ORNITOLOGIA NEOTROPICAL 22: 89–102, 2011

SEASONALITY OF TERRITORIAL AGGRESSION IN MALE TROPICAL RESIDENT RUFOUS-COLLARED SPARROWS (*ZONOTRICHIA CAPENSIS*)

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Resumen. – La estacionalidad de la agresión territorial en gorriones (*Zonotrichia capensis*) machos residentes tropicales. – Defensa territorial evoluciona cuando recursos son defendibles y cuando defensa de recursos asegura una ventaja de la salud. Sin embargo, defensa territorial puede tener substancial costos energéticos y de supervivencia, y por lo tanto sólo deben ser exhibidos cuando los beneficios son sustanciales. La residencia de territorios durante todo el a–o es común en las especies de aves tropicales y, en conjunción con menos temporadas fuertes que caractericen ambientes tropicales, proporciona una oportunidad de probar la función de la territorialidad. En general, la agresión territorial puede servir tres funciones diferentes: la atracción compa–ero o mantenimiento de relaciónes de la pareja, la protección de la paternidad y / o de la defensa de los recursos alimentarios. En cada caso, patrones temporales diferentes son expectados. diferentes Probamos la función de agresión territorial masculina a través de etapas de vida en una población residente de gorriones (*Zonotrichia capensis*) ecuatoriales en los Andes húmedos del oriente de Ecuador. Para comparar los patrones individuales de la estacionalidad, simultáneamente revisamos la sincronía de etapas de vida en el población-nivel. Los individuos fueron identificados y fueron clasificados en uno de cinco etapas de vida: pre-criando, la nidificación, alimentando volantones (jóvenes fuera del nido), mudando, o no-criando. Para determinar agresividad masculina, nosotros realizamos intrusiones territoriales simuladas con un cimbeo montado. Los machos fueron apreciablemente más agresivos durante pre-criando y anidando que al alimentar volantones, mudar, o en no-criando. Encontramos a individuos dentro de la población en todas las etapas de vida durante los dos períodos de muestreo de tres meses, demostrando población-nivel asincronía. Por lo tanto, machos individuales en esta población defienden los territorios según etapa de vida, no según temporada ambiental. Basado en estos resultados, nosotros sugerimos que las fuerzas selectivas de atracción de una embra y mantenimiento de relaciónes de la pareja y protección de paternidad pueden explicar mejor la model territorial de agresión observado.

Abstract. – Territorial defense evolves when resources are defensible and when resource defense secures a fitness advantage. However, territorial defense can involve substantial energetic and survival costs and thus should only be exhibited when the benefits are substantial. Year-round residency is common in tropical bird species and, in conjunction with low seasonality, provides an opportunity to test the function of territoriality. In general, territorial aggression can serve three different functions: mate attraction, paternity protection, and/or food resource defense. In each of these cases different temporal patterns of aggression are expected. We tested the function of male territorial aggression across life history stages in a resident population of equatorial rufous-collared sparrows (*Zonotrichia capensis*) in the humid eastern Andes of Ecuador. To compare individual patterns of seasonality, we simultaneously examined the synchrony of life history stages at the population-level. Individuals were identified and classified into one of five life history stages: pre-breeding, nesting, feeding fledglings (young out of the nest), molting, or non-breeding. In each stage we tested male territorial aggression using a simulated territorial intrusion with a mounted decoy. We found that pre-breeding and nesting males were significantly more aggressive than males that were feeding fledglings, molting, or non-breeding. However, individuals were found in all life history stages during the two three-month sampling periods, demonstrating population-level asynchrony. Thus, individual males in this population defend territories according to life history stage, not according to environmental season. Based on these results, we suggest that the selective forces of mate attraction and maintaining the pair bond and paternity protection may best explain the territorial aggression pattern observed. *Accepted 10 February 2011.*

Key words: reproductive synchrony, seasonality, territoriality, tropical, *Zonotrichia capensis*.

INTRODUCTION

Reproduction and territorial behavior are two of the best studied behaviors as they are typically easy to observe, test, and compare (e.g., Murton & Westwood 1977, Wingfield & Kenagy 1991). The majority of year-round resident species show predictable seasonality in these behaviors, correlating with environmental seasonality both in the temperate-zone and the tropics (Murton & Westwood 1977, Stutchbury & Morton 2008). However, in environments such as the humid equatorial tropics, where environmental seasonality is considerably less pronounced and less predictable, the phenology of behavior is predicted to be more flexible or even aseasonal (Stutchbury & Morton 2001, Dawson *et al.* 2008, Hau *et al.* 2008). Nevertheless, few studies have attempted to characterize the seasonality of territorial behaviors throughout the year in resident species existing in humid equatorial environments.

