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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 melanocephalus*, 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.

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 takeover 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