Sympatric black-headed and elegant trogons focus on different plumage characteristics for species recognition

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The ability of individuals to distinguish conspecifics from similar-looking congeners has important evolutionary consequences, yet few studies have determined which specific visual characteristics are used for species recognition, and whether closely related species use the same characteristics. In particular, sympatry with similar-looking congeners may influence which traits are important in species recognition. We presented elegant trogons, *Trogon elegans*, and black-headed trogons, *Trogon melano-cephalus*, with models that closely resembled conspecifics and models that differed in either the colour of the belly, the colour of the upperparts or the tail-barring pattern, while broadcasting species-specific songs. Elegant trogons showed significantly more aggression towards the conspecific and tail models, suggesting that belly and back colour, but not tail-barring pattern, are important for species recognition in this species. In contrast, the black-headed trogon approached all models very closely, except for the conspecific model. We interpret this counterintuitive behaviour as reluctance to approach an unknown conspecific, suggesting that all three plumage traits are important for species recognition in black-headed trogons. Because the elegant trogon is not sympatric with a similar-looking congener, we argue that they may lack the ability to discriminate fine-barring tail differences or overlook this trait. Sympatry with the similar-looking violaceous trogon may have influenced species recognition in black-headed trogons, favouring the use of all three plumage characteristics, including tail-banding patterns, which differ between these species. Alternatively, it is possible that incongruent stimuli are attended to differently, with elegant trogons focusing on the acoustic traits and black-headed trogons focusing on visual cues. Nevertheless, our study provides the first experimental evidence that specific plumage patches are used for species recognition and that closely related species may use different traits for species recognition. Our findings also suggest that the presence of a similar-looking congener can influence which traits are important in species recognition.

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The ability of individuals to discriminate between members of the same species and members of other closely related species has important evolutionary consequences (Ord & Stamps, 2009). Most animals defend territories against conspecifics to prevent the take-over of important ecological resources such as foraging and nesting sites (Maher & Lott, 1995) and nonecological resources such as mates (Schlicht, Valcu, & Kempenaers, 2015). These actions can incur large costs such as expending energy during displays (e.g. Brandt, 2003), time lost to other activities such as foraging (e.g. Barnett & Briskie, 2011) and possibly sustaining injuries during physical contests (e.g. Lombardo, 1986). When closely related species coexist, species-specific characteristics are assumed to allow accurate species recognition and prevent unnecessary interactions with heterospecifics (Andersson, 1994; Bradbury & Vehrencamp, 2011). Mistakes in species recognition can also lead to potential cross-species mating, which often produces offspring with reduced viability (Martin & Martin, 2001). Thus, the evolution of species recognition traits is important in the context of both male–male aggression and female mate choice.

Characteristics used to distinguish conspecifics from heterospecifics are varied and span all sensory modalities. Across taxa, acoustic traits (e.g. de Kort & ten Cate, 2001; Rollo & Higgs, 2008; Teufel, Hammerschmidt, & Fisher, 2007), olfactory traits (McLennan & Ryan, 1999; Nunes, Nascimento, Turatti, Lopes, & Zucchi, 2008; Rollmann, Houck, & Feldhoff, 2003; Shine, Reed, Shetty, Lemaster, & Mason, 2002) and visual traits (Couldridge & Alexander, 2002; Michaelidis, Demary, & Lewis, 2006; Ord &

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Stamps, 2009; Pearson & Rohwer, 2000) have all been implicated in species recognition. In a limited number of taxa, even electric discharges (Hopkins & Bass, 1981) and vibrations (Hill, 2008) are species specific. In birds, the ability to discriminate between traits of closely related species has usually been evaluated using vocal characteristics (Ord & Stamps, 2009). In *Streptopelia* doves, for example, species respond more aggressively towards vocalizations of their own species, and the degree to which they respond to the calls of congeners reflects their phylogenetic relationship (de Kort, den Hartog, & ten Cate, 2002; de Kort & ten Cate, 2001; den Hartog, de Kort, & ten Cate, 2007). While recent studies have shown that sympatry has an important influence on plumage divergence among closely related species (Martin, Montgomerie, & Lougheed, 2015), the plumage colours or patterns used in species recognition have rarely been studied (reviewed in: Ord, King, & Young, 2011; Ord & Stamps, 2009), with some notable exceptions. For example, Montagu's harriers, *Circus pygargus*, and hen harriers, *Circus cyaneus*, which are sympatric and only differ subtly in the colour of underparts and the upperwing, are less aggressive towards taxidermied models of heterospecifics than conspecifics (García, 2003). Blackcaps, *Sylvia atricapilla*, can also discriminate between their own species and taxidermied models of garden warblers, *Sylvia borin*, which differ in contour feather colour and the presence or absence, respectively, of a black crown (Matyjasiak, 2004). Furthermore, in an experiment involving taxidermied incipient *Monarcha* flycatchers, Uy, Moyle, and Filardi (2009) demonstrated increased aggressive responses with increased similarity in plumage. While the evidence thus far suggests that overall plumage patterns alone are sufficient for species recognition, no study to date has demonstrated the extent to which plumage patches must differ for proper species recognition to occur and whether closely related species assess the same traits. Furthermore, no study has directly manipulated plumage traits in model presentation experiments to exclude the possibility that other cues such as bill shape and size and body size could be used for species recognition. Because the divergence of secondary sexual characteristics is an important step in premating isolation (Price, 2007), insight into how species recognize members of their own species, and whether sympatry with a similar-looking congener is necessary for discrimination to evolve, is central to understanding the speciation process.

