A TEST OF THE FEMALE MIMICRY HYPOTHESIS IN PAINTED BUNTINGS (*Passerina ciris*)

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While female mimicry and lower status signaling hypotheses of delayed plumage maturation have received much discussion in the literature, the experimental tests of these hypotheses have been infrequent. Those experimental tests often use a simulated intruder method with artificial model intruders rather than using live conspecific birds as intruders. Subadult male painted buntings (*Passerina ciris*) possess delayed plumage maturation where they appear visually identical to adult females during their first potential breeding season, while adult males are strikingly different in plumage coloration. Here I test the behavioral responses in a territorial population of painted buntings that exhibits extreme delayed plumage maturation using a simulated territorial intrusion experiment to measure territorial male behavioral response when presented with live caged intruders of both subadult and adult males. Territorial adult males were significantly more likely to initiate an attack and continue to attack caged adult male intruders than compared to caged subadult male intruders. This result supports both the female mimicry and status signaling hypotheses, and does not support the cryptic hypothesis. Additionally, in anecdotal observations, territorial males occasionally performed mating display behaviors to caged subadult male intruders. These results further suggest that territorial male painted buntings may identify subadult males as potential mates, supporting the female mimicry hypothesis for subadult males in this species. To what degree subadult males may benefit from DPM deserves further study.

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A TEST OF THE FEMALE MIMICRY HYPOTHESIS IN PAINTED BUNTINGS (*Passerina ciris*)

General Introduction

My research investigates the behavioral ecology of the painted bunting (*Passerina ciris*), a dimorphic Neotropic migratory songbird. Painted buntings are of interest both to better understand color signaling in birds and because they are in need of conservation efforts. Painted bunting populations have steadily declined in recent decades and have been listed as a "species of concern" by the US Fish & Wildlife service and "near threatened" by the IUCN (BirdLife International, 2016; Sauer et al., 2017; USFWS, 2017). This species breeds in two most separate ranges in North America (Gilbert, Horne, & Trent, 2019) and each population has distinct migratory behavior and molt timing (Thompson, 1991a). My research uses members of the western breeding population, which has historically received less study than the eastern population, though that has begun to change in recent years (e.g., Contina, Bridge, Ross, Shipley, & Kelly, 2018; Contina, Bridge, Seavy, Duckles, & Kelly, 2013; Linck, Bridge, Duckles, Navarro-Sigüenza, & Rohwer, 2016). Understanding the behavioral ecology of this species will not only provide information to the understanding of basic avian research, but can also provide context for conservation efforts in the painted bunting's breeding range.

Figure 1: Adult male painted bunting.

Like many migratory songbirds, adult male and female painted buntings are strikingly dimorphic: females are camouflaged a dull brownish green, and adult males are bright blue and red with lime green shoulders (Inset image). In most songbird species, the males get their bright colors before their first potential breeding season, but in some species like the painted bunting, young males ("subadults") do not immediately gain all their adult coloration (Rohwer, Fretwell, & Niles, 1980; Lyon & Montgomerie, 1986), a phenomenon known as delayed plumage maturation (DPM). Various studies have found that DPM can serve different purposes in different species, so that there is no single explanation for this phenomenon (Hawkins, Hill, & Mercadante, 2012). Painted buntings are an unusual case of DPM, because subadult males are identical to females for their first breeding season (Lanyon & Thompson, 1986). Delayed plumage maturation may be adaptive for these young green males, specifically to mimic females. This might be beneficial by allowing subadult males to establish territories without facing aggression from older males (Rohwer, Fretwell, & Niles, 1980), or allowing them to sneak access to mated females (Lanyon & Thompson, 1986). Another explanation is that younger males might not yet have the skills to avoid attracting predators' attention, so they retain their camouflage for an extra year before acquiring their colorful adult plumage (Thompson, 1991b). In my research, I was interested in painted buntings as a possible case of female mimicry because young males all have coloration far more similar to females than is typical. Several species closely related to painted buntings also show DPM, but support for female mimicry is lacking in those species. For example, lazuli buntings (*Passerina amoena*) have DPM, but the young males are visually distinct from females, and conspecific males are aggressive toward young males but not toward females in their territories; in this example species, the available data are inconsistent with the female mimicry hypothesis (Muehter, Greene, & Ratcliffe, 1997).