Territorial behaviors occur when resources are defendable and when the defense of resources secures a reproductive advantage (Brown 1964). Though territorial behaviors can be costly in terms of increased energy expenditure and predation risk associated with active displays, the costs are considered to be outweighed by the advantages gained by defending a territory, such as access to resources and mates (Marler & Moore 1988, Wingfield *et al.* 1990, Dunn *et al.* 2004). Three principal selective forces are hypothesized to shape the seasonality of territorial aggression: 1) mate attraction or maintaining the pair-bond, where territorial aggression secures a territory space to attract and secure a mate(s) 2) paternity protection, where territorial aggression is primarily aimed against conspecific male intruders because of the potential paternity threat of extra-pair copulations, and/or 3) food resource defense, where the territorial aggression is necessary to defend valuable food resources on a territory for mates and young (Brown 1964). These selective forces each predict distinct seasonal patterns of territorial aggression across life history stages, but their predictions are not mutually exclusive (Brown 1964).

Theory suggests that territorial aggression should vary across life history stages (e.g., pre-breeding, molting) according to which critical resource(s) needs to be defended and during what time period defense is critical to securing a fitness advantage. Thus, for mate attraction or maintaining the pair-bond, we would predict individual males to display high territorial aggression when they first establish a territory during the pre-breeding period. This prediction is commonly suggested to explain the phenology of male territorial aggression in temperate-zone migrant passerines (90% of temperate-zone breeding bird species), as males typically return to their breeding grounds and attempt to attract mates by fiercely defending a territory during the pre-breeding season (Stutchbury & Morton 2001). Paternity protection also predicts that males will show peak levels of territorial aggression during pre-breeding as females are fertile and clutches are not yet laid, so the threat of cuckoldry is high (Brown 1964, Wingfield & Moore 1987, Weatherhead & Yezerinac 1998, Griffith *et al.* 2002, Kokko *et al.* 2006, Stutchbury & Morton 2008). Food resource defense predicts that males will show peak territorial aggression during periods when they are most dependent on food resources (Brown 1964). Protecting high quality territory-specific resources can effectively decrease the physiological and temporal cost of foraging and increase the consistency and efficiency of provisioning (e.g., when young are immobile during pre-breeding and nesting periods), leading to higher offspring survival (Hogstedt 1980, Nilsson & Svensson 1996, Pribil & Searcy 2001). By studying the seasonal pattern of territorial aggression we can begin to understand the selective mechanisms acting on territorial aggression.

Strong environmental seasonality constrains breeding to a season of the year in which climate is favorable and resources are abundant (Baker 1938, Murton & Westwood 1977). This is most visible in temperate-zone breeding migratory birds, which migrate seasonally to take advantage of periods of high productivity and benign climate to breed, and escape the low temperatures and low productivity of temperate-zone winter by migration (Murton & Westwood 1977, Wingfield & Kenagy 1991). Importantly for territorial behavior, migration imposes an extensive re-assortment of individuals and territories that does not occur in the majority of tropical resident species (Karr 1971, Ketterson & Nolan 1993).

Tropical residents do not experience the temporally constrained fierce competition for territories and mates, but may face selection pressure to keep mates and defend territories year-round when high-quality territory space and/or mates are limited (Brown 1964, Smith 1978). Tropical year-round territorial resident populations existing in habitats with low environmental seasonality are therefore likely to experience constant low-level turn-over according to stochastic demographic and environmental events, but turn-over will depend on territory and mate availability (Stonehouse 1962, Brown 1964, Smith 1978). However, there are few investigations of territorial behavior of tropical species without well-defined breeding seasons.

Previous studies investigating territorial aggression in tropical *Zonotrichia capensis* have led to some mixed results. In seasonally breeding populations of *Zonotrichia capensis* in Ecuador, high levels of territorial aggression occur during the pre-breeding life history stage, similar to temperate-zone breeding *Zonotrichia* (Moore *et al.* 2002, Busch *et al.* 2004, Moore *et al.* 2004a, 2004b, 2005). Intriguingly, Addis *et al.* (2010) found that behavioral responses of territorial male *Z. capensis* to simulated territorial intrusions (STIs) differed between rainy and dry seasonal periods independently of life history stage. That is, overall aggression scores did not differ between life history stages except that the number of songs sung by males was lower in the non-breeding season (Addis *et al.* 2010). Busch *et al.* (2004) and Smith (1978) found that territorial aggression typically occurs within sexes, thus males aggressively defend their territories from other males and not females. Here we examine territorial behavior within a population existing in an humid equatorial environment in the eastern Andes of Ecuador, where there is markedly less climatic seasonality than previously studied equatorial and Costa Rican populations (e.g., Ecuador: Moore *et al.* 2005, Costa Rica 2010: Addis *et al.* 2010). In this resident population we tested whether there is selection acting to maintain intense territorial aggression through all life-history stages in an environment exhibiting low climatic seasonality.