The avian genus *Trogon* comprises approximately 20 species distributed throughout Central and South America (Collar, 2001; Forshaw, 2009). Two or more species are often found in the same habitat, and up to six species coexist in some lowland areas. Given this high degree of sympatry, it is likely that species recognition traits, including visual characteristics, mediate interspecific interactions in this group. While trogons are known for their bright plumage colours, the distribution pattern of colours across species is highly conserved. Males of all species possess a red or yellow belly (orange in one subspecies and one race) and display iridescent upperparts that range in colour from copper–green to purple–blue. Patterns on the ventral surface of the large and conspicuous tail vary from completely white to completely black, to banded with thin and/or thick white-on-black bands. As such, these three plumage characteristics (belly colour, upperpart colour and tail-barring pattern) are potential candidates for species recognition traits in males of this genus. In this study, we experimentally tested in two species of trogons (1) which plumage characteristics are used in species recognition and (2) whether the presence of a similar-looking sympatric congener influences which traits are used in species recognition. We conducted our study on black-headed trogons, *Trogon melanocephalus*, and elegant trogons, *Trogon elegans* (Fig. 1). At our study site in Costa Rica, both of these species are sympatric with another congener, the violaceous trogon, *Trogon violaceus*. While the black-headed trogon looks very

similar to the violaceous trogon, the elegant trogon looks very different from the other two species. We presented our focal trogon species with conspecific models and modified models that differed in breast colour, upperpart colour or tail-barring pattern to assess which traits are important for species recognition in each species. We hypothesized that larger differences (i.e. belly and back colour) would be used more than more subtle plumage differences (i.e. tail barring) and that black-headed trogons would be more discriminating towards plumage differences compared to elegant trogons due to sympatry with a similar-looking congener.

METHODS

We conducted our experiment during the breeding season of all three trogon species, between May and July 2012, in the Guanacaste Conservation Area, Sector Santa Rosa, Costa Rica (10°40′N, 85°30′W). Our study site of nearly 10 km^2 is composed of secondary tropical dry deciduous forest, which has been regenerating since the 1980s, and older forest stands of evergreen species (Janzen, 1988).

The male elegant trogon displays green upperparts and a red belly (Fig. 1). Its tail pattern is a series of thick white bars interspersed by equidistant thin white and black bars (Pyle, 1997); no other bird in our study area shares similar characteristics (Stiles & Skutch, 1989). The male black-headed trogon displays a yellow breast and belly, a black head and blue–green to purple–blue upperparts. The ventral surface of its tail is solid white. The violaceous trogon is very similar in appearance to the black-headed trogon but its head is purple–blue, which often appears black from a distance. The tail-banding pattern of the violaceous trogon is very similar to that of the elegant trogon. The black-headed and violaceous trogons are not known to hybridize (McCarthy, 2006) or compete for nest sites, but they can be seen in the same trees foraging for fruit or insects, especially caterpillars, which both species feed to their young (Forshaw, 2009). Males can easily be distinguished from females by plumage in both focal species (Fig. 1).

Models

To determine which plumage characteristics might be used as species recognition traits by the two focal species, we presented individuals of each species with bird models that were as similar as possible to conspecifics and models that were different from conspecifics in either tail-banding pattern, upperpart colour or belly colour. Experiments that involve model presentations often rely on taxidermied specimens (e.g. Götmark, 1992, 1997; Uy et al., 2009). However, we preferred to produce realistic models from materials and feathers rather than risk damaging valuable museum specimens or collecting animals for the purpose of this experiment (Caro & Melville, 2012). Moreover, we have shown previously that elegant trogons respond as expected to predator and control models (Bitton & Doucet, 2014). We produced models that were as similar as possible to elegant and black-headed trogons ('Conspecific' models) and models that differed from these only in the back colour ('Back' model). In addition, we produced interchangeable plastrons and tails, which, when placed on the Conspecific model, allowed us to produce models that differed only in belly colour ('Belly' model), or tail-banding pattern ('Tail' model). We modified elegant trogon models so that they would look more similar to black-headed trogons. Back models were produced with blue upperparts, Belly models displayed yellow bellies and Tail models bore solid white undertails. Similarly, we modified black-headed trogon models so that they would look more similar to elegant trogons; Back models were produced with green upperparts, Belly models displayed red bellies and Tail models bore barred

Black-headed trogon   Violaceous trogon   Elegant trogon

Figure 1. Our experimental trials were conducted on the black-headed trogon (*T. melanocephalus*), which is similar to the violaceous trogon (*T. violaceus*) and the elegant trogon (*T. elegans*), which does not have a similar-looking congener in our study area. Artwork credit: John Sill.

undertails. One consequence of these modifications is that the black-headed trogon Tail models looked similar to violaceous trogons since they also have a barred tail. As a control, we constructed models resembling the squirrel cuckoo, *Piaya cayana* ('Control' model), a similarly sized species that does not prey on trogons and does not parasitize nests (Payne, 1997). This cuckoo is common in the study area and does not elicit aggressive responses from elegant trogons (Bitton & Doucet, 2014).