To study the adaptive purpose of DPM and how DPM may influence painted bunting interactions during breeding season, I conducted a simulated intruder experiment to quantify how territorial adult males behave toward live intruders of different age classes. Whether or not my results support the female mimicry hypothesis, this would provide a new example of a rarely documented phenomenon to better understand the benefits or adaptive significance of female mimicry, and help frame future questions to explain why female mimicry is apparently rare in class Aves. My results will serve as an additional case study to contribute to our understanding of DPM in birds, and provide context about the reproductive behavior of a species of conservation concern.

An Experimental Test of the Female Mimicry and Lower Status Signaling Hypotheses in the Painted Bunting

Introduction

Delayed plumage maturation (DPM) is a condition in which young birds, or subadults, do not acquire their definitive adult plumage until after their first potential breeding season (Lowther, Lanyon, & Thompson, 2015). DPM occurs in birds across a wide range of taxonomic groups, body sizes, trophic levels, and habitat types, and while its function varies, there is increasing evidence that DPM is a product of adaptive mechanisms rather than a result of developmental constraints (Hawkins, Hill, & Mercadante, 2012). Potential adaptive hypotheses for DPM fall into three general functional categories: crypsis, status signaling, or mimicry of females.

The cryptic hypothesis proposes that inconspicuous subadult plumage decreases the risk of predation (Selander, 1956), and has no specific predictions about differences in aggression between age classes or about whether subadult male plumage is similar to female plumage. It seems logical that cryptic plumage would allow young birds more time to learn critical survival skills before acquiring more conspicuous adult plumage, particularly for species with brightly colored adult males. Some species where data appear to support the cryptic hypothesis include the American Redstart (*Setophaga ruticilla*), in which adult males are equally aggressive toward both adult males in definitive plumage and female-like subadult males (Procter-Gray, 1991). Despite this example, few studies have investigated this hypothesis directly, and studies on whether bright plumage increases predation risk have produced mixed results (Hawkins, Hill, & Mercadante, 2012). For the purposes of this study, I will take the view of Hawkins et al. (2012) that the cryptic hypothesis may apply to many bird species with DPM regardless of whether predator avoidance was the selective pressure influencing development of DPM. The cryptic hypothesis could apply to species with DPM without precluding either of the other two major hypotheses (status signaling and mimicry). Here, I focus on whether DPM serves primarily as a tactic to reduce predation, as in the cryptic hypothesis, or whether it serves as a signal to conspecifics, as in the status signaling or female mimicry hypotheses.

The female mimicry and lower status signaling hypotheses have some mutually exclusive predictions. The most commonly supported explanation for DPM is the lower status signaling hypothesis, which asserts that subadult plumage is an honest signal of subordinate status to reduce aggression by more experienced conspecifics (Lyon & Montgomerie, 1986). This hypothesis asserts that territorial conspecifics treat subadult males with reduced aggression compared to adult males, and that conspecifics are able to distinguish subadults from adult males. The female mimicry hypothesis asserts that first-time breeding males develop similar morphology to females to gain access to resources, such as familiarity with territories (Rohwer, Fretwell, & Niles, 1980) or to sneak copulations (Lanyon & Thompson, 1986). For example, Muehter et al. (1997) investigated the function of DPM in Lazuli Buntings (*Passerina amoena*) using a simulated intruder experiment, in which they compared territorial males' responses to model intruders painted to resemble adult males, subadult males, and adult females. Muehter et al. (1997) found that subadult male models were attacked and female models were not attacked, and adult males sometimes attempted to copulate with female models. They also found that subadult models were treated less aggressively than adults but more aggressively than female models, and concluded that DPM in Lazuli Buntings is consistent with the status signaling hypothesis and inconsistent with female mimicry. In a plumage analysis of a related species, Rohwer (1986) found that subadult male Indigo Buntings (*Passerina cyanea*) were visually distinct from adult females by March of their first potential breeding season, and their brown body plumage was replaced with mostly or entirely blue adult plumage the end of May. Based on this molt sequence, Rohwer concluded that female mimicry is unlikely to explain DPM in Indigo Buntings, whereas the lower status signaling hypothesis was supported. In both of these bunting species, the subadult male plumage is visually distinct from that of adult males and adult females, such that subadult males have a patchwork of blue definitive male plumage and brown female-like plumage (Pyle, 1997).

