



Original Article

A multifunctional visual display in elegant trogons targets conspecifics and heterospecifics

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Avian visual displays often target either conspecifics or heterospecifics, but few visual displays have been described where both conspecifics and heterospecifics are the intended receivers. In this study, combining observational and experimental approaches, we present evidence that a tail-raising display performed by the elegant trogon (*Trogon elegans*) is used in multiple contexts and is directed at conspecifics and heterospecifics. We observed tail-raising displays toward conspecifics in both intersexual and intra-sexual contexts, as well as toward heterospecifics. Displays performed toward heterospecifics were directed at humans, monkeys, or birds of prey, all of which could have been perceived as potential predators. We experimentally tested the possible functions of tail-raising behavior in the presence of a predator by presenting elegant trogons with models of a natural predator and a nonthreatening control. Tail-raising displays were much more likely to occur when trogons were in the presence of a predator model (48% of trials) than a control model (6% of trials). The presence of conspecifics did not influence tail-raising propensity (conspecifics present: 44% of trials and conspecifics absent: 50% of trials). Our results suggest that tail raising in trogons is a multifunctional visual display that may function as an intersexual and intrasexual conspecific signal as well as a pursuit-deterrent signal directed at predators.

Key words: communication, courtship, display, elegant trogon, pursuit deterrent, territorial, visual.

INTRODUCTION

Visual displays in animals can take many different forms and are often directed at specific receivers. In the presence of other males during agonistic encounters, for example, cuttlefish display specific body patterns (Adamo and Hanlon 1996), hermit crabs wave enlarged chelipeds (Arnott and Elwood 2010), and many birds perform ritualized threat displays (Hurd and Enquist 2001). These displays can prevent the escalation of aggression between individuals and reduce the probability of harmful interactions. In the presence of females during mate attraction and courtship, male fireflies use bioluminescent flashes (Branham and Wenzel 2003; Lewis and Cratsley 2008), anoles bob their heads while presenting an extended colorful dewlap (Tokarz 1995), and many birds perform stereotyped dances (Gill 2007). In many species, the same displays can be used in both intrasexual and intersexual contexts. For example, male ruby-crowned kinglets (*Regulus calendula*) will raise their conspicuous red crest when confronting territorial intruders or when displaying to a female during courtship (Martens and Päckert 2006).

Not all visual displays are directed toward conspecifics; a number of behaviors appear to be targeted at heterospecifics. In birds, for example, the turquoise-browed motmot (*Eumomota superciliosa*) wags its tail from side to side in the presence of potential predators, a behavior identified as a pursuit-deterrent signal (Murphy 2006, 2007). This display warns potential predators that they have been detected and that a capture attempt would be unprofitable. The sunbittern (*Eurypyga helias*) also displays toward heterospecifics. It spreads out its wings, exposing large “eyespot,” to scare away predators or individuals of other species with which they compete for food resources (Frith 1978). The tail wagging in the turquoise-browed motmot and wing spreading of the sunbittern are used in the presence of heterospecifics but do not seem to be used for signaling to conspecifics. In fact, relatively few visual displays have been adequately demonstrated to serve in both intraspecific and interspecific contexts, especially in birds (Table 1). One exception is the crest raising display of the royal flycatcher (*Onychorhynchus coronatus*). In this species, males and females raise their crests during courtship, during aggressive intrasexual encounters, and when confronting heterospecifics near their nests (Rievey 2010).

Elegant trogons (*Trogon elegans*) perform a conspicuous visual display whereby the tail is rapidly lifted above the horizontal and

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returned to its normal vertical position in a slow, controlled manner. When performing this display, birds can usually be heard producing a clucking sound (described in Taylor 1994). When positioned with their green back facing the observer, elegant trogons appear generally inconspicuous against the background vegetation; this display increases an individual's detectability because of the movement involved and because it exposes the bright red belly and undertail coverts. This behavioral display has been mentioned twice in the literature. Cully (1986) was the first to note that

elegant trogons produced this display in the presence of a live, tethered, great horned-owl (*Bubo virginianus*) near their nest, and Hall and Karubian (1996) described this behavior in the context of a mating display. The production of tail-raising displays in the presence of heterospecifics and conspecifics raises questions regarding the general function of this display and the evolution of multifunctional displays in general. The first objective of our study was to characterize the contexts in which elegant trogons perform tail-raising displays. For this purpose, we conducted behavioral observations of

Table 1
Summary of evidence for visual pursuit-deterrence behaviors in vertebrate animals

