the non-overlapping distribution of plumage colour among the two sister species pairs (Table 1).

Results

White-capped vs. nominate chestnut-bellied pair

A nested, mixed model ANOVA revealed a significant effect of song type in the latency to respond to song playbacks, with homotypic songs eliciting a quicker response over heterotypic songs, regardless of plumage type (Table 2, Fig. 3). There was no effect of study taxon, as well as specific mount nested within plumage type and specific recording nested within song type. Likewise, there was no interaction effect between song and plumage type. Post hoc, pairwise comparisons (Fisher's LSD) of the four treatment groups (homotypic mount and song, homotypic mount and
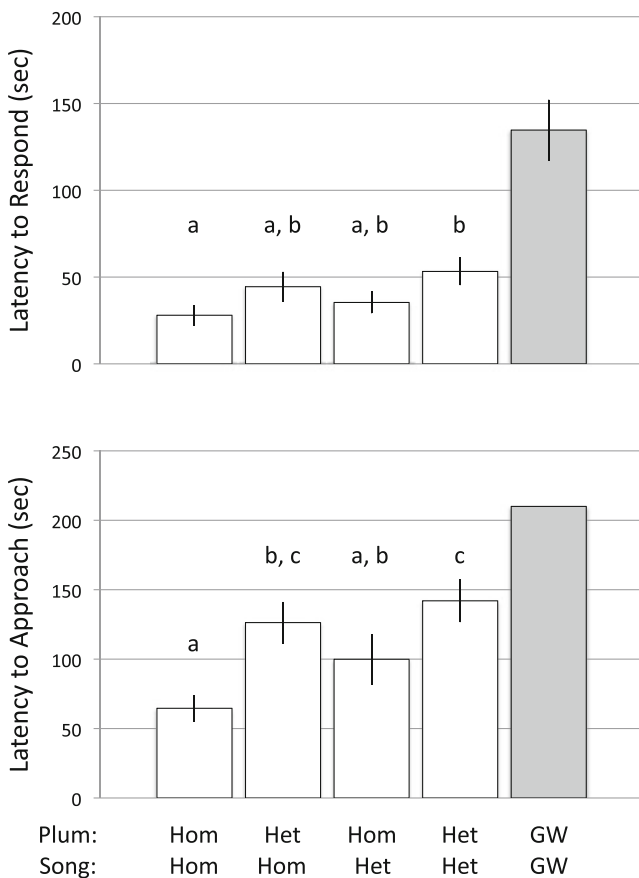
Fig. 4 Latency (second) to respond to (*top*) and approach (*bottom*) the test stimuli for melanic and Makira chestnut-bellied territory owners

heterotypic song, heterotypic mount and homotypic song, heterotypic mount and song) indicated that the treatments with homotypic song and homotypic mount did not differ significantly from the treatment of homotypic song and heterotypic mount. These two treatments, however, differed from the two treatments with heterotypic song (Fig. 3).

With respect to the latency to approach the mount, there were significant plumage type, song type, song × plumage type, and taxon effects. The taxon effect was due to the chestnut-bellied form (136.12±8.13 s) approaching the test stimuli more quickly than the white-capped form (173.97±10.24 s). There was no effect of specific mount nested within plumage type or specific recording nested within song type. Post hoc, pairwise comparisons (Fisher's LSD) of the four treatment groups indicate that only the treatment with homotypic song and homotypic mount differed significantly from any of the three treatments (Fig. 3).

A PCA collapsed the four measures of song/whistle characteristics (duration, minimum and maximum frequency, and frequency of maximum amplitude of whistle notes) into two PC scores, explaining 97.37 % of the total variation in song characteristics between sister taxa. PC 1 was positively associated with the maximum (factor loading, 0.99),

minimum (factor loading, 0.99) and peak (factor loading, 0.92) frequencies of whistle notes. PC2 was positively associated with the duration (factor loading, 0.99) of whistle notes. A one-way ANOVA revealed that PC2 was significantly different between taxa ($F_{1, 10}$=157.01, $p<0.001$) but not PC1 ($F_{1, 10}$=0.00, $p=0.99$; see Fig 2a). All 60 *M. c. richardsii* males/territory owners had white-caps, while all 60 *M. c. castaneiventris* males had black/iridescent blue caps (Fisher's exact test, $p<0.001$). All males from both subspecies had chestnut bellies (Table 1).

