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# Non-vocal sounds produced by the wings of Inca doves, *Columbina inca*, and seasonal effects on communication behavior in Costa Rican dry-moist lowland forest

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## ABSTRACT

Recent studies have shown that many birds communicate non-vocally using highly modified feathers in their wings. Several columbid species (pigeons and doves) are believed to produce these non-vocal sounds when they are alarmed and take-off in flight, conveying threat-related information to other birds. This study investigated the communicative significance of the buzzing wing-sounds created during the flight of the Inca dove in dry to moist lowland forest of the Guanacaste province of Costa Rica and characterized seasonal changes in communication behavior. Recordings of alarmed and non-alarmed flight were acoustically analyzed and used for playback experiments to determine if wing-sounds can convey threat-related information. Playback experiments revealed that Inca doves interpret information from the wing-sounds of other individuals just like they interpret information in the coos of rivals. Responses to wing-sounds were significantly different than responses to coos, indicating that they convey a different kind of information. Wing-sound analysis could not confidently identify Inca dove wing-sounds as whistles or claps, instead suggesting wing-buzz as a more accurate descriptor. Additionally, changes in the seasons significantly affected the behavior of Inca doves, increasing territoriality and courtship behaviors during regular activities and in response to played-back coos. Seasonal changes in the response to wing-sounds could not be fully characterized. Several Inca dove nests were also discovered and characterized, finding that birds prefer to nest in trees and shrubs with thorns to deter nest predation.

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## RESUMEN

Recent studies have shown that many birds communicate non-vocally using highly modified feathers in their wings. Several columbid species (pigeons and doves) are believed to produce these non-vocal sounds when they are alarmed and take-off in flight, conveying threat-related information to other birds. This study investigated the communicative significance of the buzzing wing-sounds created during the flight of the Inca dove in dry to moist lowland forest of the Guanacaste province of Costa Rica and characterized seasonal changes in communication behavior. Recordings of alarmed and non-alarmed flight were acoustically analyzed and used for playback experiments to determine if wing-sounds can convey threat-related information. Playback experiments revealed that Inca doves interpret information from the wing-sounds of other individuals just like they interpret information in the coos of rivals. Responses to wing-sounds were significantly different than responses to coos, indicating that they convey a different kind of information. Wing-sound analysis could not confidently identify Inca dove wing-sounds as whistles or claps, instead suggesting wing-buzz as a more accurate descriptor. Additionally, changes in the seasons significantly affected the behavior of Inca doves, increasing territoriality and courtship behaviors during regular activities and in response to played-back coos. Seasonal changes in the response to wing-sounds could not be fully characterized. Several Inca dove nests were also discovered and characterized, finding that birds prefer to nest in trees and shrubs with thorns to deter nest predation.

## INTRODUCTION

Birds are well-known for their complex repertoires of songs and vocalizations (Clark & Feo 2008). This acoustic communication is essential for many bird behaviors including those

related to courtship, sexual selection, territoriality, and predator avoidance (Johnston 1960, Krams 2001, Clark & Feo 2008, Hunter 2008, Hingee & Magrath 2009). Recent studies have shown that many birds are capable of communicating using non-vocal sounds (Bostwick & Zyskowski 2001, Bostwick & Prum 2003, Bostwick 2006, Clark and Feo 2008, Coleman 2008, Doran 2009, Hingee & Magrath 2009). These non-vocal sounds are produced by a variety of mechanisms in a surprisingly large number of bird species (Bostwick 2006) including hummingbirds (Trochilidae: Miller & Inouye 1983, Bostwick 2006, Clark 2008, Clark & Feo 2008, Hunter 2008), ducks (Anatidae: Doran 2009), manakins (Pipridae: Prum 1998, Bostwick 2000, Bostwick & Prum 2003, Bostwick 2006), and doves and pigeons (Columbidae: Johnston 1960, Mahler & Tubaro 2001, Coleman 2008, Hingee & Magrath 2009). These non-vocal sounds were first described by Charles Darwin (1871), who originally called them 'instrumental music.' Today, they are often referred to as mechanical sounds (Miller & Inouye 1983, Prum 1998, Bostwick 2000, Bostwick & Zyskowski 2001) and more specifically, some mechanical sounds are further classified as 'sonations' (Bostwick & Prum 2003, Bostwick 2006, Clark & Feo 2008, Coleman 2008). A mechanical sound is any non-syringeal sound produced by other parts of the animal including wings, tails, feathers, feet and bills (Clark & Feo 2008), while sonations are mechanical sounds that are intentionally modulated and communicative (Bostwick & Prum 2003).

Most birds sonate with their wings, creating two different classes of sound; first are relatively loud, brief, broad-frequency wing-claps, and second are airy, pulsed, wing-whistles (Prum 1998, Bostwick & Prum 2003, Bostwick 2006). Wing-claps are generally created by wing-to-wing feather contact above and/or below the body, wing-to-body contact, contact between adjacent secondary feathers, or the sudden interruption of air-flow between wing-flaps (Bostwick & Prum 2003). Wing-whistles are created when air is forced over or through feathers at relatively rapid speeds creating sound in the form of a conventional whistle, Aeolian whistle, or by fluttering at resonance frequency (Bostwick & Prum 2003, Clark & Feo 2008).