METHODS

Study population and area. Zonotrichia capensis is a socially monogamous, omnivorous, emberizid sparrow ranging from Chiapas, Mexico to Tierra del Fuego, Argentina and from sea level to ~4000 m elevation (InfoNatura 2007). *Zonotrichia capensis* is the only member of the *Zonotrichia* genus with tropical resident populations (InfoNatura 2007). Throughout its range, *Z. capensis* occupies diverse habitats including, urban areas, páramo grasslands, pasture, deserts, forest gaps and early second-growth (Miller & Miller 1968, Wolf 1969, King 1973, Moore *et al.* 2005). In this species males are primarily responsible for the defense of territories, with the tightness of territorial association decreasing outside of breeding periods, when birds can form loose foraging flocks (Miller & Miller 1968, Busch *et al.* 2004). Nevertheless, pairs are frequently on their territory and roost on their territory throughout the year, at least in the focal population (Class pers. obs.). "Floaters" are non-territorial birds that move through established territories freely, and can also associate with territory holders and can take over newly opened territories as opportunities arise (Smith 1978, Busch *et al.* 2004). Seasonal reproduction has been documented in populations of *Z. capensis* in Costa Rica (Wolf 1969), Panama (Kalma 1970), Colombia (Miller 1962), Ecuador (Moore *et al.* 2005), Peru (Davis 1971), and Argentina (King 1973). Yet, the timing and duration of breeding seasons varies considerably across the latitudinal and altitudinal range of *Z. capensis.* Extra pair paternity has been found to be prevalent (~50%) in a population in Papallacta, Ecuador as well as the focal population of this study (Bonier unpub. data).

The study population of *Z. capensis* is located in the rural township of Las Caucheras in Napo Province of eastern Andes of Ecuador (0°37'S, 77°55'W; ~2100 m a.s.l.). In this habitat there is only three minutes difference in daily photoperiod over the course of the year (Kaplan *et al.* 2009). Monthly accumulated rainfall is between 130–240 mm from October–March and 280–390 mm from April through September and temperature remains nearly constant circannually ~17° C in Las Caucheras (Instituto Nacional de Meteorologíca, Ecuador).

Birds were caught passively with mist nets each morning. Additionally, we used targeted mist-netting with a decoy and playback to capture specific territorial residents to determine their life history stage (see below). At capture, each bird received a unique combination of color bands and a numbered aluminum band. Measurements of reproductive morphology, molt scores (the number of primary molting wing feathers) and behavioral observations were used to categorize individuals as belonging to one of five life history stages: pre-breeding, nesting, feeding fledglings, molting and non-breeding (see Table 1). Reproductive morphology included evaluating the brood patch (developed to brood eggs and young) for females, and length and width of the cloacal protuberance (an extension of the cloaca used to deposit sperm during copulation) for males. Cloacal protuberance size closely tracks testis volume in this species (Moore *et al.* 2005). We used a five-point brood patch score: 1) defeathering, 2) defeathered, 3) edematous with hyperplastic epidermis (fluid-filled distended skin pouch used for incubation), 4) refeathering, wrinkled/scaly skin, and 5) nearly refeathered (about 10% sheathed, regrowing feathers; scaly skin may still be visible) (DeSante *et al.* 2007). We made additional observations of each territory pair for 30 minutes on alternate days to verify the accuracy of our categorizations by asking whether: pre-breeding birds had completed nest building, nesting birds continued to incubate and/or feed young, birds feeding fledglings had continued to feed

TABLE 1. Observations and characters used to categorize five life history stages of individuals.

Life history stage	Character/behavior
Pre-breeding	Female with defeathering or defeathered brood patch or male with cloacal protuberance > 2.5 mm and observed with nest material, constructing nest, or focal territory found with freshly lined nest (no eggs laid). Captured without molting primary flight feathers.
Nesting	Male cloacal protuberance > 5 mm length or female with edematous brood patch (for incubating eggs or nestlings), and/or known to have a clutch of eggs, or be feeding nestlings, and not molting primary flight feathers.
Feeding fledglings	Observed feeding and following fledglings in or around defined territory and were not molting primary flight feathers.
Molting	Caught with 1 or more primaries molting prior to experiment, recaptured with progressed molt or having completed molt post-experiment; male with cloacal protuberance < 1 mm length; female without brood patch. Focal pair was not constructing a nest, incubating, nor feeding young.
Non-breeding	Male cloacal protuberance < 1 mm length or female without brood patch and two or more of the following observations: not building a nest or incubating, not feeding fledglings, not molting any primary flight feathers.

and associate with their young, whether birds captured molting showed molt progression upon recapture, and whether non-breeding birds continued to show no signs of breeding behavior.

Definition of territories and simulated territorial intrusion protocol. In both sampling periods, 16 March–10 June 2007 and 6 September–3 December 2007, we identified, observed, and captured residents to determine their life history stage, since preliminary data showed males in all life history stages during any given period of time. During observational periods of one or more hours, we noted the frequency of use of specific landmarks (such as bushes, fence posts and trees) by focal males while they were singing, foraging, and perching. Landmarks and areas most frequently occupied by the residents were used as guide to approximate territory boundaries. We placed the decoy and playback equipment for simulated territorial intrusions (STIs) in the center of each territory. We attempted STIs only when territories, occupants, and life history stage of the resident male was determined, and when weather permitted.