Melanic vs. Makira chestnut-bellied pair

In contrast to the previous species pair, a nested, mixed model ANOVA revealed a significant effect of plumage type but not song type in the latency to respond to song playbacks and mount presentation, with homotypic plumage eliciting a quicker response over heterotypic plumage (Table 3, Fig. 4). Song type did not influence latency to respond, and there was no effect of specific mount nested within plumage type or specific recording nested within song type. Likewise, there was no interaction effect between song and plumage type. Post hoc, pairwise comparisons of the four treatment groups indicate that only the treatment with homotypic mount and homotypic song, and the treatment with heterotypic mount and heterotypic song differed significantly (Fig. 4).

With respect to latency to approach the mount (within 2 m), again only plumage type had a significant effect (Table 2). Post hoc, pairwise comparisons (Fisher's LSD) of the four treatment groups indicate that the treatment with homotypic mount and song differed significantly from the two treatments with the heterotypic mounts. Treatment with homotypic mount and song, however, did not differ from the treatment with homotypic mount but heterotypic song, suggesting a strong mount effect, but not song. The two treatments with heterotypic mounts do not differ significantly from each other (Fig. 4).

A PCA collapsed the four measures of song/whistle characteristics (duration, minimum and maximum frequency, and frequency of maximum amplitude of whistle notes) into two PC scores, explaining 82.23 % of the total variation in song characteristics between sister taxa. PC 1 was positively associated with the maximum (factor loading, 0.92) and the peak (factor loading, 0.88) frequencies of whistle notes. PC2 was positively associated with the duration (factor loading, 0.82) and minimum frequency (factor loading, 0.91) of whistle notes. A one-way ANOVA revealed that PC2 was significantly different between taxa ($F_{1, 10}$=7.59, $p=0.02$) but not PC1 ($F_{1, 10}$=0.01, $p=0.94$; see Fig 2b). All 55 *M. c. megarhynchus* males/territory owners had chestnut bellies, while all 60 *M. c. ugiensis* males had black/iridescent bellies (Fisher's exact test, $p<0.001$). All experimental

males from both subspecies had black/iridescent blue caps (Table 1).

Discussion

Sequential vs. simultaneous assessment of multimodal signals in *Monarcha* flycatchers

In a previous study, Uy et al. (2009a, b) found that both divergent plumage colour and song mediated conspecific recognition between the two incipient flycatcher species pairs in this study. Uy et al. (2009a, b) did not, however, explore the relative roles of song and plumage colour in sequential recognition because some of the experiments started with territory owners already singing, so that the latency to respond to the test stimuli could not be measured. In our current analyses, we excluded all experiments with territory owners calling at the start of the experiment, reducing the sample size of our study, but allowing us to address how quickly territory owners responded to various combinations of plumage colour (mounts) and song (recordings), and thereby determine how visual and acoustic signals influence receiver behaviour.

In the white-capped and nominate chestnut-bellied sister taxa experiments, we found that song type influenced the latency to respond, with territory owners responding more quickly to homotypic over heterotypic songs, regardless of the plumage colour of the taxidermic mounts. In contrast, the latency to approach the mount was predicted by both plumage colour and song, but with plumage colour having a stronger effect. Treatments with a mismatched plumage colour and song had intermediate values for the latency to approach. Overall, these patterns suggest that song and plumage colour are assessed sequentially, with song being used at a distance, followed by plumage at closer range.

In the melanic and Makira chestnut-bellied sister taxa, on the other hand, we only consistently detected a strong effect of plumage colour in predicting both the latency to respond and approach the test stimuli, with song having a marginal effect. In our previous study within this sister taxa comparison (Uy et. al. 2009b), we found that both divergent plumage and song influenced the likelihood of territory owners attacking the mount. Therefore, song and colour are important in overall conspecific recognition, but plumage colour has a stronger effect both in long- and close-range communication. These results suggest that divergent song and plumage are not assessed sequentially, as in the white-capped and nominate chestnut-bellied forms, but rather simultaneously.

Why are the patterns of assessment inconsistent between these two closely related, sister taxon pairs? At least two non-mutually exclusive hypotheses may explain these

patterns. First, the extent of divergence in song is different between the two sister taxon pairs (Fig. 2). That is, even though whistles are distinct among all subspecies, they are not as different between the melanic and Makira chestnut-bellied pair as between the white-capped and nominate chestnut-bellied pair (Fig. 2). Thus, differences in song may be harder to discern, and so, less useful in recognising conspecifics from a distance for birds of the Makira clade. Song, however, did ultimately influence conspecific recognition (Uy et al. 2009b), suggesting that perhaps it takes longer to assess song differences or that divergent song is assessed simultaneously with plumage colour in the Makira clade.