In the family Columbidae, 31 of about 300 species are believed to produce mechanical wing-sounds, however only one (the crested pigeon, *Ocyphaps lophotes*) is known to produce these sounds intentionally as sonations (Mahler & Tubaro 2001, Hingee & Magrath 2009). The crested pigeon produces both wing-claps and wing-whistles during take-off and during flight to convey predator-related information to other members of the flock (Hingee & Magrath 2009). Mourning doves (*Zenaida macroura*) were found to have similar traits to produce similar sounds, apparently for predator avoidance (Coleman 2008). The rock pigeon (*Columba livia*), ground dove (*Columbina passerina*), and Inca dove (*Columbina inca*) are also suspected to produce these types of sonations, but they have not yet been formally studied (Johnston 1960, Davis 1975). In particular, the Inca dove, a common resident of dry lowlands ranging from SW U.S.A. to Costa Rica (Stiles & Skutch 1989), creates a characteristic buzzing sound during flight, however it has been speculated that this buzzing probably does not serve as a warning sound to other individuals (Johnston 1960).

In the northernmost edge of its range (southern Texas) Inca doves experience a drastic change in behavior with the onset of winter (Johnston 1960). As days begin getting shorter, the birds begin defending territories and building nests in preparation for their breeding season (Johnston 1960). By December, birds in temperate regions have established territories and are building nests (Johnston 1960). According to Stiles & Skutch (1989) Costa Rican Inca doves begin building nests in April, with the onset of the rainy season, however, some sources claim that tropical Inca doves have no distinct nesting period (Dickey & van Rossem 1938). Other

changes in behavior, such as territory defense, aggressive vocalizations, and time allocation, have not been described. Behavioral seasonality is very common in tropical birds and often has drastic impacts on acoustic communication and responses to acoustic communication (e.g. clay-colored robin, *Turdus grayi* behavioral and song-behavioral changes in response to seasons; Stiles & Skutch 1989). Therefore, it seems likely that the Inca dove will show seasonal behavior similar to its kin in southern Texas. Additionally, the impact of seasonal changes in behavior on mechanical sound production and interpretation has never been studied. It is also surprising to note that Inca dove nests have not been described in full detail (Johnson 1960).

This study has three main objectives: 1) to determine whether or not the Inca dove is capable of conveying and interpreting information from conspecific wing-sounds; 2) to investigate how seasonal changes affect Inca dove responses to various forms of communication including mechanical wing-sounds and territorial coos; 3) to characterize Inca dove nests.

## METHODS

**RECORDING AND AUDIO ANALYSIS** – To determine exactly what sounds are produced by Inca dove wings, two sound recordings of birds in alarmed take-off were collected using a small directional microphone (Doran 2009, Hingee & Magrath 2009) attached to an iPod. These sounds were analyzed using RAVEN software (Charif *et al.* 2007, Clark & Feo 2008, Doran 2009, Hingee & Magrath 2009) in order to identify whistle structure and composition (*i.e.* tonal/atonal element types, amplitude, rate of repetition of element types, and peak fundamental frequency of element types; Doran 2009, Hingee & Magrath 2009). Background noise below 4000 Hz was filtered out of both wing-sounds for analysis. A third wing-sound was captured by the microphone of a Sony DSC-W80 digital still camera during video recording. Unlike the previously mentioned recordings, this sound was not analyzed due to differences in sound quality.

Wing-sounds were recorded at three regularly visited foraging sites in the San Luís Valley in Monteverde, Costa Rica. The first of these, WS-1, was located at the Beneficio de Café Monteverde in San Luís Abajo (10°16'16" N, 84°49'21" W; 705m asl). The second and third sounds, WS-2 and WS-3, were recorded in San Luís Alto on la Finca Leitón and la Finca Espinoza (10°17'13" N, 84°47'47" W, 1165m asl, and 10°17'09" N, 84°47'54" W, 1155m asl, respectively). The wing-sounds collected at la Finca Espinoza (WS-3) were captured by a camera microphone and were of lesser sound quality, as previously mentioned.

Sound recordings at the Beneficio de Café Monteverde (WS-2) were collected by placing the small iPod-microphone set-up on the ground near a foraging immature dove. When the bird was within two or three meters of the microphone, it was frightened off (by my approach), producing the desired wing-sounds. Wing-sounds recorded at la Finca Leitón (WS-1) were collected by gradually sneaking up on a foraging adult pair (with the recording device in-hand) until the birds were frightened off by my presence. The third wing-sound was recorded during a preliminary video recording trial in which an unsuspecting individual (of unknown age) briefly landed within one meter of the camera. The bird very suddenly became aware of my presence took-off in response. The sound file was extracted from the video file using AOA AUDIO EXTRACTOR software and was used for later playback experiments. All three wing-sound recordings were edited into clips of less than ten seconds in length using RAVEN.

Two territorial coo sounds were also recorded in the San Luís Valley including one at the San Luís Escuela Alto (10°16'60" N, 84°48'15" W, 1090m asl) and another at the San Luís

Escuela Bajo (10°16'22" N, 84°49'05" W, 770m asl). A third coo was acquired from Xeno-Canto, an online community database of shared bird sounds from around the world (see [www.xeno-canto.org](http://www.xeno-canto.org)), which was recorded by Doug Knapp at Intermezzo del Bosque, Managua in Nicaragua (12°07'60" N, 86°14'59" W, 105m asl).

**PLAYBACK EXPERIMENTS** – Playback experiments were conducted on 11 small groups of Inca doves (1-3 individuals) found foraging on the ground and roosting in trees in the San Luís Valley and Punta Morales area, Costa Rica. Each playback trial consisted of observing behavioral responses to a variety of the abovementioned recordings. Behavioral responses to playback experiments were video recorded and analyzed later. All playbacks were conducted using an iPod nano attached to Logitech mm28 portable speakers. Video recordings were conducted with a Sony DSC-W80 digital still camera.