Species	Behavior	Type and strength of evidence for pursuit-deterrence function	References	Context of conspecific signaling	References
Birds					
<i>Eumomota superciliosa</i>	Tail wag	Experimental; excluded other possible functions	Murphy 2006, 2007	No evidence	Murphy 2006, 2007
<i>Gallinula chloropus</i>	Tail raise	Observational and experimental; conspecific signaling not excluded	Alvarez 1993, Randler 2007	Intrasexual and intersexual	Bannor and Kiviat 2002
<i>Motacilla alba</i>	Tail wagging	Observational; conspecific signaling not excluded	Randler 2006	No evidence	Randler 2006
<i>Porphyrio porphyrio</i>	Tail raise	Observational; conspecific signaling not excluded	Alvarez 1993, Woodland et al. 1980	Intrasexual and intersexual	West and Hess 2002
<i>Sayornis nigricans</i>	Tail pump	Observational; conspecific signaling not excluded	Avellis 2011	No Evidence	Wolf 1997
Lizards					
<i>Anolis cristatellus</i>	Push-up; dewlapping	Experimental; excluded other possible functions	Leal and Rodriguez-Robles 1997, Leal 1999	Intrasexual and intersexual	Losos 2009
<i>Anolis sagrei</i>	Dewlapping	Observational; conspecific signaling not excluded	Vanhooydonck et al. 2009	Intrasexual and intersexual	Vanhooydonck et al. 2009
<i>Callisaurus draconoides</i>	Tail waving	Experimental; excluded other possible functions	Hasson et al. 1989, Cooper 2010a, 2010b, 2011a, 2011b, Eifler and Eifler 2010	Intrasexual and intersexual	(Clark 1965)
<i>Carlia jarnoldae</i>	Tail display	Observational; conspecific signaling not excluded	Langkilde et al. 2004	Intrasexual and intersexual	Langkilde et al. 2004
<i>Cnemidophorus murinus</i>	Arm waving	Experimental; excluded other possible functions	Cooper et al. 2004	No evidence	Magnusson 1996
<i>Cophosaurus texanus</i>	Tail raising	Experimental; excluded other possible functions	Dial 1986	No evidence	Clark 1965, Dial 1986
<i>Holbrookia propinqua</i>	Tail raising	Experimental; excluded other possible functions	Dial 1986	Intraspecific and Interspecific	Clark 1965
<i>Gonatodes albogularis</i>	Tail wave	Experimental; conspecific signaling not excluded	Alonso et al. 2010	No evidence	Alonso et al. 2010
<i>Leiocephalus carinatus</i>	Tail curling	Observational; excludes other possible functions	Cooper 2001, 2007	Intrasexual and intersexual	Cooper 2001, 2007
<i>Ophurus cuvieri</i>	Push-up; dewlapping	Experimental; conspecific signaling not excluded	Ito and Mori 2012	Intrasexual and Intersexual	Randriamahazo and Mori 1999
<i>Podarcis muralis</i>	Foot shaking (type 3)	Experimental; conspecific signaling not excluded	Font et al. 2012	No evidence (types 1 and 2 signal conspecifics)	Font et al. 2012
Mammals					
<i>Alcelaphusb uselaphus</i>	Stotting; leaping	Experimental; conspecific signaling not excluded	Caro 1994	No evidence	Caro 1994
<i>Aepycerosm elampus</i>	Stotting; leaping	Experimental; conspecific signaling not excluded	Caro 1994	No evidence	Caro 1994
<i>Connochaetesta urinus</i>	Stotting; leaping	Experimental; conspecific signaling not excluded	Caro 1994	No evidence	Caro 1994
<i>Damaliscus korrigum</i>	Stotting; leaping	Experimental; conspecific signaling not excluded	Caro 1994	No evidence	Caro 1994
<i>Eudorcas thomsonii</i>	Stotting; leaping	Experimental; conspecific signaling not excluded	Caro 1994	No evidence	Caro 1994
<i>Gazella granti</i>	Stotting; leaping	Experimental; conspecific signaling not excluded	Caro 1994	No evidence	Caro 1994
<i>Odocoileus virginianus</i>	Tail raise	Experimental; conspecific signaling not excluded	Bildstein 1983, Caro et al. 1995	No evidence	Bildstein 1983, Caro et al. 1995

free living birds. The second objective of our study was to determine the function of tail raising in the presence of heterospecifics. For this purpose, we conducted an experiment testing the predictions of 3 competing hypotheses.

The conspecific warning signal hypothesis was developed in the kin selection framework (Maynard Smith 1965; Sherman 1977) and presumes that displays in the presence of a potential predator are directed at related individuals (kin). The display is designed to inform individuals that have not yet detected the predator of the potential threat. A specific prediction of this hypothesis is that birds should not display in the presence of a potential threat if conspecifics, specifically kin, are not in visual range of the individual producing the displays.