We used a plastic dove decoy similar in shape and size to the trogons as a base for all our models, and we glued feathers on top. We used a base layer of wind-sensitive downy feathers and covered these with pennaceous feathers to make the models realistic looking (for details on the importance of life-like models, see Němec et al., 2014). We used a similar technique to produce the belly plastrons using rigid fabric as a base. We placed Velcro® (Curacao, Netherlands Antilles) on the plastic dove models and on the plastrons and tails to facilitate the interchange of the modifications. For each of the two experimental subject species (elegant and black-headed trogons), we produced three Conspecific base models and three Back base models. In addition, we produced five red and five yellow belly plastrons, as well as three elegant trogon-type tails and three black-headed-type tails for each of the two back colours (i.e. 12 tails in all). Therefore, by combining the bases (three), plastrons (five) and tails (three), we could generate 45 'different' models for each treatment ($3 \times 5 \times 3$). This allowed us to use a unique stimulus for each trial to avoid simple pseudoreplication (Kroodsma, 1989; Kroodsma, Byers, Goodale, Johnson, & Liu, 2001). We also produced three squirrel cuckoo control models.

To ensure that the model feather colours matched those found on real trogons, we measured dyed feathers and real feathers using reflectance spectrometry and compared their colours using a tetrachromatic avian visual model. We first produced a library of coloured feathers by mixing commercially available fabric dyes (Rit©, Phoenix Brands LLC, Stamford, CT, U.S.A.). We objectively measured the reflective properties of the dyed feathers and those of real birds (three males of each species) obtained from museum specimens using an Ocean Optics USB 2000 spectrophotometer in conjunction with a PX-2 xenon light source (Ocean Optics, Dunedin, FL, U.S.A.). To measure the dyed feathers and the red and yellow belly trogon feathers, we used a bifurcated probe fitted with a rubber stopper at the tip. The stopper kept the probe at 5 mm from the feather surface and excluded the ambient light. To capture the iridescent nature of green and blue upper-back feathers of the trogons, we used two standard fibre-optic probes (instead of the

bifurcated probe) in conjunction with a goniometer, which permits measurements of specular and diffuse iridescence (Meadows, Morehouse, Rutowski, Douglas, & McGraw, 2011). For each of three green and three blue feathers, we collected reflectance measurements at 10° increments between near-normal incidence (85°) and 55°. We accomplished this by concurrently moving both the light source arm and the spectrophotometer arm of the goniometer to measure specular reflectance and by moving the spectrophotometer arm alone to capture diffuse reflectance. Reflectance measurements were all relative to that of a diffuse pure white standard (WS-1; Ocean Optics). For each colour, we chose the dyed feathers that best matched the real feathers (all measurements included) by selecting colours that were either included in or very near the three-dimensional volume created by the colours of the real trogons in tetrahedral colour space (all data presented in
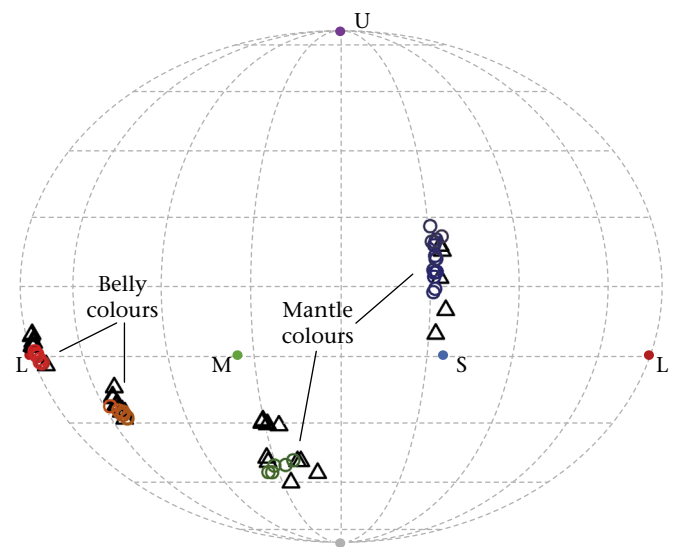

Figure 2. The hue of the dyed feathers (coloured circles) on the models closely matched the hue of museum specimens (black triangles) in avian colour space. Black-headed trogons have blue upperparts and yellow bellies, elegant trogons have green upperparts and red bellies. The Mollweide projection is a two-dimensional representation of the three-dimensional tetrahedral colour space. Colours of the open circles are approximations of the perceived hues generated from the spectral data. U, S, M and L denote ultraviolet-, short-, medium- and long-wavelength-sensitive photoreceptors, respectively, which are also each marked with a solid circle symbol.