Five flocks were found foraging on the ground and were subjected to playback experiments with all three wing-sounds and a coo sound. Three of these flocks were located in the San Luís Valley and two were in the Punta Morales area. Six flocks were found interacting in trees and were subjected to similar playback experiments using wing-sounds and all three coos. Flocks were located between one and five meters from the speakers and volume was adjusted freely to compensate for both long and short ranges. One flock was tested at a range of greater than seven meters which was later concluded to be too far for wing-sounds to be heard clearly, but still within audible range of coos.

Each trial began with a coo sound in order to ensure that the volume was high enough to be heard, but not so high that it disproportionately frightened the birds. Next, wing-sounds and coos were played in a random order. After each stimulus, I waited for the birds to return to the behavior they were exhibiting before stimulation (*i.e.* preening, foraging, etc.) and then gave them at least one additional minute of recovery. Various recordings were replayed to further characterize some behavioral responses. Three trials on grounded flocks were conducted prior to the first rains of the year (11 April 2010 at 0921 h, 13 April at 0948 h, 13 April at 1207 h), and two were conducted after the first rains (20 April at 1015 h, 20 April at 1429 h). One playback experiment on treed Inca doves was conducted prior to the first rains of the year (14 April 2010 at 1339 h) and the other five were conducted after the first rainy day (18 April at 0802 h, 18 April at 0845h, 18 April at 0950, 20 April at 1232 h, and 20 April 1303 h).

**BEHAVIORAL OBSERVATIONS AND VIDEO ANALYSIS** – The first rains of the Costa Rican wet season in 2010 arrived on 15 April. Behavioral observations were made in conjunction with playback experiments for flocks in the San Luís Valley and Punta Morales areas both before and after this date. This change in season coincides with drastic changes in bird behavior. To characterize these behaviors I observed four flocks before and seven after 15 April. I used video recordings to observe various behaviors as the seasons changed. Specifically, I quantified 13 behaviors including (1) increased vigilance, (2) time spent vigilant, (3) startling, (4) self-preening, (5) foraging, (6) mutual-preening/pecking, (7) preen/peck initiation, (8) territorial/aggressive tail displays, (9) number of displays, (10) territorial vocalizations, (11) number of vocalizations, (12) types of vocalizations and (13) spontaneous stimulus-induced flight reactions (unrelated to startling). I quantified baseline levels of each of these 13 actions by analyzing video recordings of Inca dove behavior without artificial stimuli. When possible, I also noted the gender of each individual by using a variety of behavioral and morphological cues. In particular, individuals observed mounting and chasing others were clearly male. In such

situations, the other individual being mounted was assumed to be female. When side-by-side, female Inca doves clearly have more heavily scaled breasts and napes than males (Stiles & Skutch 1989).

Definitions of behaviors are as follows: (1) Increased vigilance: the cessation of a previous behavior to assume an alert, head-up posture; measured as the proportion of a flock vigilant. (2) Time spent vigilant: the amount of time (sec) that it took for the first individual of a flock to return to its previous behavior. (3) Startled behavior: any bird that lifted its wings, readying itself for take-off, or jumped into the air; measured as the proportion of a flock that is startled. (4) Self-preening: any individual picking at or cleaning their feathers; measured as the proportion of a flock self-preening. (5) Foraging behavior: seed or grit collection on the ground; measured as the proportion of a flock foraging. (6) Mutual preening/pecking behavior: two birds, facing the same direction, sitting with wing-to-wing contact, and pecking at feathers on the other individual's breast, neck and upper back; measured as the proportion of a flock engaged in mutual preening/pecking. (7) Preen/peck initiator: the first bird (male or female) to contact the feathers of its mate. (8) Tail displays: lifting and fanning of the tail; measured as the proportion of a flock displaying. (9) Number of tail displays: recorded for each displaying individual. (10) Territorial vocalizations: throaty, harsh growls and territorial coos; measured as the proportion of a flock vocalizing. (11) Number of vocalizations: recorded for each vocalizing individual. (12) Type of vocalizations: recorded for each vocalizing individual. (13) Non-startled stimulus-induced flight reaction: flying to a new perch in response to a stimulus (playback or natural); measured as the proportion of individuals in a flock that respond with this type of flight.

I calculated the mean proportion of individuals within a flock that exhibited any of these behaviors as well as the mean amount of time spent vigilant and the mean number of displays and vocalizations. Lastly, I determined differences between behaviors (1-13) before and after the rains.

**NEST DESCRIPTIONS** – In search of Inca dove nests, I surveyed approximately six hectares of cow pasture, forested wind-breaks, and secondary-growth patches on la Finca Leitón, la Finca Espinoza, and la Finca Vargas between 21 April and 2 May 2010. I systematically investigated every tree and shrub with a height greater than one meter to find occupied and unoccupied Inca dove nests. Most trees and shrubs in this area (*Citrus* spp. and *Bougainvillea*) were short enough for me to see into nests and dense foliage with the help of a mirror. Taller trees (*Pinus* spp. and *Psidium guajava*) had foliage sparse enough for me to investigate all branches with binoculars. Additionally, I briefly searched seven kilometers of roadside forest between San Luís Alto and el Beneficio de Café Monteverde.

Upon discovering a nest, its height above the ground, widest diameter, and depth were measured. In addition, I recorded the tree species in which the nest was found as well as the number of eggs or squabs.

## **RESULTS**

**RECORDING AND AUDIO ANALYSIS** – Inca dove wing-sounds consisted of broadband claps with some whistle-like properties. The sounds appeared to be atonal in that they span a broad range of frequencies (generally between 5500 and 22000 Hz). Additionally, each of these broadband claps contained repeated and predictable tonal elements with fundamental peak frequencies at 5857.0,

6201.6, and 7752.0 Hz (Fig. 1). Herein, broadband claps with whistle elements shall be called wing-buzzes.