The self-preservation alarm signal hypothesis states that signals target conspecifics with the intent to trigger a reaction to deter or reduce the chance of a predator being successful by mobbing or confusing the predator (Sherman 1985). A specific prediction of this hypothesis is that on detecting a predator and after a display, conspecifics should approach the individual displaying (to form a larger and threatening group), mob the predator, or scurry in all directions to confuse the predator.

The pursuit-deterrence hypothesis states that signals in the presence of predators target the potential predator, not conspecifics, and informs that predator it has been detected and an attempt at capture would be unprofitable (Woodland et al. 1980; Caro 2005). A specific prediction of this hypothesis is that individuals should display in the presence of potential predators regardless of the presence or absence of kin within visual range.

METHODS

The elegant trogon is a member of the Trogoniformes and ranges from the southern United States to northern Costa Rica (Collar 2001; Forshaw 2009). The species is sexually dimorphic: males have bright iridescent green upperparts, whereas females have coffee-brown upperparts. Females display white feathers on their breast and faded red feathers on their undertail coverts; males display brightly colored red feathers on their breast and undertail coverts. Immature males, which exhibit delayed plumage maturation, have patchy brown and red breast feathers (Kunzmann et al. 1998). They can be easily discriminated from mature males for more than 1 year after fledging. Differences between immature females and adult females are more subtle, but the two can be discriminated by tail feather wear: immature females leave the nest with well-frayed feathers, which are first molted at least a year after fledging (personal observation). Furthermore, immature females have a white tip on the tertials, which is lacking in older females (Pyle 1997). Both the male and female contribute to modifying nest cavities by taking turns to enlarge the opening. Males and females share responsibilities when incubating the eggs and feeding the nestlings (Kunzmann et al. 1998).

We conducted our research in Sector Santa Rosa, Guanacaste Conservation Area, Costa Rica (10°40'N, 85°30'W). Our study site of nearly 9 km² is characterized by a mix of secondary dry deciduous forest, which has been in a regeneration state since the 1980s, and older forest stands of evergreen tree species (Janzen 1988). Elegant trogon breeding density at this location is high; surveys during 2010 and 2011 estimated 20–30 breeding pairs per square kilometer across the entire study area.

Observation of natural tail-raising occurrences

We recorded observations of trogons raising their tails during two 2.5-month periods: 18 April to 28 June 2010 and 30 April to 12

July 2011. Trogon observations were conducted in 3 different contexts: 1) opportunistically during trail surveys, 2) when following individuals located on a previous day to document their behaviors and find their nests, and 3) during focal nest watches. We estimate that approximately 300 h were dedicated to observing elegant trogons to quantify tail-raising behaviors in 2010, and 150 h in 2011. Nest initiation and the start of the breeding season in Santa Rosa is triggered by the arrival of the seasonal rains, which usually start early to mid-May. Therefore, in both field seasons, we collected behavioral data both before and during the breeding season.

When tail-raising behaviors were observed, we noted the sex and age (immature or adult) of the individual raising its tail and of any conspecifics in the area. Individuals were considered in the area when they could be seen or heard within visual range of the displaying individual. We noted the location of each observation to the nearest 5 m by GPS and locations were georeferenced on ArcGIS (ESRI 2013). We inferred the context of the display based on the interactions of the individuals and species present. The elegant trogons in our population are not banded; therefore, we could not determine the exact identity of individuals we observed displaying. However, based on local breeding density and time spent following individuals on foraging bouts, we estimated that territory size extend 100 m from the nest site at most. Therefore, we considered any locations separated by more than 200 m of each other to be observations of different individuals. On several occasions, we observed trogons raising their tails when we, the observers, were most likely the cause of the behavioral displays. This most often occurred when flushing an unsuspecting bird, immediately triggering a tail-raising response. On other occasions, we were certain that the displaying individuals were unaware of our presence because 1) we first heard the trogons displaying and crept-up to observe the displays without the birds ever looking in our direction or 2) we observed the display when conducting nest watches under camouflaging textile from at least 20 m away. None of the tail-raising responses reported here were triggered on purpose by approaching birds or by making our presence obvious.

To avoid including the same individual in the same group context more than once in our analyses, we randomly selected a single observation in each year from those made in any given area (separated by at least 200 m). Although an individual from a specific location could have been included twice (from 2 different years) in our observations, the group context would always have been different.