The female mimicry hypothesis predicts that the subadult male plumage is selected to mimic the plumage of adult females, resulting in conspecifics being unable to visually distinguish subadult males from adult females, and the subadult males receiving reduced aggression from adult males as a result. Although the female mimicry hypothesis has received much discussion over several decades in the literature (e.g., Procter-Gray, 1991; Rohwer & Butcher, 1988; Vergara & Fargallo, 2007), female mimicry has very rarely been supported in birds (Hawkins, Hill, & Mercadante, 2012). Based on my review of the literature, I found studies on four bird species that seem to support the female mimicry hypothesis (Chen, Xia, Dong, Lyu, & Zhang, 2019; Hakkarainen, Korpimaki, Huhta, & Palokangas, 1993; Jukema & Piersma, 2006; Slagsvold & Sætre, 1991).

Of those studies, female mimicry has probably been best demonstrated in two flycatcher species, the Pied Flycatcher (*Ficedula hypoleuca*) (Slagsvold & Sætre, 1991) and the Green-Backed Flycatcher (*Ficedula elisae*) (Chen, Xia, Dong, Lyu, & Zhang, 2019). In the Pied Flycatcher, males of all age classes display a morphological gradient, with plumages ranging from visually identical to females to strongly dimorphic (dark upper parts contrasting strongly with white patches). Slagsvold and Sætre (1991) used a simulated live intruder experiment to show that territorial male Pied Flycatchers attacked subadult intruders with male-like plumage, but responded the same to female and female-like male intruders. Meanwhile, resident females behaved aggressively toward female-like intruders, suggesting that subadult Pied Flycatchers were successful female mimics, able to deceive both male and female conspecifics. Chen et al. (2019) also used a simulated live intruder experiment to show that territorial male Green-Backed Flycatchers responded aggressively to adult intruders and had indistinguishable responses to subadult male and female intruders. This study also included plumage spectrophotometry measurements to account for differences in human and avian visual systems. They accomplished this by taking spectrophotometry measurements from six plumage patches to on adult males, subadult males, and females, and then calculated whether recorded color differences in spectrophotometry curves could be perceived by the birds, using a model of the visual system of the European Starling (*Sturnus vulgaris*) for reference. They found that conspecifics were unlikely to have the physical ability to distinguish visually between subadult and female plumages. The combination of findings by Chen et al. (2019) provide evidence to add Green-Backed Flycatchers to the short list of species potentially exhibiting female mimicry.

Here I examine the effect of delayed plumage maturation on the territorial behavior of adult painted buntings (*Passerina ciris*) in response to intruders of different age classes. The painted bunting is a sexually dimorphic Neotropical migratory songbird in which males aggressively defend breeding territories primarily through vocal and behavioral displays (Lanyon & Thompson, 1984). The subadult plumage of painted buntings is unusual among migratory passerines in that subadults consistently and nearly identically resemble adult females, rarely possessing any patches of definitive plumage (Lanyon & Thompson, 1986). Indeed, subadult painted buntings cannot be reliably sexed in the hand outside the breeding season, and even during the breeding season, the sex of some subadult individuals cannot be determined by experienced observers (Thompson, 1992). The definitive adult male plumage includes a bright green back, blue head, and bright red rump, underparts, and eye ring. In contrast, both subadult males and adult females have uniformly green plumage with no distinctive patch or marking (Fig. 1); both sexes occasionally have irregular small patches of blue feathers on the head (Pyle, 1997). This unusually female-like subadult plumage distinguishes the painted bunting from almost all other species exhibiting DPM, in which subadults have patches of adult-like plumage, such as their previously mentioned sister taxa Lazuli and Indigo Buntings. Additionally, based on the fact that subadult painted buntings undergo extensive body molt and the replaced feathers are the same female-like green (Thompson, 1991, 1992), subadult plumage is unlikely to be a result of molt constraint in this species (Hawkins et al, 2012). Painted buntings are therefore an ideal study species to test the female mimicry hypothesis.

To test whether subadult male painted buntings are treated less aggressively than adult males, I presented known territorial males with 20 live caged intruders (Slagsvold & Sætre, 1991). Simulated territorial invasion is the most straightforward way to test the function of DPM because it allows researchers to systematically observe interactions between wild individuals in a scenario very similar to natural encounters (e.g., Chen, Xia, Dong, Lyu, & Zhang, 2019). If the female mimicry hypothesis is supported, I would expect to see subadult male painted buntings treated not only less aggressively than adult males, but that subadults males would receive the same low level of aggression as females and possibly even mating displays (Sætre & Slagsvold, 1992).