Spectrographic analysis of WS-1 revealed five measurable wing-buzzes with a high frequency at 17684.0 Hz (3<sup>rd</sup> buzz) and low frequencies measuring  $5160 \pm 130$  Hz (mean  $\pm$  SD). The mean rate of wing-buzz repetition was  $16.81 \pm 0.003$  Hz (Fig. 1a). Spectrographic analysis of WS-2 revealed seven measurable wing-buzzes with high frequencies above the measurable range ( $>22050$  Hz) and low frequencies measuring  $5350 \pm 900$  Hz (Fig. 1b). Frequencies of WS-2 were only slightly higher than WS-1 ( $t=-0.446$ ,  $df=10$ ,  $p=0.665$ ). The mean rate of wing-buzz repetition was  $20.07 \pm 0.001$  Hz which was significantly faster than WS-1 ( $t=6.18$ ,  $df=7$ ,  $p<0.001$ ).

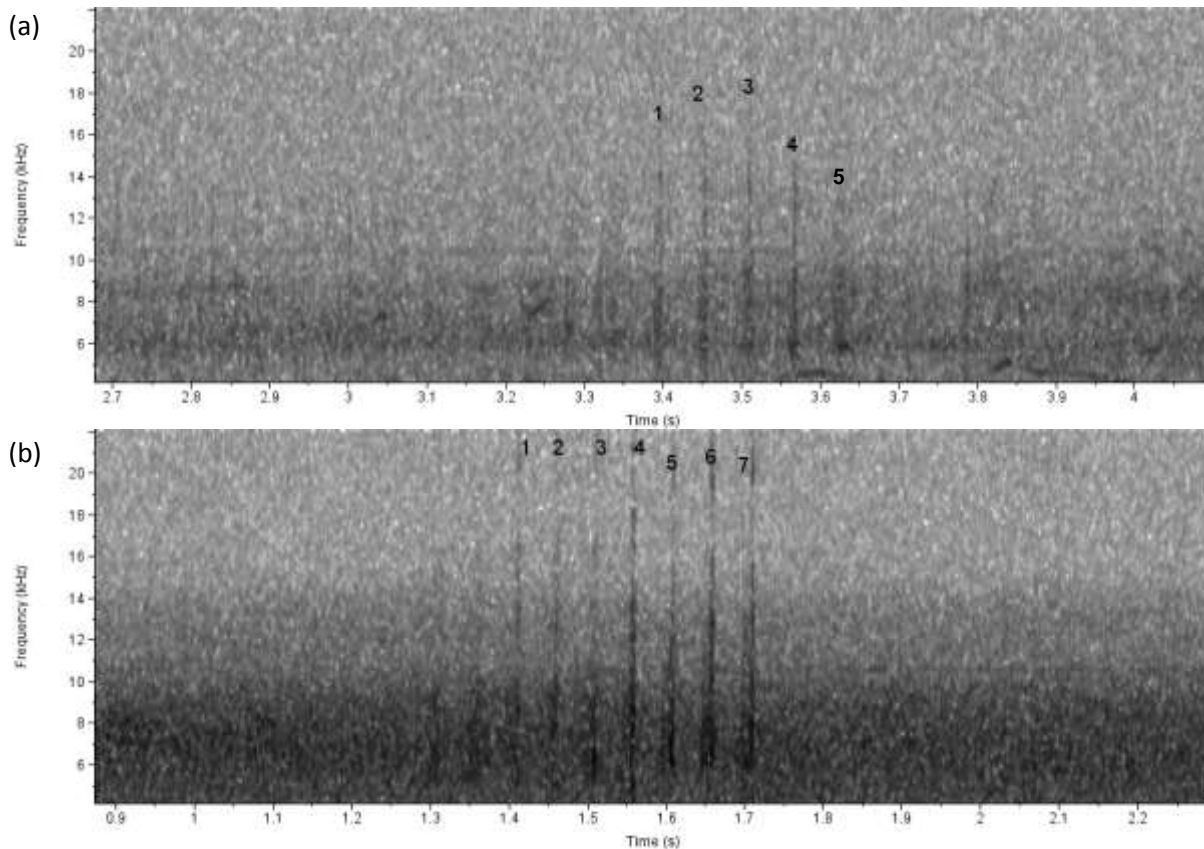


FIGURE 1. Spectrograms of wing-sounds produced by *Columbina inca* during alarmed take-off. Both spectrograms produced in RAVEN. Grayscale depicts relative sound energy where black indicates high sound energy and white indicates low sound energy. Background noise below 4000 Hz has been filtered out. (a) WS-1 showing five measurable wing-sound elements (labeled) that repeat about once every 0.06 seconds, corresponding to wingbeat rate. (b) WS-2 showing seven measurable wing-claps (labeled) that repeat about once every 0.05 seconds, corresponding to wingbeat rate.

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PLAYBACK EXPERIMENTS: VIGILANCE – The proportion of individuals in a flock that exhibited increased vigilance differed significantly between treatments ( $F_{4,96}=40.613$ ,  $p<0.001$ ), however, the proportion of individuals that increased vigilance in response to WS-1, WS-3, and coo stimuli were the same (Fisher's LSD:  $p>0.05$ ; Fig. 2a). Additionally, the proportion of individuals that increased vigilance during baseline activities was significantly lower than the proportion of individuals that increased vigilance in response to any of the four stimuli (Fisher's LSD:  $p<0.01$ ; Fig. 2a). WS-3 and coo stimuli always prompted birds to increase vigilance. Flocks responded to WS-1 by increasing vigilance 90% of the time ( $\pm 28\%$  SD).