Second, general forest structure may differ between the two sister taxa pairs, which, in turn, could dictate the utility of divergent song as long-distance signals for conspecific recognition. The territories where we conducted the playback experiments for the white-capped and nominate chestnut-bellied forms were in more mature rainforests, with relatively complete canopies (e.g. Tetepare Island is the largest unoccupied island in the South Pacific). In this type of habitat, song would be more useful in long-range communication than plumage colour, as obstructions from vegetation and longer distances from the canopy to the test stimuli could favour the use of acoustic over visual signals. In contrast, the territories we used for the playback experiments in Makira and Santa Ana were in more open and disturbed secondary forests. The entire Solomon Islands is subject to periodic cyclones, and cyclones play a major role in shaping canopy structure (Whitmore 1969). However, the southeastern section of the Solomon Islands, where the Makira island group is found, is subject to more intense and frequent cyclones (Brookfield 1969), which results in more disturbed forests and fewer climax communities. For instance, Santa Ana Island and the coastal forests of Makira where we conducted our experiments were devastated by Cyclone Ursula in December 1971 (Bureau of Meteorology 1975). This is not to say that song is not important in communication, as males clearly use song in territorial defence and song influenced the likelihood of territory owners attacking taxidermy mounts (Uy et al. 2009b). Therefore, with respect to song and plumage acting as signals in conspecific recognition, song may be assessed simultaneously with plumage colour, as more open canopies allow territory owners to more easily view visual signals.

Multimodal signal assessment in other taxa

Most studies of multimodal signals have focused on determining signal content or how different signal components affect receiver behaviour in controlled laboratory trials (reviewed in Candolin 2003; Hebets and Papaj 2005; Partan and Marler 2005; Bro-Jørgensen 2009).

Consequently, sufficient data for a systematic and unbiased analysis of published studies to test if selection for sequential assessment favours the evolution of multimodal signals are currently not available. However, a broad survey of studies that directly and indirectly explored multimodal signal assessment suggests three interesting observations. First, multimodal signals are assessed sequentially in many cases across a diverse set of taxa and sensory modalities (Table 4). These examples range from crickets using acoustic and olfactory signals to frogs and birds using acoustic and visual signals (Table 4). Second, our broad survey revealed that certain signalling modalities are associated with specific spatial scales or communication distances. In many terrestrial systems, for instance, acoustic signals are commonly used in long-distance attraction, while visual and tactile signals are often assessed at close range (Table 4). Likewise, in fish, olfactory signals may more often be used in long-range communication, while visual signals are assessed at close range (Table 4). Third, the incidence of sequential signal assessment of multimodal signals seems to be relatively independent of signal content. That is, there is evidence of sequential assessment for multimodal signals that convey both redundant and independent information (Table 4). Therefore, (1) the widespread incidence of sequential assessment of multimodal signals across diverse taxa and modalities, (2) the pattern of certain sensory modalities being used consistently in long versus close-range communication and (3) the observation that signal content is not necessarily associated with sequential assessment suggest that the detectability of certain signalling modalities at various distances may favour multimodal communication, as communication often requires individuals first identifying conspecifics from a distance before approach or further assessment. Understanding how signals are assessed is therefore important in understanding the evolution of multimodal signals.

Multimodal signal divergence and the origin of species

Signalling traits are critical components in mate choice and conspecific recognition (Andersson 1994). Accordingly, changes in signal characteristics between closely related populations could lead to recognition errors and eventually premating reproductive isolation (Lande 1981; West-Eberhard 1983; Kirkpatrick and Ravigne 2002). As such, changes in the characteristics of signals across multiple sensory modalities could further enhance premating reproductive barriers. For instance, divergent visual and olfactory signals result in premating reproductive isolation between closely related three-spined stickleback *Gasterosteus aculeatus* populations (Boughman 2001; Rafferty and Boughman 2006) and closely related species of mollies

Xiphophorus spp. (Hankison and Morris 2003). Likewise, simultaneous assessment of divergent plumage and song results in stronger premating isolation than assessment of only divergent plumage or song in closely related buntings (Baker and Baker 1990). Overall, however, few studies have explicitly tested the relative roles of divergent multimodal signals in conspecific recognition or premating reproductive isolation (Candolin 2003; Bro-Jørgensen 2009).