Methods

Study Population and Capture Methods

This research took place using a color banded study population of painted buntings at the Lewisville Lake Environmental Learning Area (LLELA) in Lewisville, Denton County, Texas. LLELA is an approximately 1,000-ha nature reserve located at the transition between the Blackland Prairie and Cross Timbers ecoregions (Griffith, Bryce, Omernik, & Rogers, 2007). The study area is comprised of approximately 30 ha and includes a mosaic of tallgrass prairie, shrubland, and wooded habitat, and supports a median of 47 territorial males annually, or 1-2 territorial males per ha (Bednarz & Gurley, Unpubl. data). Adults and subadults have been captured and marked with metal USGS bands and unique combinations of color bands in this study area since 2017.

A preliminary version of the trial method was piloted in 2017 and refined to conduct trials during the 2019 and 2020 summer breeding seasons. Resident painted buntings arrive at this site in the last week of April and depart between late July and early August. Trials were conducted starting mid-May to allow territorial birds enough time to establish territories at the beginning of the season. I have observed gradual reductions in intensity of territorial behavior in the latter half of the nesting season, consistent with the seasonal plasticity in territorial behavior observed in numerous other songbird species (Brenowitz, 2004). Additionally, monitoring of painted buntings with radio-telemetry at this site suggests some of the territorial males begin to depart for migration during the final weeks of July (Bednarz & Gurley, Unpubl. data; see also Rohwer, Rohwer, & Wingfield, 2020). I therefore conducted the majority of trials in the first half of summer and concluded all trials by the second week of July.

New and previously marked adults were captured either with targeted mist netting or passive mist netting between dawn and about 1100 hours. Targeted mist nets (6 x 2.6 m; mesh 30 mm) using a playback of male song and a model painted as an adult male. Passive mist nets (12 x 2.6 m; mesh 30 mm) were deployed in sets of 9-10 nets and checked at least every 20 minutes. A unique four-band color combination was given to each captured bird, including a USGS metal band stamped with an identifying number and three color bands (i.e., two bands per leg). Subadult males were sexed in the hand based on a combination of factors, including wing molt characteristics (Thompson 1991b) and the presence of a large cloacal protuberance. Ambiguous individuals which could not be confidently sexed in the hand were not used as intruders in this experiment.

Territories of adult males were identified primarily by repeated spot map surveys supplemented with incidental observations. To conduct spot map surveys, the study area was divided into 2 grids with grid points marked 50 m apart. The surveyor walked along the marked grid points of one grid (i.e., half the study area) between dawn and 1100 hours, alternating grids and rotating start points so that each part of the study area was observed evenly across different months of the breeding season and across different times of day. At least 8 spot map surveys were conducted annually on each grid (half) of the study area between May and July. Once an adult male’s territory was identified, an appropriate location for each trial was determined in advance to ensure the trial could be observed accurately. Although subadults occasionally defend territories (pers. obs.), I have only used intruder trials where the resident was an adult male. To avoid potential neighbor effects related to the interactions of neighboring territorial males (Ydenberg, Giraldeau, & Falls, 1988), intruders were presented in territories at least 150 m from their capture location, and were never presented in territories contiguous to their capture location.

Field Intruder Trials

Experimental trials follow a similar setup to Slavgsvold and Særte (1991), in which a live caged “intruder” of known age and sex is placed temporarily in a conspecific’s territory, allowing me to record the responses of the resident male. To simulate territorial intrusion, a captured adult or subadult male was placed in a covered bird cage and transported to a documented adult male’s singing territory. The cage containing the intruder was kept covered during transportation, and the cage was uncovered after being placed in the territory selected for that trial. As the primary observer, I hid 10-30 m from the caged intruder before starting playback using a remote controlled speaker. I played a recording of the painted bunting primary song to attract the resident male within visual range of the uncovered cage, and confirmed resident male’s arrival based on hearing a song response or visual confirmation of a responder arriving. Playback was stopped when the resident male arrived, and then his behavior was recorded for 10 min. Specifically, I recorded the resident male’s number of songs, calls (e.g., chirps), approaches within 3 m of the cage, and attacks (landing on cage or swooping within 0.5 m). I also recorded additional behaviors such as the duration of each attack and number of wing quivers, if observed, and any change in the intruder’s behavior. Behavior terminology follows Lanyon and Thompson (1984) unless specified otherwise. To minimize stress to captive “intruders,” caged birds were used only in a single trial, were kept covered during transportation, and were immediately returned to their capture location and released after the completion of a trial.