The amount of time a flock spent vigilant differed significantly between treatments ( $F_{4,96}=38.459$ ,  $p<0.001$ ; Fig. 2b). Flocks spent the same amount of time vigilant in response to WS-1 as they did in response to WS-2 and WS-3 (Fisher's LSD:  $p=0.246$  and  $p=0.068$  respectively), however, the response time for WS-2 was significantly shorter than the response time for WS-3 ( $p=0.014$ ; Fig. 2b). In addition, all birds were vigilant for the same amount of time in response to WS-3 as they were for coo stimuli ( $p=0.035$ ; Fig. 2b). Lastly, the amount of time flocks spent vigilant in response to WS-2 did not appear to be significantly different from baseline levels of vigilance ( $p=0.403$ ; Fig. 2b). Overall, birds spent the least amount of time vigilant during baseline activities ( $0.4 \pm 0.8$  sec; mean  $\pm$  SD) and the most time vigilant in response to coo stimuli ( $7.4 \pm 4.2$  sec).

PLAYBACK EXPERIMENTS: OTHER BEHAVIORS – In general, the proportion of birds exhibiting self-preening behavior was the same in response to all four treatments and during baseline activities ( $F_{4,96}=0.574$ ,  $p=0.682$ ; Fig. 2c), however, this behavior was more commonly observed in birds in trees (50% observations) than on the ground (11% of observations). Only one bird startled in response to a stimulus (WS-3), and birds were never observed startling without stimulation. Birds never responded to a stimulus with foraging behavior, however during baseline activities, approximately  $80 \pm 36\%$  (mean  $\pm$  SD) of the individuals in a flock were observed foraging while on the ground. Mutual preening behavior was only observed in trees and in response to the playback of territorial coo sounds. Approximately  $30 \pm 51\%$  (mean  $\pm$  SD) of played-back coo sounds resulted in individuals responding with mutual preening behavior. This mutual preening behavior was always initiated by the male. In 20% of mutual preening interactions, the female did not participate, instead remaining very still and submissive in a slightly hunched posture. Tail display behavior was only observed in trees during the wet season



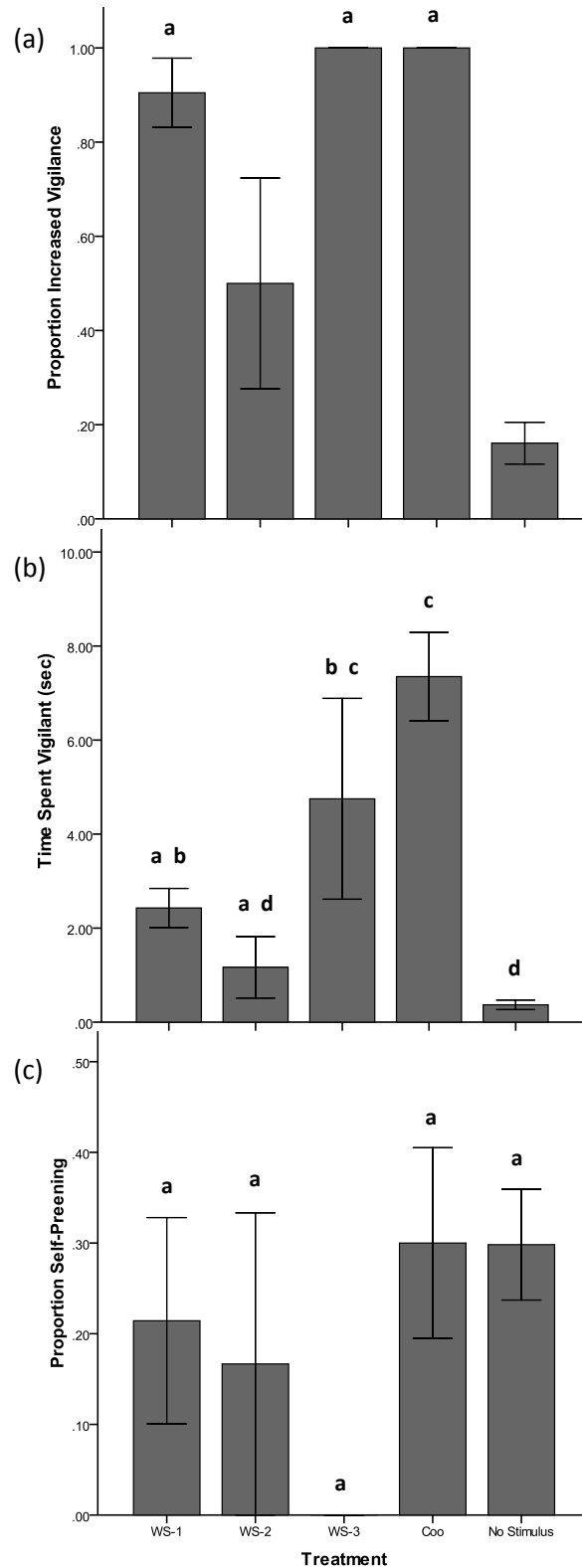


FIGURE 2. Effect of playbacks of three alarmed wing-sounds (WS-1, WS-2, and WS-3) and one territorial coo sound on three aspects of Inca dove behavior and compared to standard behavior without playback stimuli. Panel (a) shows the proportion of individuals in a flock that respond to playback treatments by increasing vigilance. Panel (b) shows the shortest length of time that any one individual spent vigilant following the playback of a stimulus. Panel (c) shows the proportion of individuals in a flock that respond to playback treatments by self-preening, a possible displacement behavior. All bars represent means  $\pm$  SE. Bars that share letters above them are not significantly different ( $p > 0.05$ ).

and in response to the playback of territorial coo sounds. An individual responded to  $40 \pm 51\%$  (mean  $\pm$  SD) of played-back coo sounds with tail display behavior. There was a large amount of variation in the number of tail displays exhibited by displaying individuals ranging from 1 to 14 displays (mean 5.25). Birds only responded vocally to the playback of coo sounds. In addition, they only responded vocally while in trees during the wet season. On average, an individual responded vocally to the playback of coo sounds  $30 \pm 50\%$  of the time. Growls were the most common vocalization that I observed. All growl responses were also accompanied by tail displays. The number of vocal responses an individual exhibited varied widely from 2 to 23 vocalizations (mean 7.75). Lastly, birds only took-flight in response to stimuli twice. In both of these instances birds in trees were repositioning themselves in response to a played-back coo sound.