In avian studies, where the role of divergent mating signals in speciation has been addressed extensively (reviewed in Price 2007), the response to mounts or song playbacks by territorial males have been used as an indirect proxy of reproductive isolation (e.g. Ratcliffe and Grant 1985; Baker 1991; Irwin et al. 2001; Grant and Grant 2002a, b; Balakrishnan and Sorenson 2006; Seddon and Tobias 2007), especially if the experiment incorporates appropriate controls (e.g. ecologically similar, sympatric heterospecific stimuli). Therefore, assuming that male response is linked to female mating preferences, our field experiments in *Monarcha* flycatchers suggest that in one sister taxa comparison, assessment of divergent multimodal signals can result in a predictable temporal and spatial sequence of conspecific recognition—song is first assessed, then plumage colour. This pattern suggests the possibility that components of divergent multimodal signals may act in sequence as premating barriers, much like premating and postmating reproductive barriers also act sequentially (see Coyne and Orr 1989; Ramsey et al. 2003). Alternatively, divergent multimodal signals may be assessed simultaneously, with both signal modalities enforcing the information being conveyed (e.g. Hankison and Morris 2003). Both scenarios of sequential and simultaneous assessment of acoustic and visual signals suggest that multimodal signal divergence can lead to enhanced conspecific recognition or reproductive barriers, which may explain why premating reproductive isolation evolves more quickly than postmating isolation in birds (Price and Bouvier 2002). Additional studies explicitly testing the temporal and spatial scale of assessment of divergent multimodal signals across a wide range of taxa should shed light on how communication in multiple sensory modalities relates to speciation.

To complement empirical studies focused on divergent sister taxa, broad-scale comparative studies need to test the hypotheses that divergence in multimodal signals can promote speciation. Previous comparative studies indicate that proxies of intensity of sexual selection predict species diversity (Barraclough et al. 1995). However, in most of these studies, only a single modality is considered (e.g. plumage dichromatism). That is, taxa where multimodal signals are used should have more species than those that rely primarily on a single modality. Analogously, comparisons of hybrid zone dynamics should reveal that incipient species that come into secondary contact have lower incidences of

Table 4 Empirical studies that explore how multimodal signals are assessed

Taxon/taxa	Signal modalities	Assessment: sequential or simultaneous	Signal content	Type of data (observational, field experiment, lab experiment)	Reference
Birds					
Long-tailed manakin *Chiroxiphia linearis*	Song/courtship then visual	Sequential	Signal intensity shown to covary with female choice	Observational field study on wild animals	McDonald (1989)
Sage grouse	Acoustic then display rate	Sequential	Not indicated	Observational field study on wild animals	Gibson (1996)
Satin Bowerbird *Ptilonorhyncus violaceus*	Physical display (bower decoration) then male behavioural display intensity then bower	Sequential	Redundant signals of male quality: physical and behavioural displays are correlated	Combinations of observation and experiments in a field setting (e.g., male bowers were manipulated)	Borgia (1995), Patricelli et al. (2003), Coleman et al. (2004), Robson et al. (2005)
Reptiles, amphibians, fish					
Squirrel tree frog	Acoustic then visual	Sequential	Attractiveness to females	Phonotaxis and visual stimulus experiments in outside enclosures using field-caught individuals	Taylor et al. (2007)
Tungara frog *Physalaemus pustulosus*	Acoustic paired with visual signal (inflated vocal sac)	Simultaneous	Attractiveness to females	Experiments in the lab using field-caught individuals	Rosenthal et al. (2004), Taylor et al. (2008)
Sand goby *Pomatoschistus minutus*	Male body size and nest size	Simultaneous	Each cue separately does not predict mate choice but the simultaneous presentation of both does	Experiments in the lab using wild caught individuals	Lehtonen et al. (2007)
Stickleback	Olfactory then visual	Sequential	Olfactory cues used in location	behavioural trials in the lab using field-caught individuals	McLennan (2003)
European bitterling *Rhodeus sericeus*	Male behaviour and red colour then quality of oviposition site (mussel)	Sequential	Unclear as male traits do not indicate oviposition site quality in all cases	Courtship trials in the lab using field-caught individuals; oviposition site density experimental manipulated	Candolin and Reynolds (2001)
Foot-flagging frog *Staurois guttatus*	Acoustic signals then behaviour and visual signals (foot flags)	Sequential	Support of the alerting hypothesis: acoustic signals alert receiver to location of signaler for closer inspection of visual signals	Experimental study on wild animals (playback experiments)	Grafe and Wagner (2007)
Bornean rock frog *Staurois parvus*	Acoustic signals then behaviour and visual signals (foot flagging and foot flashing)	Sequential	Support of the alerting hypothesis: acoustic signals alert receiver to location of signaler for closer inspection of visual signals	Experimental study on wild animals (playback experiments)	Grafe et al. (2012)
Arthropods					
Wolf spider *Pardosa milvina*	Chemical then visual	Sequential then simultaneous	Chemical used in location, both chemical and visual used in assessment of whether females are virgin	Behavioural trials in the lab using field-caught individuals	Rypstra et al. (2009)
Wolf spider *Schizocosa stridulans*	Visual and seismic	Simultaneous	Seismic signals are necessary for copulation; visual signals may be used for detectability	Behavioural trials in the lab using field-caught individuals	Hebets and Papaj (2005), Hebets (2008)
House cricket *Acheta domesticus*	Acoustic then visual	Sequential	Both are signals which indicate body size; acoustic is a long distance transmission signal whereas visual signals are used in close proximity	Behavioural trials in the lab using field-caught individuals	Stoffer and Walker (2012)
False garden mantid *Pseudomantis albofimbriata*	Olfactory and visual	Simultaneous	Chemical cues used by males to locate females; visual cues used to assess fecundity	Behavioural trials in the lab using field-caught individuals	Barry et al. (2008)
Fruit fly *Drosophila melanogaster*	Acoustic and chemical	Simultaneous	Attractiveness to females	Experiments in the lab	Rybak et al. (2002)
Field cricket *Gryllus integer*	Long distance calls then close up chemical cues	Sequential	Multiple messages hypothesis supported	Observational study (behavioural trials) in the lab using field-caught individuals	Leonard and Hedrick (2010)