The same resident was presented with both an adult and subadult intruder whenever possible to reduce potential error resulting from differences among resident responsiveness. In case an intrusion temporarily increased the responsiveness of a resident, the same resident was not presented with another intruder until at least 24 hours had passed since the last trial using their territory. Residents were never presented with more than one intruder per day. When the same resident was presented with more than one intruder, the order of which age class was presented first was opportunistic dependent upon which age class of intruder could be captured. A total of 23 trials were conducted, with eight trials with four residents that were shown both an adult and subadult caged intruders (adult first, n = 3; subadult first, n = 1) and 15 trials where the resident was shown only one age class of intruder (adult only, n = 5; subadult only, n = 10). A total of 6 control trials were also conducted, where residents were drawn in using playback and presented with an empty cage to quantify a baseline number of vocalizations in the absence of an intruder and to control for any change in behavior related to the cage itself. These controls were conducted in 2020 without a secondary observer. Residents were not presented with an empty cage first in the experimental trial sequence.

In trials where one observer could not see all the typical singing perches of the known resident, a secondary observer assisted with confirming the age class, arrival time, and identity (color band combination or lack of bands) of the resident. When present, the secondary observer was hidden 15-30 m from the cage before initiation of playback. The same primary observer recorded resident responses in all trials to avoid observer inconsistencies. Both primary observer and secondary observer (when present) wore cryptic clothing, hid behind shrubs or in tall vegetation before the start of playback, and did not move from their hidden location until after the conclusion of the trial. Observers were placed so their location would be partially concealed while still allowing direct sight of the cage. A secondary observer was present at all 2019 trials (adult intruder n = 6, subadult intruder n = 4), and some trials conducted in 2020 (adult intruder n = 1, subadult intruder n = 3). Eight trials were conducted with only a primary observer and no secondary observer in 2020 (adult intruder n = 1, subadult intruder n = 7) due to COVID-19 safety restrictions on shared field vehicles. One trial from the

2017 pilot study was included in the results of this study, and that trial used a secondary observer following this same protocol (adult intruder n = 1).

This research protocol was reviewed and approved by the University of North Texas IACUC (Protocol No. 18-013) and conducted under the appropriate state and federal permits.

Statistical Analysis

Resident responses to adult and subadult male intruders were compared using Mann-Whitney U tests. All statistical analysis was conducted using the stats package in R (R Core Team, 2019). Statistical analysis was repeated with the “complete” data and a “conservative” version of the data, in which up to 5 of 23 trials were removed from one or both datasets based on potential confounding factors observed in the field (n = 4) or due to responses being flagged as potential upper outliers (n = 1). The resulting complete dataset contained 21 trials, including 9 adult intruders and 11 subadult intruders, and the conservative dataset included 18 trials, with 8 adult intruders and 10 subadult intruders.

To prepare these two datasets for analysis, I assessed trials with one of three types of potential confounding factors in the field: (a) the age class of the resident could not be confirmed during the trial (n = 1), (b) a conspecific neighbor was singing from within 100 m of the targeted resident’s territory (n = 4), or (c) an additional green painted bunting besides the resident and intruder was present during the trial (n = 1). The trial in which the age class of the resident could not be confirmed was excluded from both datasets. The trial in which an additional green bunting was present was used in the complete data and excluded from the conservative data. In this trial, the unknown bird sat in the same tree with the resident during the trial, and the resident followed this other bird out of sight of the observers partway through the 10 min observation period and did not return.

For the 4 trials where another male was singing during the trial period within 100 m of the territory of the targeted resident, I excluded 2 trials from both versions of the data, and chose to include the other 2 because for the latter trials it appeared that the neighbor did not affect the responder's behavior. For the 2 trials that were excluded, these trials may have been affected because the neighbor was within 60 m of the responding resident. In both of the trials in question, the song timing of the resident matched that of the neighbor (countersinging) and both resident and neighbor were on high perches, likely allowing a direct line of sight between them. For comparison with one of the two trials that were not removed: in one trial, a conspecific song was audible roughly 60 meters away from the trial location during part of the trial period, but the resident remained singing from a low branch within 10 m of the caged intruder with a direct line of sight between them and no direct line of sight to the neighboring singer.