**THE EFFECTS OF SEASONALITY: VIGILANCE** – The proportion of individuals that increased vigilance in response to playback stimuli was dependent on season ( $F_{1,91}=2.730$ ,  $p=0.034$ ; Fig. 3a). During baseline activities, three times as many birds were vigilant in the dry season than in the wet season ( $t=2.209$ ,  $df=55$ ,  $p=0.031$ ; Fig. 3a). The amount of time a flock spent vigilant in response to playback stimuli was dependent on the season ( $F_{1,91}=3.055$ ,  $p=0.021$ ; Fig. 3b). Without stimuli, birds were vigilant three times longer in the dry season than in the wet season ( $t=2.551$ ,  $df=55$ ,  $p=0.014$ ; Fig. 3b).

**THE EFFECTS OF SEASONALITY: OTHER BEHAVIORS** – The change in seasons appeared to have significant effects on several additional behaviors, including foraging, territorial vocalizations and displays. Foraging behavior was only observed on the ground during baseline activities (never in response to stimuli), however, the proportion of individuals foraging was slightly greater in the dry season than in the wet season ( $t=1.754$ ,  $df=55$ ,  $p=0.085$ ; Fig. 4). Mutual preening behavior was only observed in birds responding to territorial coos while in trees. Approximately  $20 \pm 45\%$  (mean  $\pm$  SD) of individuals in a flock were engaged in mutual preening during the dry season. In the rainy season, I observed no change in mutual preening behaviors ( $20 \pm 41\%$ ;  $t=0.000$ ,  $df=18$ ,  $p=1.00$ ). As previously noted, tail displays and territorial vocalizations were wet season behaviors only. Additionally, these behaviors were only exhibited in response to the playback of coo sounds. Lastly, Inca doves appear to increase self-preening behavior in the wet season, but this slight change was not significant ( $F_{1,91}=0.386$ ,  $p=0.818$ ; Fig 3c).

**ADDITIONAL BEHAVIORAL OBSERVATIONS AND NEST CHARACTERISTICS** – In addition to observing Inca dove flocks in response to playback stimuli, I also observed many additional behaviors and behavioral changes in Inca dove flocks. Specifically, after the first rains of the year, Inca doves became increasingly territorial. Before the rains, the foraging site at the Beneficio de Café Monteverde normally attracted a flock of two breeding pairs and two juveniles. Just before the rains began, however, a pair began constructing a nest in a building overlooking the foraging site. This pair began defending the territory surrounding their nest and the remaining four individuals never returned to the site in the duration of my study.

I also discovered that the playback of territorial coo sounds can prompt all male Inca doves within earshot to begin responding with their own coos. This was especially evident when I played a coo sound at full volume on a quiet morning in Punta Morales (20 April 2010 at approximately 1030 h). At least four individuals began cooing in response to the sounds I had

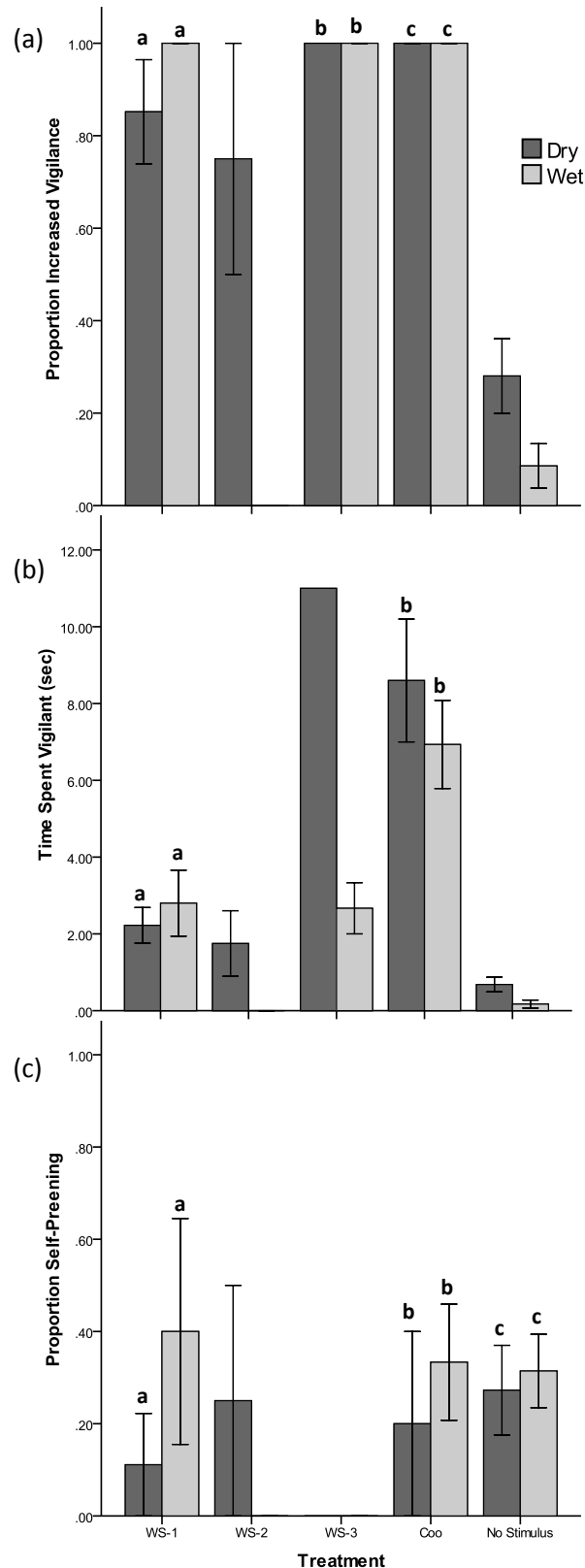
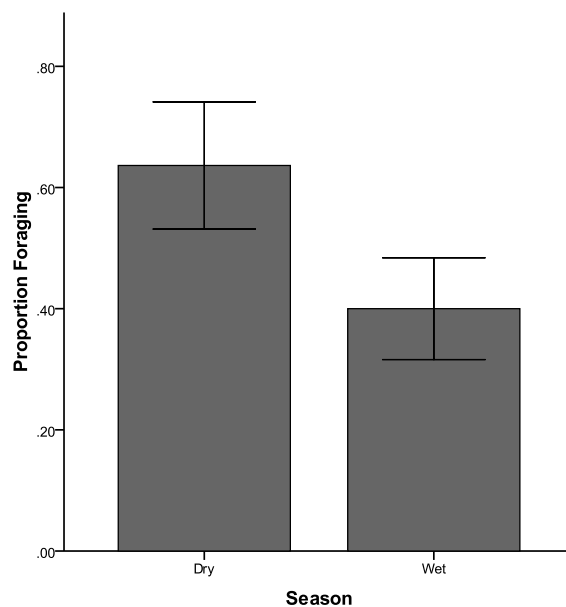