hybridisation if they have diverged in multimodal signals. That is, after controlling for other traits and factors that influence trait introgression (e.g. mating system, dispersal rate and distance, genetic distance), taxa that diverged in multimodal signals should have steeper clines than taxa that have diverged in only a single modality.

Future directions and conclusions

Variable ecological and social conditions can favour the evolution of (1) complex signals, (2) multicomponent signals of a single modality and/or (3) multimodal signals (Candolin 2003; Hebets and Papaj 2005; Bro-Jørgensen 2009) to insure that information is conveyed across a wide range of situations and conditions. Given selection favouring multicomponent signals, why then evolve multimodal, rather than unimodal signals?

One likely explanation is that most animals use multiple sensory modalities in daily, critical activities not related to mate choice or conspecific communication, such as foraging/hunting, navigating and escaping predators (Partan and Marler 2005). Most animals are therefore predisposed to communicate in multiple sensory modalities. In addition, although complex unimodal displays may effectively capture the attention of and attract receivers (e.g. Persons et al. 1999), stimulating multiple sensory modalities may better facilitate learning or the decision making process (Hebets and Uetz 1999; Hankison and Morris 2003; Kulahci et al. 2008; Uy et al. 2009b). For instance, bumblebees, *Bombus impatiens*, learn to find rewarding flowers faster when trained with multimodal (olfactory and visual) rather than unimodal (visual only) signals (Kulahci et al. 2008). Likewise, exposure to both visual and acoustic signals elicits a stronger response from female pigeons, *Columba livia*z, than either visual or acoustic signals presented in isolation (Partan et al. 2005).

Finally, a broad temporal and spatial scale of communication may favour the use of multiple sensory modalities. To some degree, complex signals of a single modality may be effective in sequential assessment at different spatial scales; however, larger scale communication may ultimately require multimodal signals, as each signalling modality will have different ranges and limits ("efficacy trade-off" in Hebets and Papaj 2005). For instance, in bowerbirds, components of multifaceted visual signals appear to have distinct functions: larger decorations away from bowers attract females to a male's bower, while smaller decorations on bowers are used to assess potential mates (Borgia 1995). However, these visual signals may not be effective for attracting females to the male's general area or territory, which may require signals that travel much further, such as advertisement calls (Tack et al. 2005). Likewise, in aquatic systems, visual signals may work well in close range, but, because visual signals attenuate

quickly in aquatic habitats, other sensory modalities, such as acoustic (Winn and Winn 1978) and olfactory (McLennan 2003) signals, may be more suitable for long-range communication. It remains possible, however, that a single signalling modality can be used across broad spatial and temporal scales, like in field crickets, *Teloegryllus oceanicus*, where acoustic signals are used for both long- and close-range communication (e.g. Zuk et al. 2008). Overall, because communication involves interactions between signalers and receivers in predictable spatial and temporal sequences, sequential assessment may favour the use of signals of multiple sensory modalities. To gain a better understanding of multimodal signal evolution, we therefore need studies that explore not only signal content but also how signals are assessed in natural conditions.

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