Fig. 2). In the visual model, we used an ideal illuminant (pure white light) and the visual system of an average bird possessing a short-wavelength cone that peaks in the ultraviolet, as found in another species of trogon (Ödeen & Håstad, 2013). Therefore, we used photoreceptor peak sensitivity (λ_{max}) values of 367 nm, 444 nm, 501 nm and 564 nm for short-wavelength-sensitive (SWS1, SWS2), medium-wavelength-sensitive (MWS) and long-wavelength-sensitive (LWS) cones, respectively; for cone oil droplets, we set λ_o, the wavelength at which oil droplet transmittance is $1/e$, at 426 nm, 529 nm and 591 nm, and we set b, the transmission rate of decay, at 0.085/nm, 0.062/nm and 0.058/nm for clear (C-type), yellow (Y-type) and red (R-type) oil droplets, respectively. We used these idealized parameters because trogons are found at different heights in the forest canopy and in a variety of habitats where light and background conditions change substantially. The avian visual model values were generated using the 'pavo' package in R (Maia, Eliason, Bitton, Doucet, & Shawkey, 2013; R Development Core Team, 2014).

Field Experiment

For each focal species (elegant and black-headed trogon), we presented five types of models in an arbitrary order at each trial location: (1) a Conspecific model with correct back colour, belly colour and tail patterning; (2) a Belly model with a different belly colour (red for black-headed trogons and yellow for elegant trogons); (3) a Back model with a different back colour (copper–green for black-headed trogons and purple–blue for elegant trogons); (4) a Tail model with a different tail-barring pattern (barred for black-headed trogons and solid white for elegant trogons); and (5) a Control model of a squirrel cuckoo.

Trogon territory sizes at our study site are less than 100 m in radius (Bitton & Doucet, 2014), as in other parts of their range (Corcuera & Butterfield, 1999). To prevent testing the same individuals more than once with the same treatment, we separated trial locations by at least 200 m. Up to 10 different trials could be conducted at the same location (five treatments for each species), but some trial sites were used fewer times because birds could not be attracted to the models. We raised the models to 3 m near a natural perching branch using a camouflaged-painted tripod, below which a remotely controlled camouflaged loudspeaker (Scorpion X1-B, Foxpro, Lewistown, PA, U.S.A.) was hidden. We hid the models under camouflaging textile, which could be removed using a clear fishing line. The observer was also under camouflage, at least 10 m away from the model. After the initial set-up was complete, the observer waited 10 min before beginning the trial to avoid potentially influencing the behaviour of the experimental subjects. We attracted trogons to the area using playback of an adult male species-specific territorial vocalization obtained in a previous year (2011). The playback vocalization was that of a single individual unfamiliar to the test subjects (recorded outside of the study area) and consisted of a loop of the same 1 min vocalization bout. We broadcast playbacks a maximum of 10 min to attract a subject. Model presentation trials were either initiated as soon as a focal individual was in direct sight of the model feature of interest (i.e. subjects had to be able to see the tail in Tail model trials), or aborted if no bird approached within sight of the model after 10 min of playback. The playback vocalization continued throughout the trial for two main purposes: to maintain the attention of the focal individual and to simulate a territorial intrusion.

We initiated model presentation trials by removing the camouflaging textile from the model; trials always lasted 10 min in addition to the time needed to attract a focal subject, regardless of whether or not the experimental subjects remained within view of the model. We recorded behavioural observations with a small hand-held recorder (Edirol R-09, Roland, Japan) and supplemented our data by collecting measurements after the trial had ended. For each successful trial we recorded the distance between the observer and the model (in metres), the time until a bird was heard or sighted after initiating the playback (in seconds), the time between the start of the playback and the exposure of the model (in seconds), the perches used and at what time, and any kind of aggressive display. Elegant trogons, but not black-headed trogons, are known to perform tail raises as a signal of aggression in the presence of conspecifics (Bitton & Doucet, 2014). Therefore, aggressive displays included tail raises and flights at the model (displacement or attack attempts) for elegant trogon trials, but we did not detect tail raises by black-headed trogons and only recorded flights at the model in black-headed trogon trials. After the end of a trial, we measured the horizontal distance between perches to the nearest 10 cm using a measuring tape and estimated the height of the perch by eye to the nearest 0.5 m. We calculated the linear distances between the model and the perches based on those measurements for use in the analyses. To measure each focal subject's motivational state, we used the amount of time before the focal subject was heard or visually located in the immediate area ('first response') and the time to the beginning of a trial (focal subject in view of the model feature of interest). Trials in which birds could be heard calling before the start of the playback were excluded from analyses that included first response time as a factor. In addition to observations of tail raises and displacement attempts, we investigated the effects of model type on the distance of closest approach and the time at which birds reached this location (henceforth latency to closest approach).

We conducted successful trials of at least one model presentation at 49 different locations (average ± SE distance between locations = 270 ± 8 m; range 200–420 m). We initiated 427 trials, of which 200 were successful at attracting a trogon near enough to conduct a full trial. We conducted 99 trials with elegant trogons (Control: $n = 19$, Conspecific: $n = 20$, Tail: $n = 20$, Back: $n = 20$, Belly: $n = 20$) and 101 trials with black-headed trogons (Control: $n = 20$, Conspecific: $n = 20$, Tail: $n = 20$, Back: $n = 20$, Belly: $n = 21$). The average distance between the observer and the model did not differ between model types for the elegant trogon trials ($P = 0.99$) or the black-headed trogon trials ($P = 0.70$), or between trials conducted to each of the two species ($P = 0.66$). Moreover, the average distance between the model and the focal individual at the beginning of each trial did not differ between model types for the elegant trogon trials ($P = 0.43$) or the black-headed trogon trials ($P = 0.87$), or between trials conducted to each of the two species ($P = 0.58$).