FIGURE 3. Three behavioral responses to the playback of three alarmed wing-sounds (WS-1, WS-2, and WS-3) and one territorial coo sound for Inca doves in the dry and wet seasons. Each set of stimuli are also compared to standard behavior without playback stimuli. Panel (a) compares the proportion of a flock showing increased vigilance in response to stimuli in both dry and wet seasons. Panel (b) makes a similar comparison for the amount of time spent vigilant during both seasons and panel (c) shows self-preening behavioral responses for both seasons. Note that birds never increased vigilance in response to WS-2 in the wet season (n=2). All bars represent means  $\pm$  SE. Bars that share letters above them are not significantly different ( $p > 0.05$ ).




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FIGURE 4. The effects of seasonality on the proportion of individuals in a flock of Inca doves that were observed foraging during normal daily activities. Bars represent means  $\pm$  SE and are marginally different ( $p=0.085$ ).

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played. In addition, I discovered that coo sounds played within an individual's territory would often prompt the male defending that territory to seek out the bird responsible for the calls.

It is also interesting to note that coo sounds were almost always produced by male Inca doves. During all of my behavioral observations, I only observed one female give cooing calls. Her mate, sitting next to her, was responding to a coo that I had played, prompting her to begin cooing as well. Her coos were not as strong as the male's and she cooed only twice.

All of the major behavioral changes I observed in Inca doves with the changing seasons were in conjunction with the start of the nesting season. I discovered three fully constructed nests in the weeks following the first rains. Additionally, I found seven partially constructed pigeon nests (belonging to either red-billed pigeons, *Patagioenas flavirostris*, or Inca doves). All nests that I discovered were built in spiny trees and shrubs including *Citrus* (Rutaceae) and *Bougainvillea* (Nyctaginaceae). One nest was also constructed in the overhang of a building at the Beneficio de Café Monteverde as previously mentioned.

Of the three fully constructed nests, one was located in a *Citrus* tree, one in *Bougainvillea* and one in a building overhang. The *Citrus* nest had a diameter of 9.03cm at the widest point, a depth of 4.05cm, and was located 168cm above the ground. The *Bougainvillea* nest was 10.12cm at the widest point and 3.86cm deep. The Beneficio nest was approximately 11.56cm wide and was 213cm above the ground. Nest depth could not be determined due to its inaccessible location.

## DISCUSSION

RECORDING AND AUDIO ANALYSIS – Inca dove wing sounds appear to have both clap- and whistle-like properties. Analysis of crested pigeon wing-sounds (Hingee & Magrath 2009)

revealed distinct clap and whistle elements. This was not seen in Inca dove wing-sounds, rather, tonal (whistles at 5857.0, 6201.6, and 7752.0 Hz) and atonal (broadband claps) elements occurred in the same moment. Additionally, conventional clap sounds occur in a very short moment of time (<0.001 sec) and have abrupt, very distinct moments of initiation. Inca dove wing-claps are much longer (0.007 sec) and have abrupt moments of termination, rather than initiation. This provides further evidence to suggest that Inca dove wing-sounds are not exactly claps.