We conducted each STI on a unique male. All STIs occurred between 1200 and 1800 h. We used three stuffed decoys from the study population, mounted on a stick, for all STIs. We measured a 5 m radius around the territory center a day prior to each STI to ensure more accurate estimates of distance and time. Immediately prior to each experiment, we placed the decoy and song playback equipment in the territory center, after focal males were located visually. During the experiments, we stood at least 15 m from the territory center, a distance at which we were presumably not perceived as an obvious threat (i.e., no chipping/flights directed to the observer).

Each STI (30 min total experiment duration) was conducted on a different male and consisted of three consecutive 10 min observation periods. In the first 10 min of the observation period (min 0–10) the decoy was covered and there was no song playback. This period was used to determine the individual background level of territorial aggression. After this initial 10 min period, we uncovered the decoy and started a song playback track that ran for the next 10 min period of observation. This period corresponded to active territorial defense. For the third 10 min observation period (min 20–30), we re-covered the decoy and turned off the song playback. For each STI we selected a single song for playback from 12 song tracks, each recorded from a different male in 2006 from a field 6 km away. None of the recorded males were subjects or neighbors of focal males in experiments described here. Each song track had a single, randomly selected song (to avoid pseudoreplication; Kroodsma *et al.* 2001), followed by 9 seconds of silence, to approximate the natural song rate of *Z. capensis* in this population. Playback volume simulated normal ranges of observed song volume, adjusted for locale. During all three periods, we recorded the duration of time the focal male was within 5 m of the decoy, his closest approach to the decoy (m), number of songs, number of song switches (number of times each bird used a different song type; Kramer *et al.* 1985), number of attacks, and number of flights over the decoy. During the STI period (min 10–20), we also recorded latency, or the time elapsed, until the male responded to the intruder. During the post-STI (min 20–30) we recorded the persistence of aggressive response, or the time the male continued to display aggressive behavior, despite the disappearance of the threat.

Data analyses. To compare territorial aggression across life history stages and among STI periods, we generated a single aggression score (Busch *et al.* 2004, Moore *et al.* 2004a) for each of the 89 focal males using principal components analysis (PCA). As we did not observe any attacks during any STI, we did not include this in the PCA. We used the first principal component (PC1) as the aggression score for each male tested (Table 2). Means of PC1 scores were compared using a two-way repeated measures ANOVA among the five life history stages and the three STI periods including interactions between life history stage and STI periods. We also examined the measured behaviors individually to determine what exactly changed, if anything, among life history stages using two-way ANOVAs. For instance, we examined whether birds in the nesting life history stage sang more frequently in response to a decoy than pre-breeding, feeding fledglings, molting or non-breeding birds within the STI period of the experiment. The latency and persistence of aggressive responses were measured only during the STI (latency) and post-STI periods (persistence); they were each analyzed two-way ANOVAs. Where there were significant differences, we used Tukey-Kramer post-hoc tests to clarify where differences existed in all of our analyses.

To examine the synchrony of life history stages within the population, we compiled all data on life history stages of identified territorial individuals. Data from the two sampling periods was further divided into approximately 30-day time periods during each of the two sampling periods. We combined the pre-breeding, nesting and feeding fledgling life history stages (though some individuals in each life history stage were observed in all sampling periods) into a general “breeding” category for simplicity of the analysis. Sampling effort in each of the two field periods was approximately equal. However, the subdivision of 30-day periods and times when we conducted STIs led to a few more or less territories each category. All statistical analyses

TABLE 2. Principal component loadings for behavioral responses to simulated territorial intrusions.

Measured behavior	PC1 Loading
Time within 5 m	0.50
Closest approach (m)	0.51
Number of songs	0.50
Number of song switches	0.37
Number of flights	0.31
Percent variance explained	54.7

were performed in SAS v. 4.1 and figures were prepared using SigmaPlot v. 11.0.

RESULTS

There was a significant effect of life history stage on the male aggression score (Fig. 1; two-way repeated measures ANOVA: $F_{4, 84}$ = 28.54, $P < 0.0001$). Post-hoc analysis revealed that pre-breeding and nesting males were significantly more aggressive than males that were feeding fledglings, molting or non-breeding (Tukey-Kramer HSD: $P < 0.0001$). There was no difference in aggression between pre-breeding and nesting males (Tukey-Kramer HSD; $P = 0.667$), nor between males that were non-breeding, molting and feeding fledglings (Tukey-Kramer HSD; non-breeding versus molting, $P = 0.117$; non-breeding versus feeding fledglings, $P = 0.211$; feeding fledglings versus molting, $P = 0.999$).