Analyses

To best capture the aggressiveness of focal individuals when presented with models, we combined six behavioural measures using a principal component analysis. We included (1) the distance (in metres) to closest approach and (2) the latency to closest approach (in seconds) from the beginning of the trial. We also calculated (3) the distance travelled between the location of the bird when the trial started (perch 1) and the next perch it travelled to (perch 2) and (4) the time before it relocated (i.e. time at perch 1). We also calculated (5) the distance travelled between perch 1 and the perch of closest approach and (6) the amount of time needed to reach closest approach from the start of the trial. All measures were first log transformed to correct for non-normal distributions. The first component, PC1, explained 38.9% of the variation and was more heavily loaded by measures related to distance from model (Supplementary Table S1) such that lower PC1 scores represented

individuals that approached closer to the model by travelling longer distances from their original perch (spatial aggression). We interpreted lower PC1 values as more aggressive. The second component explained 33.2% of the variation and was more heavily loaded by measures related to speed of approach (Supplementary Table S1) such that lower PC2 scores represented individuals that approached quickly towards models (temporal aggression). We also interpreted lower values of PC2 as more aggressive.

To determine the influence of model type on our measures of aggression (PC1 and PC2), we used linear mixed models fitted by restricted maximum likelihood using the 'lmer' function from the package 'lme4' (Bates, Maechler, & Bolker, 2012; R Development Core Team, 2014), with model type, species and the interaction between the terms as fixed effects. Because we did not know the identity of the individuals in each trial, and because several trial sites were used for more than one experimental treatment, we included trial site as a random factor in our analyses. We estimated *P* values for the fixed effects by iteratively comparing the full model to one reduced by each factor using likelihood ratio tests, and we present the difference in deviance as a chi-square approximation with degrees of freedom associated with the change in number of parameters. Variance explained by the fixed effects (marginal R^2) and variance explained by the fixed effects and random variables (conditional R^2) were calculated following Nakagawa and Schielzeth (2013). Post hoc tests were conducted using the 'glht' function from the 'multicomp' package (Hothorn, Bretz, & Westfall, 2008). To understand the influence of model type on the number of tail raise displays and displacement attempts, we first conducted a 1×5 Fisher's exact test because the distribution of values did not meet the assumptions of standard contingency table analyses (see Results). This was followed by targeted contrasts of model types using 1×2 Fisher's exact tests. We adjusted the *P* values for multiple comparisons by controlling the false discovery rate, following methods by Benjamini and colleagues (Benjamini & Hochberg, 1995; Benjamini & Yekutieli, 2001). We present results ± SE and all data are available upon request.

RESULTS

There was a significant effect of the model type by species interaction on spatial aggression (PC1; LRT: $\chi^2_4 = 30.44$, $P < 0.001$; full model: marginal $R^2 = 0.20$; conditional $R^2 = 0.24$). To understand the interaction term, we fitted linear mixed models separately for each species (model type as a fixed effect and trial site as a random factor). There was a significant difference in spatial aggression values between model types during black-headed trogon trials (PC1; LRT: $\chi^2_4 = 24.25$, $P < 0.001$; full model: marginal $R^2 = 0.22$; conditional $R^2 = 0.29$). Post hoc Dunnett's tests revealed that experimental subjects were more aggressive towards the Control (estimate $= -1.36 \pm 0.35$, $z = -3.90$, $P < 0.001$), Back (estimate $= -1.62 \pm 0.35$, $z = -4.68$, $P < 0.001$), Belly (estimate $= -1.40 \pm 0.35$, $z = -4.05$, $P < 0.001$) and Tail (estimate $= -1.39 \pm 0.35$, $z = -4.04$, $P < 0.001$) models than they were towards the Conspecific model (Fig. 3). There was also a significant difference in spatial aggression values between model types during elegant trogon trials (PC1; LRT: $\chi^2_4 = 11.07$, $P = 0.026$; full model: marginal $R^2 = 0.11$; conditional $R^2 = 0.15$). Post hoc Dunnett's tests revealed that experimental subjects were more aggressive towards the Conspecific model than they were towards the Control (estimate $= 1.58 \pm 0.53$, $z = 3.01$, $P = 0.009$), Back (estimate $= 1.28 \pm 0.52$, $z = 2.46$, $P = 0.047$) and Belly models (estimate $= 1.53 \pm 0.52$, $z = 2.94$, $P < 0.012$), but not the Tail model (estimate $= 1.06 \pm 0.53$, $z = 1.99$, $P = 0.144$; Fig. 3). There were no effects of the interaction term (PC2; LRT: $\chi^2_4 = 1.94$, $P = 0.746$) on temporal aggression. Removing the interaction term did not
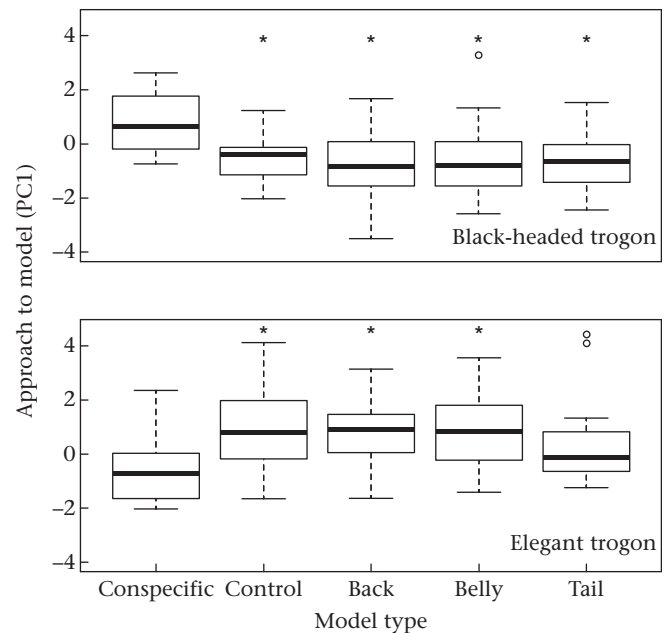