Assuming that pigeon wing-sounds are created by primary feathers, Inca dove wing-sounds could be caused by the sudden interruption of airflow between three different feathers. Although in-depth feather analyses were not conducted for the Inca dove, personal observations of mounted specimens and information provided by Johnston (1960) lead me to hypothesize that these sounds may be torque-induced feather-claps. The greater degree of torque in primary feathers (greater torque in Inca doves as compared to red-billed pigeons which do not produce buzzing flight sounds; pers. obs.) gives feathers a twisted rachis and may cause individual feathers to clap against one another as moving air forces them to straighten while the torqued rachis forces them to snap back into place. It is possible, therefore that three torqued feathers are responsible for the tonal elements observed in Inca dove wing-sounds. The gaps between feathers that are created as feathers twist and untwist could also be responsible for the tonal wing-sound elements. If gaps create the tones, then four feathers would be involved in forming the gaps. As in other pigeon wing morphology studies, (Johnston 1960, Mahler & Tubaro 2001, Bachman *et al.* 2007, Hingee & Magrath 2009) the 10<sup>th</sup>, 9<sup>th</sup>, 8<sup>th</sup>, 7<sup>th</sup>, and/or 6<sup>th</sup> primaries are most likely involved in sound-production.

It is also interesting to note that the pitches of these three whistle-like tones did not change between wing-sound recordings that had significantly different wing-beat rates. One would assume that as the rate of wing-beats increases and the airflow over feathers increases, the pitch of whistles (conventional whistles) would increase. This is not the case with the wing-sounds of Inca doves, suggesting that the tones are not conventional whistles. Clearly, further investigation of Inca dove wing-morphology is needed to determine how these “wing-buzzes” are created.

**PLAYBACK EXPERIMENTS: GENERAL BEHAVIOR** – Inca doves are clearly capable of interpreting information from wing-sounds produced during take-off. Birds responded to all three wing-sounds with a higher degree of interpretive behavior (vigilance, time spent vigilant, startling) than during baseline activities. This degree of response was very similar to the degree of response to coos, however, coos were also found to have a large variety of unique responses (mutual-preening, tail displays, vocalizations). Therefore, wing-sounds and coos are both interpreted by Inca doves, but differences in these responses indicate that they convey different kinds of information.

Wing-sounds are also capable of provoking startled flight responses. In one instance, the playback of WS-3 prompted one individual to visibly jump in fright. Of the three wing-sounds I recorded, WS-3 was the most alarmed and recorded at the closest range. These two factors most likely contributed to the high level of vigilance and this one startle behavior that I observed in response to WS-3.

The playback of coo sounds also regularly provoked high degrees of increased vigilance in Inca doves. These sounds are known to convey information regarding territoriality (Johnston 1960). Vocalizations and tail displays are also linked to territoriality, and therefore I was not

surprised to observe these behaviors in response to the playback of territorial coos. It is interesting, however, that coo playback also provoked mutual preening in mated pairs. Variations on this behavior have been observed in many pigeons and doves and in all cases, it is believed to facilitate the establishment and maintenance of pair-bonds (Johnston 1960). Unlike other columbids, Inca doves continue this behavior throughout their mated life. I would therefore hypothesize that upon hearing the coo of a rival individual, mutual preening was initiated in order to reinforce the strength of the pair-bond. The fact that males initiated mutual preening in 100% of my observations supports this theory, as it seems logical that pair-bond maintenance behaviors should be initiated by males when there is high competition for females.

**PLAYBACK EXPERIMENTS: THE EFFECTS OF SEASONALITY** – During the dry season, Inca doves appear to allocate more of their time to foraging and vigilance than in the wet season. In addition, Inca doves were observed performing a significantly greater amount of territorial and courtship behaviors in the wet season than in the dry season. In Costa Rican dry to moist, lowland forests, Inca doves are known to coordinate their breeding season with the rains, beginning nest construction in April (Stiles & Skutch 1989). For this reason, territorial and courtship behaviors would be expected to increase with the rains. In fact, my observations revealed that these behaviors did not even begin until the dry season had ended.

In addition, it seems logical that they would allocate less time to foraging if they are spending more time constructing nests, courting and defending territories. The general decrease in the level of vigilance that I observed after the rains, may be due to the fact that flocks were most often found on the ground, foraging, in the dry season and most often in the trees during the wet season. While on the ground, birds generally exhibit a higher level of vigilance than they do while perched in a tree. These trends were observed during baseline activities (without playback stimuli) and also in response to playback stimuli.

Although behaviors during baseline activities were significantly different in the dry and wet seasons, responses to wing-sounds did not show such defined changes. With the change in seasons, I observed marginal changes in the level of vigilance in response to wing-sounds. This change might have been more defined if birds didn't also reduce the amount of time they spent on the ground. As previously mentioned, birds normally spent more time vigilant while on the ground than in trees, and in addition, birds spent more time in trees than on the ground in the wet season. These two behavioral changes combined would dilute any changes I observed in the level of vigilance in response to wing-sounds in the dry versus wet seasons.

**NEST CHARACTERISTICS** – After finding three confirmed Inca dove nests and six likely (but uninhabited) nests only in spiny trees and shrubs, I would confidently conclude that Inca doves are selecting these spiny plants for nest locations. The two plant species in which I regularly found nests, *Citrus* and *Bougainvillea*, are introduced species. It would be interesting to investigate how the large-scale introduction of these species to dry Costa Rican lowlands has affected the nest and brood success of Inca doves and other birds in the area. I suspect that the added protection of thorns would decrease nest predation and therefore may be increasing Inca dove populations.

In conclusion, Inca dove wing-sounds are conveying information to other individuals, but further investigation is needed to determine if these sounds are indeed conveying predator-related information. Additionally, the intentionality of these sounds was not addressed in this study,

therefore, these sounds cannot yet be identified as sonations. Feather morphology studies combined with high-speed video analysis of flight would assist in determining the identity and mechanisms for producing wing-sounds in Inca doves. Lastly, although seasonality has a major impact on Inca dove behavior, its effects on responses to wing-sounds have yet to be fully investigated. The results of this study, I hope, will encourage further investigations of non-vocal communication via wing-sounds in Aves, a blossoming new field of animal communication.

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