There was also a significant effect of the STI period on the aggression scores of males (two-way repeated measures ANOVA: $F_{2, 168}$ = 145.64, $P < 0.0001$; Fig. 1, compare a, b, c). Post-hoc analysis of STI periods revealed pre-STI, STI, and post-STI periods were all significantly different from one another (Tukey-Kramer HSD; $P < 0.0001$). There was a trend for an interaction of life history stage and STI period (two-way repeated measures ANOVA: $F_{8, 168}$ = 1.74, $P = 0.092$).

Behaviors recorded from resident male *Z. capensis* were analyzed by STI period (pre-STI, STI, post-STI) and among life history stages. Two-way ANOVA conducted for each STI period revealed significant effects of the behaviors: time spent within 5 m of the decoy (pre-STI: $F_{4, 84}$ = 8.15, $P < 0.0001$; STI: $F_{4, 84}$ = 12.53, $P < 0.0001$; post-STI: $F_{4, 84}$ = 10.96, $P < 0.0001$); closest approach (m) to the decoy (pre-STI: $F_{4, 84}$ = 13.45, $P < 0.0001$; STI: $F_{4, 84}$ = 7.64, $P < 0.0001$; post-STI: $F_{4, 84}$ = 11.18, $P < 0.0001$), and number of songs (pre-STI:$F_{4, 84}$ = 9.9148, $P < 0.0001$; STI: $F_{4, 84}$ = 22.09, $P < 0.0001$; post-STI: $F_{4, 84}$ = 18.43, $P < 0.0001$). There were significant differences in the number of flights during the pre-STI ($F_{4, 84}$ = 5.48, $P = 0.0006$) and post-STI ($F_{4, 84}$ = 3.04, $P = 0.02$), but not during the STI period ($F_{4, 84}$ = 0.52, $P = 0.72$). Song switching was a significant effect during the post-STI period ($F_{4, 84}$ = 3.95, $P = 0.006$), but not during the pre-STI or STI periods ($F_{4, 84}$ = 0.9177, $P = 0.46$; $F_{4, 84}$ = 1.38, $P = 0.25$, respectively). The latency to respond was recorded only during the STI period. Our results showed significant differences among males in different life history stages in latency to respond (two-way ANOVA: $F_{4, 84}$ = 6.77, $P < 0.0001$). Persistence responses were only recorded only during the post-STI period. Males in different life history stages show significantly different persistence responses (two-way ANOVA: $F_{4, 84}$ = 9.27, $P < 0.0001$; see Table 3 for Tukey-Kramer post-hoc test results).

We found pairs in all life history stages during both sampling periods (Fig. 2).

DISCUSSION

In our study, *Z. capensis* males responded more aggressively to STIs during pre-breeding and nesting than while they were feeding fledglings, molting or non-breeding. Nevertheless, there was a significant aggressive response to

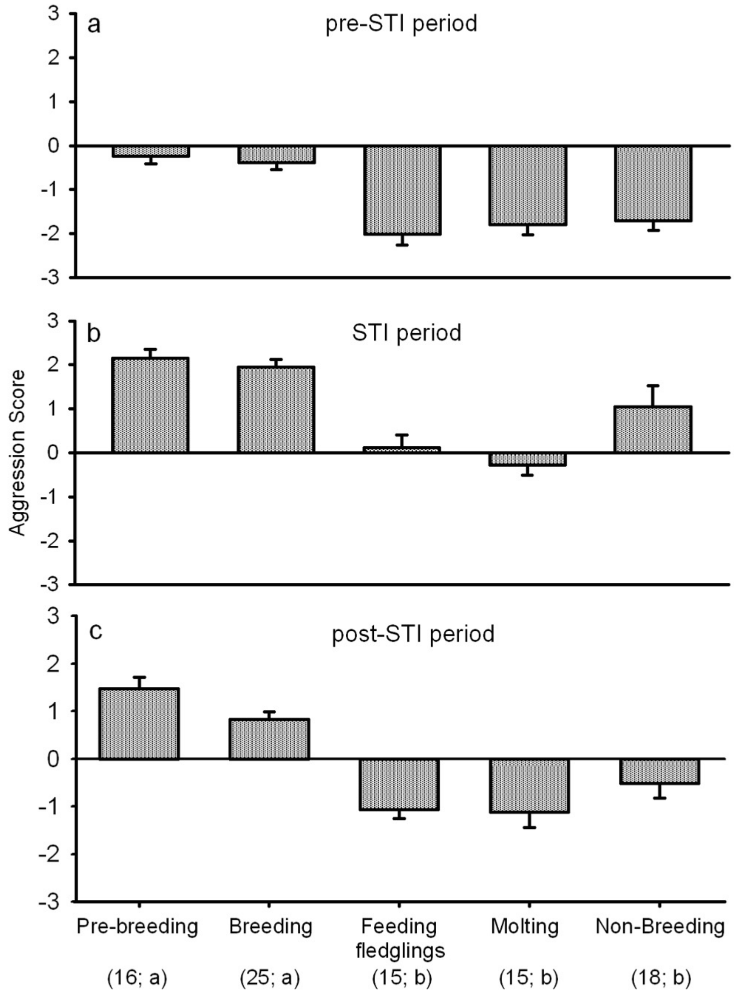

FIG. 1. Mean aggression scores (± SE) among males in five life history stages. Males in each life history stage were tested across three simulated territorial intrusion (STI) periods (a: pre-STI, b: STI, c: post-STI). Numbers in parentheses are sample sizes, different letters following these numbers show significant differences among life history stages. See results for statistics.