Figure 3. Approach to Conspecific, Control, Back, Belly and Tail models by black-headed and elegant trogons (see Methods for model descriptions). Lower PC1 scores indicate higher levels of spatial aggression (shorter distance of closest approach and longer distance travelled to approach the model). Boxes show median (50th percentile) and interquartile range (25th to 75th percentile); whiskers indicate the 95% confidence intervals; open circles are data points that fell outside the 95% confidence range. Asterisks indicate model types that differed statistically ($P < 0.05$) from the Conspecific model.

improve the model (PC2; LRT: species: $\chi^2_1 = 0.499$, $P = 0.48$; model type: $\chi^2_4 = 6.52$, $P = 0.16$; full model: marginal $R^2 = 0.04$; conditional $R^2 = 0.04$).

We detected aggressive displays in 19 elegant trogon trials: 15 trials with at least one tail-raising display. In four trials, all when presenting the Tail model, we observed at least one flight at the model. Aggressive displays were not equally distributed across all model types (Fisher's exact test: $P < 0.001$, Fig. 4). Control models did not elicit any displays, the Belly and Back models each elicited aggressive displays in one trial, the Conspecific model elicited displays in seven trials and the Tail model elicited aggressive displays in 10 trials. Fisher's exact tests (1×2) revealed that the Conspecific and Tail models elicited aggressive displays in more trials than almost all other model types (Table 1). After correcting for multiple comparisons, aggressive displays were significantly more common in trials with Conspecific models than in trials with Control models, marginally more common in Conspecific trials than in Back and Belly trials, but no different when compared to Tail model trials. In addition, aggressive displays were significantly more common in Tail model trials than in Control, Back and Belly trials. We did not detect any aggressive displays in black-headed trogon trials.

DISCUSSION

In this study, we used a model presentation experiment to investigate the plumage characteristics used for species recognition in two coexisting species of trogons: the elegant trogon, which is not sympatric with a similar-looking congener, and the black-headed trogon, which is sympatric with the similar-looking violaceous trogon. Elegant trogons displayed significantly more aggressive behaviours towards the Conspecific model and towards the model with a modified tail (Tail model), but they behaved less
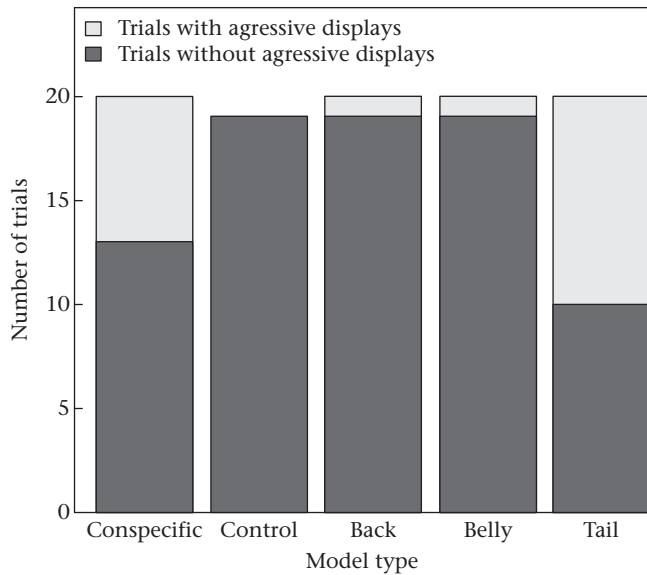
Figure 4. Relative frequency of aggressive displays by elegant trogons when presented with Conspecific, Control, Back, Belly and Tail models (see Methods for model descriptions).