Model presentation experiment

We conducted our experiment between 1 May and 15 July 2011. To simulate the presence of a potential aerial predator, we fabricated models closely resembling the collared forest falcon (*Micrastur semitorquatus*; Figure 1A,B). This species is known to consume trogons on occasions (Sandoval L, personal communication) and regularly consumes birds of similar size (Thorstrom 2000). As a nonthreatening avian control, we fabricated models closely resembling the squirrel cuckoo (*Piaya cayana*; Figure 1C,D). This species is an appropriate control to the collared forest falcon for the following 3 reasons: 1) it is very similar in total length (forest falcon 51–57 cm; cuckoo 45–50 cm), 2) it has a long narrow tail, and 3) it often perches relatively upright. Therefore, the general silhouette of the squirrel cuckoo is similar to that of the collared forest falcon. The squirrel cuckoo is not a parasitic species and its main diet is similar to that of trogons and does not include any birds (Payne 1997). Both the forest falcon and cuckoo are common in Sector Santa Rosa.

Experimental designs that involve model presentation often rely on stuffed specimens (Götmark 1992, 1997). However, we elected to produce realistic looking models from craft materials rather than risk damaging valuable museum specimens, or collecting animals for the purpose of this experiment (Caro and Melville 2012). We constructed our collared forest falcon model (Figure 1A) using peregrine falcon (*Falco peregrinus*) polyresin decoys to which we glued 2 layers of commercially available black and white feathers in the color patterns found on the forest falcon (Figure 1B). The first layer consisted of downy material and produced a lofty, wind-sensitive layer. The second layer consisted of contour feathers that were positioned on the model to reflect the natural arrangement of feathers on live birds. The long tail was produced with commercially available black turkey (*Meleagris gallopavo*) feathers, which were modified and arranged to match the shape and size of live forest falcons. We constructed our squirrel cuckoo models (Figure 1C) using generic dove plastic

decoys to which we glued 2 layers of custom-dyed feathers (Rit[®]) to match the patterns found in the live birds (Figure 1D). Two layers of feathers were applied to the decoys to give them a realistic feel and appearance. We produced 2 predator models and 2 control models.

Forty trial locations were selected from candidate sites at which individuals or groups of trogons had previously been observed, and all trials were separated by at least 200 m. The sites selected were forested (i.e., no trials in open areas), had relatively good visibility (15 m in each direction), and did not include natural (e.g., river) or artificial (e.g., trail) features within 15 m of the model, which could have influenced the behavior of the birds near the model. For all trials, the model was positioned at the top of a 3-m tall metal pole camouflaged with paint to resemble the background, near a realistic perch site. At the beginning of each session, the model was covered by camouflage textile tied to a clear fishing line. A loud speaker was hidden at the base of the pole. The observer, also hidden under camouflage textile, was located at least 10 m away from the model, sometimes up to 18 m away. After setup, the observer waited 10 min under camouflage before starting the trials to avoid influencing the behavior of the trial subjects. Trogon subjects were drawn to the trial location using playback of an adult male call recorded the previous year (2010) outside of the area in which this experiment was conducted. Individual recognition based on call characteristics has not been demonstrated in this species. However, variation among individuals is distinguishable to the human ear, and using a call recorded outside the study area was meant to exclude the possibility that the call could be recognized as kin by any of the subject individuals. Playback of the trogon call was used for a maximum of 6 min to attract individuals. If an individual did not show up during that time period, the trial was aborted.

Once a subject individual(s) arrived within visual range of the model (usually within 12 m), the camouflage was removed by drawing the line and a second playback was concurrently initiated to replace the trogon calls. The playback consisted of a series of calls characteristics of the model species being displayed. The recordings were 6 min long and consisted of 1 min of calls followed by 1 min of silence, 3 times in a row. Trials always lasted 6 min even if the subject birds had left the area. Two versions of the recording were used for the predator model and 2 versions of the recording were used for the control model so that trial subjects were presented with 1 of 4 possible combinations of model and playback.

For each successful trial, we recorded the following observations: 1) date, time, and location (georeferencing coordinates) of the trial site; 2) composition of the trial subjects (number of individuals, sex, and age); 3) perches used by the birds; 4) time at which perch changes occurred; 5) number of tail-raising displays at each perch; and 6) whether the model was attacked or harassed by the target individual or any other bird. A trial was considered successful if at least 1 bird remained within visual range of the model for at least 2 min. The actual distance between the perches used and the model was determined with a measuring tape (to the nearest 0.25 m) and the perch heights were estimated (to the nearest 0.5 m). Reported distances are the linear distance between the model and the perches. Conspecifics were considered to be in the area if they could be visually detected but also if they could be heard within 20 m of the model's location.