Trial results were also examined for potential outliers, specifically to identify whether any single trial had an unusually high or low quantity of responses compared to the median in trials with intruders of the same age. Potential outliers were flagged based on whether any values recorded fell outside the range of median ± 2 IQR (interquartile range), and each flagged trial was evaluated individually. Of these flagged trials, nothing in the field observations gave reason to suspect those data were outside the range of natural variability, nor were there any other confounding factors to indicate those trials should be removed. Only one trial had potential upper outliers in more than one behavior recorded; this trial was excluded from the "conservative" dataset as a precaution. Using these standards, Mann-Whitney U tests were repeated on two versions of the data to determine whether any particular trial was the tipping point between significant and non-significant difference.

Results

Responder Behavior

Most responses by territorial adult male painted buntings consisted of vocalizations, approaches, and attacks (Fig. 2). There was no significant difference in number of wing quivers, songs, or calls in response to intruders of both age classes (Fig. 2). There was no difference in total duration of approaches (amount of time spent within 3 m of cage), adult intruders were approached more often than subadults (Fig. 2c; p = 0.042). However, this difference became nonsignificant (p = 0.065) after the removal of one potential outlier (Table 1). Adult intruders were also approached more often than subadult intruders in the complete data set (p = 0.042), and borderline non-significant in the conservative dataset (p = 0.065; Fig. 1). In the complete data, subadult intruders were approached in 54% of trials (n = 6 out of 11 trials), and adult intruders were approached at least once in 78% of trials (n = 7 out of 9 trials).

The number and duration of attacks directed toward adult intruders was higher than toward subadult intruders, which were never attacked (Figs. 2-3). No subadult intruders were attacked during experimental trials (n = 11), compared to 5 trials where adult intruders were attacked (n = 5 of 9 trials). An adult intruder had a 56% chance of being attacked (n = 9, p = 0.007) in the complete data (Fig. 3), and a 40% chance of being attacked (n = 8, p = 0.017) in the conservative dataset. Attacks were usually brief, consisting of a dive toward or flyover the cage (i.e., only a few seconds in duration). Longer attempted attacks of 20 seconds or longer were observed in one trial with an adult intruder, and this trial had the highest total attack duration of any trial in this experiment. Attack duration was not recorded for the trial with the highest number of attacks, a trial which was conducted in 2017 and which was excluded in the conservative dataset due to the involvement of a different observer and being flagged for upper outliers in number of attacks and approaches.

There were two trials in 2019 in which the resident male displayed toward a subadult male intruder as though the intruder were a prospective mate. In one trial in 2019, the resident never approached close to the intruder, but remained more than 3 m from the intruder, and delivered a combination of songs, calls, wing quivers, bows, and lateral tail flicks. This was one of only two trials in which I observed wing quivers (one trial with an adult intruder and one with a subadult intruder) and the only trial where a resident was observed performing definitive courtship behaviors. In a different trial in 2020, I observed similar lateral tail flicks by a resident toward a subadult male intruder, with no accompanying display behavior, no approaches, and no attacks.

Trial results were assessed for potential confounding factors, and two versions of the data were developed: the complete data and the “conservative” data. Trials with potential confounding factors or potential outliers resulted in response rates and p-values similar to trials in which no such factors were present. Each potential outlier is nearly always the only outlier among all the behaviors recorded for that trial (Fig. 2). For example, a trial might show a potential upper outlier in number of songs, but have all other behavior count and duration values within the expected range (i.e., within ± 1.5 IQR of the median). In fact, there is only a single trial recorded that contains more than one outlier; in this 2017 trial, an adult intruder was approached and attacked enough times for those values to be flagged as potential upper outliers. To exercise caution, this trial was removed from the conservative dataset; this removal may have contributed to the number of approaches not being significant in the conservative dataset (Fig. 2).

Intruder Behavior

Once the bird that served as an intruder was caught for the experiment, he initially attempted to escape the cage by fluttering against its walls, but appeared to become calm and used the perches within the cage within 5 min of the observer(s) being partially out of sight (see methods) and before the start of playback. During the trials, intruders either moved to the opposite side of the cage to avoid attacks by the resident male, moved within the cage but in no consistent direction, or fluttered near or landed briefly on the cage wall regardless of when a resident was nearby. Further, none of the birds serving as intruders were observed to vocalize while in the cage, so residents likely could not use vocal cues to identify the sex of a subadult male. All individuals used as intruders were in good condition and flew without apparent difficulty at their time of release.