Table 1
Comparison of aggressive displays performed by elegant trogons when presented with Conspecific, Tail, Control, Belly and Back models

Model comparison	Odds ratio	95% CI	P
Conspecific vs Control	**0.00**	**0.00−0.59**	**0.024**
Conspecific vs Belly or Back	0.10	0.00−0.96	0.066
Conspecific vs Tail	0.55	0.12−2.27	0.52
Tail vs Control	**0.00**	**0.00−0.31**	**<0.001**
Tail vs Belly or Back	**0.06**	**0.00−0.50**	**0.005**

See Methods for model descriptions. Values are from Fisher's exact tests. *P* values are corrected for false discovery rates. Significant outcomes are shown in bold.

aggressively towards the models with modified back or belly colours (Back or Belly model). Furthermore, elegant trogons approached the Conspecific model and the Tail model more closely than the Belly and Back models. These findings suggest that Conspecific models and Tail models were both recognized as conspecifics, whereas the other models were not, indicating that back and belly colour, but not tail-barring pattern, may be important for species recognition in elegant trogons. In contrast, the black-headed trogon approached within a very short distance of all models except the Conspecific model. Thus, black-headed trogons clearly distinguished between Conspecific models and all other model types, but maintained their distance from this conspecific intruder. Although this behaviour may seem counterintuitive, reluctance to approach or even retreating from aggressive conspecific intruders has been shown in several song playback studies (e.g. de Kort, Eldermire, Cramer, & Vehrencamp, 2009; Illes, Hall, & Vehrencamp, 2006; Mennill & Ratcliffe, 2004). Black-headed trogons are monogamous and territorial, but they are known to frequently interact with conspecifics (Riehl, 2008). They sometimes aggregate in small to medium-sized groups and forage and/or visit potential nesting sites together. While in groups, both males and females take flight at other individuals (Riehl, 2008), but natural observations of interactions between individuals that encounter each other for the first time are lacking. It is possible that aggressive encounters are more common among individuals that have knowledge of one another and for which a hierarchy has been previously established, which would reduce aggressive interactions

towards unknown individuals (e.g. Müller & Manser, 2007). In addition, it is likely that black-headed trogons approached closer to models perceived as heterospecifics because they were looking for the source of the vocalization (species specific) but did not recognize the non-Conspecific models as the signaller. Closer approaches could then be interpreted as curiosity rather than aggression. Nevertheless, our findings suggest that black-headed trogons may use back colour, belly colour and tail-barring pattern in species recognition. Overall, our results demonstrate that trogons use specific plumage patches as species recognition traits, but they suggest that these two coexisting species may use different cues for species recognition and that their sensitivity to different traits may be influenced by the presence or absence of sympatry with a similar-looking congener.

Both elegant and black-headed trogons distinguished between conspecific models and models that differed in either the back or belly colour. These results are not unexpected considering that the differences between the Conspecific and Back/Belly models were large patches that differed in coloration. Much smaller differences in plumage traits have been shown to be sufficient for species recognition (Matyjasiak, 2004) and individual recognition (Godard, 1991). However, elegant trogons were more aggressive towards Conspecific and Tail models than they were towards other model types, whereas black-headed trogons behaved differently towards Conspecific models and all other model types.

Together, our results imply that elegant and black-headed trogons may not use exactly the same species recognition characteristics, but, because we used species-specific playbacks to attract subjects to our trial sites and maintain their interest in the models, we have to consider that focal individuals were faced with incongruent acoustic and visual stimuli (except during Conspecific model trials). When presented with multimodal stimuli, different species attend to these signals differently. In birds and most terrestrial species, multimodal signals are evaluated sequentially such that acoustic traits are used at a distance and visual characteristics are used at closer range (reviewed in Uy & Safran, 2013), but some species assess multimodal information simultaneously. Our main findings suggest that black-headed trogons are potentially more discriminant towards visual cues than black-headed trogons. However, it is possible that these two species differentially weigh the simultaneous information obtained from acoustic and visual stimuli. Playback recordings may drive elegant trogons to dismiss small differences in plumage even if the discrepancies are recognized, while weaker attention to the playback by the black-headed trogon could allow them to attend more strongly to the visual signals. An experiment specifically designed to test the strength of simultaneous multimodal signals in these two species could be conducted to assess the relative importance of visual versus acoustic species recognition traits. Nevertheless, our results do suggest the use of specific visual species recognition traits, and that the presence of a similar-looking sympatric congener may influence the use of species identity cues. Social learning and differential discrimination abilities at the population level could explain our results.

The ability to recognize conspecifics from heterospecifics has been demonstrated to result from social learning of songs (Catchpole & Slater, 2003) and plumage characteristics (Hansen & Slagsvold, 2003) in a number of species. While song and plumage recognition are often acquired through imprinting in nestlings, evidence shows that regular interactions with heterospecifics that use similar resources can lead to recognition of heterospecifics at later stages in life (e.g. Catchpole, 1978; Grether, Losin, Anderson, & Okamoto, 2009). This has been demonstrated in black redstarts, *Phoenicurus ochruros*, for example, where individuals are aggressive towards playbacks of common redstarts, *Phoenicurus phoenicurus*,

in areas of sympatry but not in areas of allopatry (Sedláček, Cikánová, & Fuchs, 2006). The black-headed trogons at our study site regularly come in contact with violaceous trogons, providing ample opportunities to learn the differences in tail-barring patterns between conspecifics and heterospecifics. In contrast, elegant trogons at our study site, which have bright red bellies, are only sympatric with yellow-bellied trogons and would not need to assess tail-barring patterns to recognize conspecifics. The ability of black-headed trogons to recognize violaceous trogons may be local (i.e. population level); an experiment with black-headed trogons in an area where they are not sympatric with violaceous trogons could determine whether learning plays a role in heterospecific recognition. Similarly, an experiment with elegant trogons in an area where they are sympatric with a similar-looking congener could yield important insights about the role of learning in species recognition.