the STI in all life history stages compared to the control periods (i.e., the pre-STI period). Thus, the presence of an intruder always elicited a significant response compared to background levels, regardless of the life history stage of a given resident male. Finally, we show that there is marked asynchrony in reproductive phenology the focal population.

Our examination of territorial behavior in a population of birds living in an equatorial environment with low seasonality demonstrates that active territorial defense is maintained in every life history stage, but that territorial aggression is held at a low level when the threat of cuckoldry and resource competition is low. Territorial defense may be

Table 3. Aggressive behaviors divided among simulated territorial intrusion (STI) periods (pre-STI, STI, post-STI) and among life history stages (LHSs). Means + standard error are given for all behaviors used to compile PC1 scores for individual males in each LHS (n = 16 pre-breeding, 25 nesting, 15 feeding fledglings, 15 molting, 18 non-breeding). Each behavioral response is compared for a given STI period, as well as among LHSs. Note: latency responses to intrusions were only recorded in the STI period and persistence of response was only recorded in the post-STI period, thus these were not included in PC1 scores. Distinct superscript letters denote significant differences in responses among LHSs, but within STI periods.

Measured behavior	Life history stage														
	Pre-breeding			Nesting			Feedings fledglings			Molting			Non-breeding		
	STI period			STI period			STI period			STI period			STI period		
	pre-	STI	post-	pre-	STI	post-	pre-	STI	post-	pre-	STI	post-	pre-	STI	post-
Time within 5 m	6.84 ± 0.82^{a}	9.48 ± 0.60^{a}	8.99 ± 0.77^{a}	5.12 ± 0.66^{ab}	8.73 ± 0.48^{a}	7.38 ± 0.67^{ab}	1.73 ± 0.85^{c}	5.84 ± 0.62^{bc}	3.87 ± 0.79^{c}	1.61 ± 0.85^{c}	4.33 ± 0.62^{c}	2.88 ± 0.79^{c}	2.56 ± 0.78^{bc}	7.19 ± 0.57^{ab}	5.29 ± 0.72^{bc}
Closest approach (m)	3.38 ± 0.49^{a}	1.03 ± 0.30^{a}	1.09 ± 0.41^{a}	3.00 ± 0.39^{a}	1.12 ± 0.24^{a}	1.84 ± 0.33^{a}	6.67 ± 0.51^{b}	2.20 ± 0.31^{ab}	4.13 ± 0.42^{b}	5.80 ± 0.51^{b}	2.81 ± 0.31^{b}	4.47 ± 0.42^{b}	6.00 ± 0.46^{b}	2.31 ± 0.28^{b}	3.92 ± 0.38^{b}
Number of songs	9.38 ± 1.46^{a}	32.3 ± 2.98^{a}	25.5 ± 2.56^{a}	6.96 ± 1.17^{a}	31.1 ± 2.39^{a}	19.3 ± 2.05^{a}	0.20 ± 1.51^{b}	5.53 ± 3.08^{bc}	1.13 ± 2.64^{b}	0.00 ± 1.51^{b}	4.00 ± 3.08^{c}	3.07 ± 2.64^{b}	0.50 ± 1.38^{b}	17.1 ± 2.81^{b}	6.78 ± 2.41^{b}
Number of song-switches	0.06 ± 0.05a	0.94 ± 0.42^{a}	1.13 ± 0.21^{a}	0.08 ± 0.04^{a}	0.64 ± 0.17^{a}	0.07 ± 0.22^{ab}	1.84 ± 0.33^{a}	0.40 ± 0.44^{a}	0.07 ± 0.17^{b}	0.00 ± 0.05^{a}	0.13 ± 0.44^{a}	0.20 ± 0.22^{b}	0.00 ± 0.04^{a}	1.11 ± 0.40^{a}	0.39 ± 0.20^{ab}
Number of flights	6.84 ± 0.82^{a}	7.50 ± 1.54^{a}	4.19 ± 0.66^{a}	2.24 ± 0.24^{a}	5.48 ± 1.24^{a}	2.92 ± 0.53^{a}	1.84 ± 0.33^{a}	4.73 ± 1.59^{a}	1.47 ± 0.69^{b}	1.27 ± 0.31^{ab}	5.73 ± 1.59^{a}	2.00 ± 0.69^{ab}	1.06 ± 0.28^{b}	6.78 ± 1.46^{a}	1.56 ± 0.63^{b}
Latency	<>	0.59 ± 0.52^{a}	<>	<>	0.89 ± 0.42^{a}	<>	<>	2.50 ± 0.54^{ab}	<>	<>	3.84 ± 0.54^{b}	<>	<>	2.20 ± 0.49^{ab}	<>
Persistence	<>	<>	8.66 ± 0.78^{a}	<>	<>	6.98 ± 0.63^{ab}	<>	<>	3.64 ± 0.81^{c}	<>	<>	2.91 ± 0.81^{c}	<>	<>	5.27 ± 0.74^{bc}