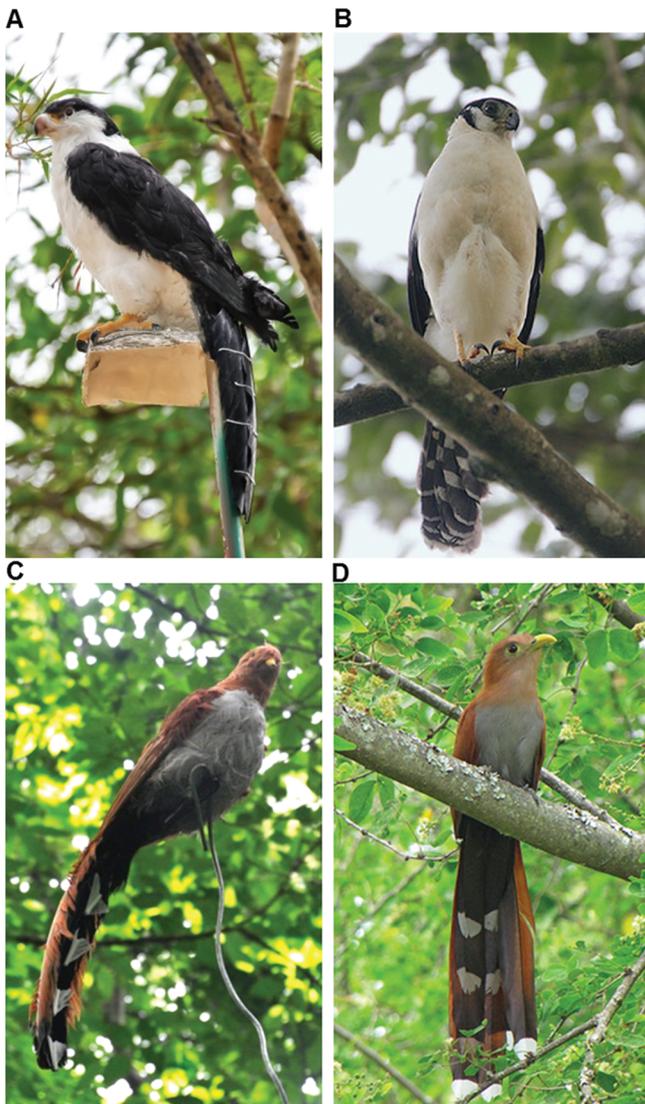


Figure 1
Examples of the models (A and C) used during experimental trials and photographs of live specimens (B and D) for comparison. (A and B) Collared forest falcon (*Micrastur semitorquatus*; Mike Dazenbaker) and (C and D) squirrel cuckoo (*Ptyana cayana*; Francisco Piedrahita).

Because we conducted both predator and control model trials at some but not all sites, and because group composition often changed between trials conducted at the same sites, we do not treat trials at the same location as paired trials. As a consequence, our results are conservative. All analyses were conducted using the R programming language (R Development Core Team 2013).

RESULTS

Observation of natural tail-raising occurrences

We documented 22 tail-raising events at 14 locations in 2010 and 18 tail-raising events at 14 locations in 2011. Across both years, individuals directed their display toward heterospecifics in 24 cases: 18 toward humans and 6 toward other species (Table 2). All displays toward humans were observed during surveys, never when discreetly following birds or when conducting nest watches. These occurred before and during the nesting period; birds were usually flushed from or located near a trail and started displaying after detecting us (distance from observer = 14.5 ± 8.6 m SD; max = 32 m, min = 7 m).

In 12 of the 40 observations, the individuals directed their display toward conspecifics, in either intraspecific or interspecific context (Table 2). Males displaying to other males lead to chases and/or displacements in 3 of the 5 interactions and we observed a nest-attending male chasing an intruding male after the paired female had raised her tail multiple times in the direction of the trespasser. In only 4 cases, we were not able to determine the context of the display because we were unsure if the individual displaying had detected us.

After removing observations from locations where we witnessed a tail-raising display on more than 1 occasion, 28 observations remained for analyses. We estimate that we observed 23 different individuals tail raising in 2010 and 15 in 2011. Tail raising was equally likely to be observed when 1, 2, or more individuals were present (13 lone birds, 15 in groups; $\chi^2_1 = 0.14$, $P = 0.71$). When observing groups, we detected multiple individuals displaying as

often as we observed lone individuals displaying within a group (7 multiple individual displays, 8 lone individual displays; $\chi^2_1 = 0.07$, $P = 0.80$). In general, males were more likely than females to be observed displaying (25 males and 13 females; $\chi^2_1 = 3.79$, $P = 0.05$), mainly because males were more likely to display toward conspecifics (11 males and 1 female; $\chi^2_1 = 8.33$, $P = 0.004$). In contrast, males were detected displaying to heterospecifics as often as females (9 males and 12 females; $\chi^2_1 = 0.43$, $P = 0.51$).