Empty Cage Control Trials

In contrast to the intruder trials, residents never attacked an empty cage during the control trials. Intruder trial data was not adjusted using baseline information from control trials because only 3 of 6 control trials could be considered valid under the same standards as trials with caged intruders. This was due to either (1) difficulty getting residents to approach trial area within sight of the observer, or (2) the presence of a countersigning conspecific neighbor, so that the vocal responses of the resident might have been directed at a neighbor rather than at the empty cage. In attempted trials where the targeted territorial male was never observed, it is possible that he might have been attracted to the trial area by playback, but because there was no intruder, the responder did not move far enough into the trial area to be recorded by the observer.

Discussion

My results indicate that delayed plumage maturation serves an adaptive function in conspecific interactions in painted buntings, consistent with both the female mimicry hypothesis and the status signaling hypothesis. Territorial males responded to adult male intruders more aggressively than subadult male intruders; adult intruders were more likely to be approached, and they were attacked more often and for a longer duration than subadult males. Aggression between male painted buntings often involves one male flying toward the other (i.e., “butterfly flight” and “flutter up” attacks (Lanyon & Thompson 1984), which were recorded as attacks in this study. While this study did not quantify behavior toward subadult males, they did record interactions between adult males and females, and found that adult males were more likely to direct these aggressive behaviors toward other males than toward females and green birds of unknown sex. A difference in attack frequency and intensity is the most clear indicator of a difference in aggression between groups, and my results indicate that that adult males respond to other adult male intruders as a greater threat compared to subadult males (Figs. 2 and 3).

The lack of difference in vocal displays toward intruders is difficult to interpret, because vocal displays cannot be identified as definitively aggressive without the presence of additional aggressive behavior. Songs and calls can serve multiple functions depending on context; the same male song might serve as a territorial warning or an advertisement to a potential mate (Berglund, Bisazza, & Pilastro, 1996). A resident male might reasonably be expected to sing in the presence of either a male competitor or a female potential mate. Thus, a resident singing in the presence of a female-like male is not necessarily a helpful indicator of whether the female mimicry hypothesis applies. While it has not been shown whether male song is used in mate attraction in painted buntings, male song is well established as an honest signal of quality used by females to select mates (e.g., Ota & Soma, 2014; Poesel, Kunc, Foerster, Johnsen, & Kempenaers, 2006). Male song could therefore be reasonably expected to serve that function in painted buntings, so an adult male could use similar song intensity in the early stages of an encounter with either potential competitor or a potential mate.

Number of approaches and wing quivers are similarly equivocal. There is a trend toward adult male intruders being approached more often, and when accompanied by an increased chance of attacks, this seems consistent with higher aggression toward adult male intruders. A lack of responses toward empty cages compared to both classes of intruder indicates that songs, calls, and approaches were likely directed specifically toward the intruders rather than general responses to playback. Note that playback was used before but not during experimental trials: playback was used to attract residents to the trial area and stopped once the resident arrived, so that trials’ 10 min observation period did not overlap with playback use.

During this study, I observed two instances where an adult male exhibited behavior toward subadult males consistent with mating displays, which I cautiously suggest supports the possibility of female mimicry by subadult males. In the most interesting example, an adult male did not attack the cage and performed wing quivers, bows, and lateral tail flicks in direct line of sight of the caged subadult male. In their observations on painted bunting visual displays, Lanyon and Thompson (1984) reported that wing quivers can be used in both territorial and courtship displays, and that bows are typically performed in the presence of a female. Lateral tail flicks were not reported in Lanyon and Thompson's systematic assessment of painted bunting displays, nor in the observational account by Parmelee (1959). In the two cases I observed, lateral tail flicks were not accompanied by attacks, so it is possible that this serves as a non-aggressive display behavior. The female mimicry hypothesis specifically predicts such cases, while the lower status signaling hypothesis does not require subadult plumage to be identical to that of females. These interactions do not provide definitive support for female mimicry, but do indicate that at least some subadult males are mistaken for females, and perhaps that a territorial male uses a combination of plumage and behavioral cues to infer the sex of an intruder. For example, male Satin Bowerbirds (*Ptilonorhynchus violaceus*) adjust mating displays based on subtle cues from females that would be difficult to observe in most behavior experiments (Patricelli, Coleman, & Borgia, 2006). Thus, males of other species, perhaps including the painted bunting, might be able to rely more heavily on behavioral responses to determine the sex of conspecifics in species with ambiguous subadult plumage.