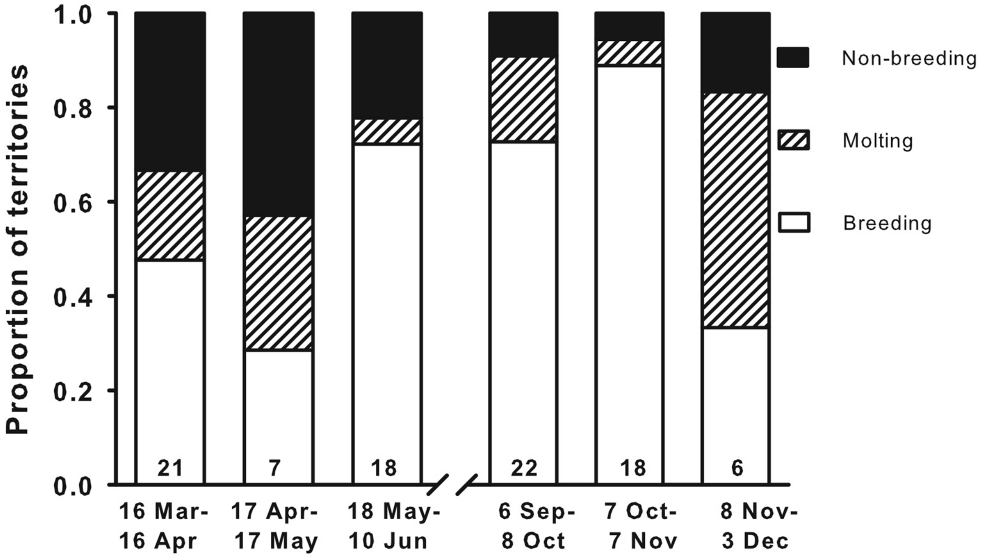

FIG. 2. The proportion of territories in each life history stage (LHS) during two periods (March - June and September–December 2007). For clarity, pre-breeding, nesting and feeding-fledglings LHSs were combined into a single 'breeding' category. Number of territories identified are at the bottom of bars. Note: three additional territories with known LHSs are included in this figure that could not be analyzed in the simulated territorial intrusion analysis.

maintained to defend territory space and quality habitat for nesting because these resources are essential for year-round mate attraction and/or to keep a current mate, in accordance with the mate attraction hypothesis. In this view, there is a shift from the significantly high aggression responses seen in pre-breeding and nesting males, directed at defense of paternity and food resources, to low territorial aggression, while males are primarily concerned with feeding fledglings or self maintenance, but still must maintain a hold on their "real estate" in order to keep their mate or for future mate attraction.

Our results demonstrate peak aggression responses during pre-breeding and breeding, despite the evidence that the focal population as a whole was markedly asynchronous. These results suggest that seasonality of aggression is determined at the individual level, not by the environment. Further, these data suggest that paternity protection may be an important selective force determining seasonality of aggression in the Las Caucheras population. During pre-breeding females are fertile and capable of extra pair copulations, thus resident males must defend against any intruding male, regardless of the number of neighboring males that are actually in breeding condition and could threaten paternity (Weatherhead & Yerzerinac 1998, Kokko 1999). Intriguingly, extra-pair fertilizations are common in this population, at rates comparable to highly seasonal temperate-zone breeding *Zonotrichia* despite population asynchrony of reproduction (Bonier unpub. data). Therefore, males must mate guard to resist cuckoldry. It is possible that commonly observed roaming groups of "floater" adults may pose a constant threat to adult males as they could be capable of extra-pair fertilizations over much of the year (Smith 1978, Busch *et al.* 2004).

An unexpected result of our STIs was that males had statistically indistinguishable high aggression responses not only during pre-breeding, but during nesting as well (see Fig. 1 including pre-STI and post-STI periods). Without the threat of extra-pair fertilizations of their females in later nesting periods, we suggest that male aggression responses during nesting may be directed at defending food resources for young and adults while they are tied most closely to territories. We did observe that *Z. capensis* generally spend more time gathering food resources within the territory during pre-breeding and nesting compared to when they are feeding fledglings, molting and not breeding, but future experiments could certainly clarify our casual observations by quantifying foraging time and compare food resource abundance and quality gathered within and around territories of pairs in different life history stages (AMC pers. observ.).