Model presentation experiment

From 74 trial attempts, we attracted 1 or more elegant trogons close enough to initiate the experiment in 40 trials. We excluded data from 1 additional trial because a male started chasing another male toward the end of the trial, potentially confounding the reasons why tail raising may have occurred. Therefore, we included 39 trials from 25 different locations in our analyses, including 23 predator trials and 16 control trials. The average distance between arenas was 274 ± 36 m SE (max: 1100 m; min: 203 m). In 24 of the trials, we attracted only 1 bird to the area; 23 were males (3 immature) and 1 was female. We attracted 2 individuals in 13 trials and 3 individuals in 2 trials.

Because we did not have any influence over where the individuals landed in the arena, our initial analyses explored the possibility that initial conditions might have influenced the behavior of the trogons during the trials. The distance separating the initial perch of the test subject and the predator model ($7.5 \text{ m} \pm 0.44$) was no different than the distance to the control model ($8.1 \text{ m} \pm 0.61$ SE; $t = 0.76$, degrees of freedom [df] = 29, $P = 0.46$). Furthermore, there was a clear indication that models were detected (subjects looking directly at the model) in the same proportion of trials (predator model: 16 of 23 trials, control model: 11 of 16 trials, odds ratio = 0.96, 95% confidence interval [CI] = 0.19–4.93, $P = 1.00$), and the experimental subjects were also started by the exposure of the model in equal proportions (predator model: 7 of 23 trials, control model: 3 of 16 trials, odds ratio = 1.87, 95% CI = 0.34–13.43, $P = 0.48$). Therefore, there was no significant difference in the initial trial conditions.

Tail-raising displays were much more likely to occur when trogons were in the presence of a predator model (Figure 2A; odds ratio = 12.9, 95% CI = 1.50–6.28, $P = 0.01$). However, the presence of conspecifics did not influence tail-raising propensity (Figure 2B; odds ratio = 0.80, 95% CI = 0.10–5.70, $P = 1.00$). Furthermore, when more than 1 trogon was present during predator model trials, we did not observe a single mobbing event.

The initial perch distance from the predator model influenced tail-raising rate, which was best described by an exponential decay model, where tail-raising rate was highest when the subject was near the predator model and decreased rapidly with increasing distance from the model (Figure 3; $F_{1,22} = 5.33$, $P = 0.03$). For birds that stayed within the arena for at least 4 min, tail-raising rate decreased over time (repeated measures $t = 3.21$, df = 8, $P = 0.01$).

DISCUSSION

In this study, we document that tail raising in the elegant trogon is performed toward conspecifics in both intersexual and intrasexual interactions, as well as toward heterospecifics. Furthermore, the results from our experiment support the pursuit-deterrent function of tail raising in the presence of potential predators. These results imply that tail raising in this species is a visual communication behavior with multiple functions and interspecific and intraspecific intended receivers. Although such display behaviors have been documented in a few species of lizards, pursuit-deterrent visual signals that are

Table 2
Elegant trogons (*Trogon elegans*) were observed performing tail-raising displays in various contexts

Receiver	Context	Observations
Intrasexual	Male–male competition for female	1
	Male–male competition for territory	5
Intersexual	Courtship display	1
	Nest building/preparation	4
	Territorial intrusion	1
Heterospecific	Spectacled owl (<i>Pulsatrix perspicillata</i>)	1
	Roadside hawk (<i>Buteo magnirostris</i>)	2
	Double-toothed kite (<i>Harpagus bidentatus</i>)	1
	Collared forest falcon (<i>Micrastur semitorquatus</i>)	1
	Geoffroy's spider monkey (<i>Ateles geoffroyi</i>)	1
	Humans	18
Unknown		4
Total		40