Differences in species recognition between elegant and black-headed trogons could arise from each species focusing on particular traits, but it could possibly also arise from differences in their discrimination ability. Indeed, the costs of incorrect species discrimination are expected to exert strong selective pressure for accurate transmission on the part of the signaller, but also on the perceptive ability of the receiver (Tobias & Seddon, 2009). For example, playback experiments in closely related Thamnophilidea antbirds with convergent songs demonstrated that females are able to distinguish between conspecifics and heterospecifics and recognize mates from strangers, even when songs are extremely stereotyped (Seddon & Tobias, 2010). This ability to discriminate among conspecifics is not present in males (Tobias & Seddon, 2009), demonstrating that even within species the perceptive abilities of the receiver can differ and are potentially influenced by the differential cost of species misidentification within and among species. Females misidentifying heterospecific males would incur much larger costs, by producing potentially unfit hybrids, while males may incur costs associated with wasted time, misdirected aggression and risk of physical injury (Seddon & Tobias, 2010; Tobias & Seddon, 2009). In areas where similar-looking congeners occur, it is therefore possible that the perceptual abilities of individuals are fine-tuned to small differences in trait differences.

Several mechanisms, in different contexts, could promote the evolution of fine discriminating abilities. For example, sympatric, closely related species in which hybrid matings sometimes occur would be expected to recognize heterospecifics within the sympatric area, but not necessarily in the adjoining allopatric zones. The increased ability to recognize a heterospecific would evolve as part of a multifaceted reinforcement mechanism, favour assortative mating, and thus decrease the opportunity for hybridization (Coyne & Orr, 2004). Similarly, incipient species would be expected to have better heterospecific discriminating ability than fully established species, especially in cases where speciation is driven by slight changes in the ecological niche of the diverging populations (Price, 2007); failure to discriminate between diverging groups could lead to a collapse of the species pair through indiscriminate hybridization (e.g. Behm, Ives, & Boughman, 2010). Finally, as in our study, it is possible that species with sympatric similar-looking congeners would have better discrimination abilities than species without sympatric, closely related congeners, even in the absence of hybridization. Since the cost of misidentification would be relatively low in this context, the precision of species recognition might be weaker than in the situations explored above, and might not evolve as a mechanism of reinforcement following secondary contact but, rather, might evolve in the context of competitor recognition. Even in the absence of competition for resources, individuals can avoid the cost of aggressive interactions by recognizing noncompetitive heterospecifics (Anderson & Grether, 2009, 2010). Because divergence in traits can occur through agonistic character displacement (Grether et al., 2009; Okamoto & Grether, 2013), perhaps interspecific interference competition could also lead to an increase in perceptual abilities that facilitate species recognition.

The elegant trogon subjects in our experiment showed the same level of aggression towards the Conspecific model and the Tail model. Even if individuals have the capacity to discriminate between different traits, it is still possible that they did not attend to these differences for two reasons. First, when species rely on several sources of information, such as multiple coloured plumage patches, individuals may not notice smaller differences when initiating a response (Hankinson & Morris, 2003). However, the aggressive behaviours of elegant trogons towards the models always came after a relatively long period of visual assessment. In fact, the earliest display of aggression occurred after over a minute of close-range evaluation, sufficient time to evaluate the differences in characteristics between the model and conspecifics. The hypothesis that elegant trogons do not assess differences in tail-barring patterns because they do not notice smaller details should be tested by presenting a range of tail-barring differences. Presenting models with a gradient of differences in belly and back colour would also help to assess whether small differences are neglected only in the tail or in other plumage characteristics as well. Second, individuals would not react towards a modified signal if their response potentially incurred greater costs (such as reciprocal aggression) than not responding (Bradbury & Vehrencamp, 2011). We consider this explanation improbable in the context of our experiment because a large majority of the aggressive displays consisted of tail raises, which are low cost because they are not energetically demanding, and, most importantly, do not risk injuring the individual. Therefore, our results suggest that elegant trogons either dismissed differences in tail barring, or did not have the ability to distinguish between the Conspecific model and the Tail model.

Our study revealed that two coexisting trogons may use different plumage traits for species recognition, and provides evidence that the presence of a similar-looking congener can influence the use of visual species recognition characteristics. The lack of discrimination between potential species recognition characteristics, as we found in elegant trogons, could result from simply ignoring those differences or from inferior discrimination ability. Our findings also suggest that learning may play a role in species recognition, since both of our focal species are sympatric with similar-looking congeners in some parts of their range but not in others. Experiments conducted in different populations, with different sympatric species present, would help elucidate the exact mechanisms responsible for our results. Nevertheless, this study provides strong experimental evidence of species recognition based on specific (and different) plumage patches in two sympatric congeners, and it is the first to demonstrate that the presence or absence of a similar-looking congener appears to influence which visual traits are used for species recognition. Because the evolution of divergent sexually selected traits and their assessment by conspecifics promotes premating isolation and speciation, our study demonstrates the importance of sympatry on these processes.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2016.03.035.

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