The switch from investing in mate and resource defense tightly associated with the territory area in pre-breeding and nesting, to investing in mobile young while adults are feeding fledglings and self maintenance during molting and non-breeding, may explain lower aggression scores during these life history stages. Thus, males that are feeding fledglings may be less aggressive as their primary concern is no longer directed at intruders threatening their paternity or resources, but to their highly mobile and needy fledglings. A similar shift in energetic and temporal investment may occur during molt, as it can present substantial energetic costs in sparrows (Murphy 1996, Schieltz & Murphy 1997, Weathers *et al.* 2003). Males that are feeding fledglings, molting, or not breeding are also not obligately dependent on their territories (Miller & Miller 1968), which suggests considerably less selective pressure for territorial defense.

In temperate-zone birds that establish breeding territories there is a characteristic decline in aggression and hormones controlling aggression, typically testosterone, from pre-breeding to nesting. This decline in testosterone is thought to occur because the hormone can interfere with the expression of paternal care and potentially can lead to misplaced aggression (Wingfield & Moore 1987, Wingfield *et al.* 2001). The relationships of testosterone and behavior that have been described in *Z. capensis* do not always follow patterns described in temperate-zone birds, even those of the same genus (Moore *et al.* 2004a, 2004b, Addis *et al.* 2010). In a Costa Rican population of *Z. capensis*, both testosterone and the stress hormone corticosterone appear to be modulated seasonally and at least somewhat independent of life history stage (Addis *et al.* 2010, Busch *et al.* 2010). Males in Ecuadorian *Z. capensis* populations do not appear to socially modulate testosterone levels but elevated testosterone does inhibit paternal care (Moore *et al.* 2004, Lynn *et al.* 2009). Given very low seasonality in the focal population, we predict that seasonal hormone variation may be very low in general, and that territorial behavior may be largely independent of androgen hormones, as suggested by several previous studies (Moore *et al.* 2004a, 2004b, Addis *et al.* 2010, Busch *et al.* 2010).

Though it is proposed that the most costly life history stages are under strong selection to overlap minimally (nesting and molting in the case of *Z. capensis*), life history stages are considered more likely to overlap in tropical resident birds (Jacobs & Wingfield 2000). Overlapping costly life history stages in tropical environments may be a function of less pronounced environmental seasonality constraining the timing of life history stages (Jacobs & Wingfield 2000). Though we are certain none of the males involved in this experiment were in overlapping life history stages, we did observe some individuals in overlapping life history stages, as have other studies of Z. *capensis* (e.g., Miller & Miller 1968, Addis *et al.* 2010, Busch *et al.* 2010). We are not sure how overlapping stages would influence territorial responsiveness and this would be worth exploring experimentally in the future.

The timing of life history stages and population-level synchrony. In our study population we observed every life history stage during each of the three-month long sampling periods, without an apparent trend toward seasonal breeding (Fig. 2). Populations of birds around the world rarely exhibit such strong asynchrony in reproduction (Baker 1938, Stutchbury & Morton 2001), but there are some conditions that could select for this, including nesting habitat limitation and inconsistent resource availability (Stonehouse 1962, Snow 1965, Ashmole 1968). For example, in some populations of tropical seabirds and perhaps in the focal population, high quality nesting territories may largely be filled, leaving many young and unmated birds "floating" as they wait for the opportunity for a random territory opening and/or mate, leading to asynchrony within the population as a whole (Stonehouse 1962, Ashmole 1968, Smith 1978). Though most Z. capensis populations studied to date are seasonal and synchronous, there is flexibility in breeding season timing in general (Moore et al. 2005). Thus, some pairs appear to be able to breed successfully during periods of the year when the majority of their population is not breeding, similar to previous findings by Miller and Miller (1968). The focal population exists in a humid equatorial environment, without strong seasonal changes in photoperiod, climate, or resource availability. In such conditions, it appears that seasonality occurs at the level of the pair rather than at population-level, suggesting that social cues between mates may be more important than environmental cues in organizing and timing reproduction.

ACKNOWLEDGEMENTS

Sincere thanks to los Flacos and la familía Luís for permitting us to use their land for research, in helping with maneuvering livestock, and in working around mist nets. Special thanks to J. F. Husak and P. Widder, who gave advice and critique on figures, statistics, and the manuscript. Thanks to B. G. Freeman, H. Wada, A. Kumar, C. Eikenaar, and J. R. Moore who provided valuable critique of manuscript drafts. Thank you to J. Chaves for help with our abstract translation. We also thank T.W. Small for logistical assistance and moral support and to P. Martin and S. Lynn for teaching specimen mounts techniques in the field. Funding was provided from the National Science Foundation (IOS 0545735 to ITM). The research described above adhered to animal care protocols by the IUCAC of Virginia Tech and Ecuadorian regulations.

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