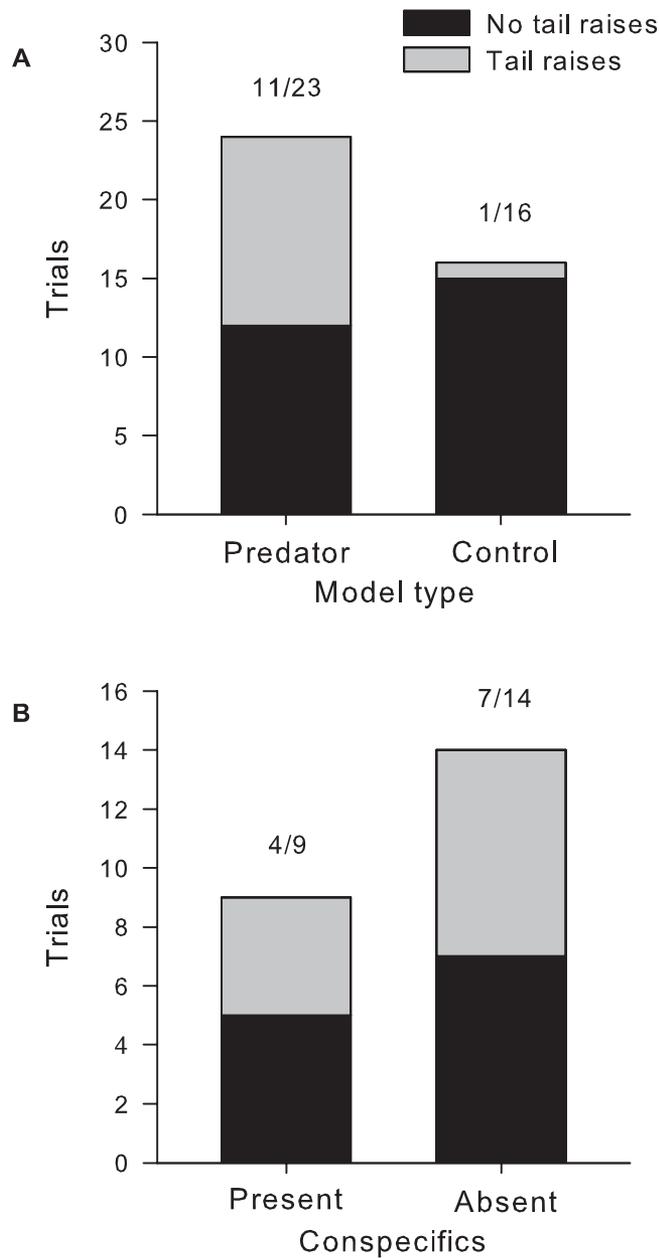


Figure 2

(A) Elegant trogons were more likely to raise their tail in the presence of a predator model than in the presence of a control model, but (B) the presence or absence of conspecifics did not influence tail-raising behavior of elegant trogons presented with a predator model. Numbers above bars indicate proportion of trials during which tail raising was observed.

also used in intraspecific communication have not previously been unequivocally demonstrated in birds or mammals (Table 1).

During natural observations, we documented individuals displaying toward conspecifics in 5 different contexts (Table 2), and these situations can be separated into 2 distinct probable functions: 1) signals of dominance or aggression and 2) behaviors associated with courtship and mating rituals. During intraspecific male–male interactions, many tail-raising displays resulted in 1 individual chasing another away. Therefore, it is probable that in certain situations, tail-raising signals dominance status and/or the intent to engage in aggressive behavior. Such preaggression signals are common in

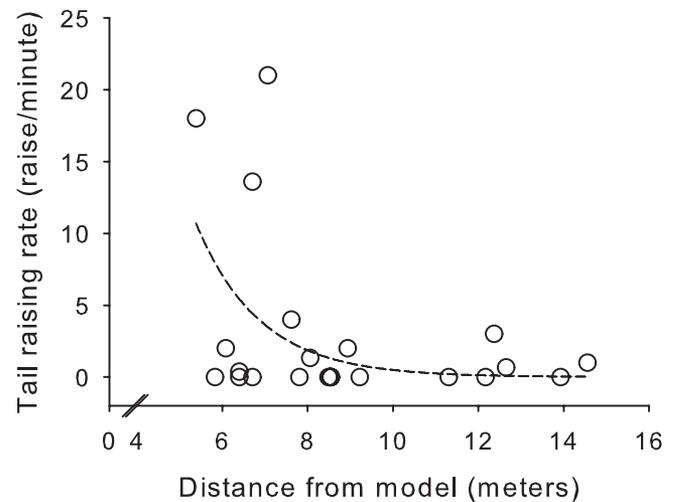


Figure 3

The influence of first perch distance from a predator model on tail-raising rate in the elegant trogon was best described by an exponential decay curve (dashed line).

birds (Andersson 1980), are often stereotyped, and can prevent violent confrontations (Hurd and Enquist 2001). However, our conclusions are based on limited observations, and further documentation of this behavior in natural and experimental contexts is needed.

When we observed elegant trogons tail raising in the presence of a heterospecific, the target receiver was always a potential predator. Of the 6 species targeted by tail-raising behavior, 4 were birds of prey that incorporate birds the size of trogons in their diets (de Silva et al. 1997; Panasci and Whitacre 2000; Schulze et al. 2000; Thorstrom 2000). Such birds of prey have been observed targeting trogons in Costa Rica, including a black-throated trogon (*Trogon rufus*) depredated by a collared forest falcon (Sandoval L, personal communication). On one occasion, we observed elegant trogons displaying toward a Geoffroy's spider monkey (*Ateles geoffroyi*), a species that is not known to include birds or eggs in their diet (Henderson 2002). However, white-headed capuchin monkeys (*Cebus capucinus*) are common in Santa Rosa and are known to depredate adult birds, their eggs, and nestlings (Wainwright 2002). It is possible that elegant trogons have not developed the ability to distinguish between monkey species and display toward any monkey encountered. It also seems highly possible that the trogons would consider humans as potential predator, explaining why we were often the target of tail-raising displays.

During our experimental trials, birds presented with predator models raised their tail regardless of the absence of conspecifics within visual range (prediction of the conspecific warning signal hypothesis), and this behavior never triggered a mobbing of the predator (prediction of the self-preservation alarm signal hypothesis). These results generally support the idea that tail raising in elegant trogons is a pursuit-deterrent signal. Caro (1995) argued that the exclusion of the conspecific warning signal and the self-preservation alarm signal hypotheses was not satisfactorily sufficient to claim a pursuit-deterrence function to behaviors; conclusive evidence of pursuit deterrent signals must include a demonstration that potential predators are deterred by the signal. However, he suggests that a reduction in rate of display once the predator retreats or is located further away as a reasonable argument (Caro 1994, 1995). In our experiment, we could not move the models once the trials had started but 2 behaviors support the idea that birds reduce their

rates of display once the potential threat had been warned that it has been detected. First, the rate of signaling decreased significantly with increase in distance between the model and the first trogon perch. This suggests that indicating presence awareness to the predator is more pressing when the threat is nearby. Second, all birds that remained in the trial arena reduced the rate at which they displayed. This further suggests that once the trogons had been satisfied that the perceived threat had been reduced, the need for signaling their awareness of the predator was also reduced. Although not directly demonstrating that predator behavior is implicitly affected by the display, the experimental results suggest that pursuit deterrence is the most likely function of the behavior.

All situations in which the elegant trogon has been observed raising its tail are contexts where high levels of excitement could be expected, and this suggests the possibility that tail raising in trogons is not meant to signal specific information but is a by-product of agitation in general. However, if this were true, trogons would not perform this display when in the presence of a potential predator, especially one that has not yet detected them. In addition, because nest depredation rates in this species and in trogons in general is very high (Gonzales-Rojas et al. 2008; Steward and Pierce 2011), displaying at the nest during the excavation process could potentially draw the attention of nest predators and impose large costs to the individuals involved in the display. Therefore, we contend that a conspicuous behavior such as tail raising serves an adaptive function and is not the result of agitation.

Multifunctional signals are not uncommon in birds (Hoi and Griggio 2008) and other taxa (Morris et al. 2007). The multiple functions of bird songs, for example, are well documented in intersexual, intrasexual, and interspecific contexts (Catchpole and Slater 1995). However, visual signals with a similar diversity of contexts and functions seem to be either very uncommon or undescribed. As previously mentioned, only the crest raising display of the royal flycatcher has been described as a visual signal to multiple receiver types (Rievey 2010), and the tail-raising behavior in purple gallinule (*Gallinula chloropus*) and common moorhen (*Porphyrio porphyrio*) may target both interspecific and intraspecific (Table 1).

Our study demonstrates that elegant trogons perform their tail-raising behavior in multiple contexts. This is a rare demonstration of a visual display targeting both conspecifics and heterospecifics, and our findings highlight an understudied topic in animal visual communication. Future studies should experimentally determine the exact functions of these displays and investigate how they evolved. This work also highlights the need for studies to successfully document the extent of multifunctional visual displays. Elegant trogons are not the only trogon species to perform tail-raising displays: we have also observed other trogon species perform tail raises when startled by humans. However, it is unknown whether or not these displays are also performed in intraspecific contexts. Furthermore, several members of other groups such as motmots (Snow 2001) and kingfishers (Woodall 2001) also raise or wag their tail in the presence of potential predators. A comparative analysis of such behaviors would provide a greater understanding of the evolutionary history of multifunctional visual displays in birds.

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