A limitation of this study is the relatively small sample size of trials, resulting in low statistical power. This sample size was mostly due to the inherent challenges of using live, wild-caught birds as territory intruders, including the time required to conduct each trial while accounting for ethical treatment of birds being presented as intruders. The use of live intruders in a simulated intruder experiment involves much greater logistical challenges than using models; however, I suggest that live intruders add movement and likely subtle behavioral cues that are completely lacking by using an inanimate model (Scriba & Goymann, 2008; Tryjanowski, Morelli, Kwieciński, Indykiewicz, & Møller, 2018). Using wild-caught intruders necessitates using many different individuals, and though this adds greatly to the time required per trial, it means that the intruders represent a range of individual variability, which would not be present in repeated experiments using the same or a few non-live models. The strong statistical patterns in my data, despite relatively low statistical power, indicate a real difference in territorial behavior toward intruders of different age classes of painted buntings.

Some studies have used painted models, which are easier to produce than taxidermy models, and either type of model would remove the logistical limitations of using live models. However, painted models may be an unreliable stand-in for live birds when the study population has previously encountered models in the context of targeted mist netting. Passerines may learn to avoid various capture methods (Camacho, Canal, & Potti, 2017; Roche, Brown, Brown, & Lear, 2013) and possibly specific lures through experience (Linhart, Fuchs, Poláková, & Slabbekoorn, 2012). In the study population used for this experiment, previously captured males seem to be more difficult to recapture with audio and model lures compared to naïve individuals. The past use of a model as a lure might therefore be a confounding factor in a territorial invasion experiment.

More importantly, painted models may not be a suitable alternative to taxidermic models, because they may not account for dimorphism in the ultraviolet spectrum between subadult male and female plumages. Plumage reflectance in the UV is sometimes present in species with DPM where subadult and female plumages appear identical in the spectrum visible to human observers (Morales-Betancourt & Castaño-Villa, 2018; Benítez Saldívar & Massoni 2018); however, dimorphism between subadults and females has not been assessed for painted buntings. Chen et al. (2019) emphasized that whether conspecifics are able to visually distinguish between subadult and adult plumages is highly relevant to questions of DPM function.

To distinguish between the lower status signaling hypothesis and the female mimicry hypothesis in painted buntings, a useful test would be to compare responses to simulated territory intrusion by females versus subadult males. To do this, I recommend planning to complete female trials as soon as territories are established at the beginning of the field season, and using multiple capture strategies to ensure a sufficient number of females can be captured (e.g., systematic passive netting as in Springborn & Meyers, 2005). Future research would be able to achieve a larger sample size and cover a more representative range of individual variation in green birds if such individuals were used in behavior experiments and their sex determined later using genetic methods (e.g., Çakmak, Akın Pekşen, & Bilgin, 2017).

While the role of the subadult male painted bunting plumage remains unclear in multiple aspects of their reproductive ecology, my research suggests that DPM in the painted bunting is consistent with the female mimicry and status signaling hypotheses. Additional research is warranted to quantify the role of subadults in territorial and reproductive behavior in this species. A few studies have variously described its breeding system as both monogamous and polygynous without providing supportive results for either breeding strategy (Lowther, Lanyon, & Thompson, 2015). Subadult males have often been explicitly excluded from studies of painted bunting reproductive behavior (Lanyon & Thompson, 1984; Springborn & Meyers, 2005). One recent study that included subadult males suggests that male age class influences male-male interactions and population density in at least one point in their life history (Rohwer, Rohwer, & Wingfield, 2020). Painted buntings in the western half of the range molt at migration stopover sites during the fall, and display high aggression before the initiation of molt. At one of these stopover sites, adult males displaced conspecifics including subadults and adults, while green birds never displaced adult males in aggressive conflicts (Rohwer, Rohwer, & Wingfield, 2020). These results indicate that subadult males should not be assumed to behave the same as adult males, and I suggest this should be extended to studies of breeding behavior as well. During the breeding season, subadult male painted buntings do at least occasionally defend territories (Lanyon & Thompson, 1986; pers. obs.), which may be a critical limiting resource for reproductive success, as high site fidelity has been reported in this species for all age-sex classes at human supplemented feeding sites (76% annual return rate; Sykes et al., 2019) and for both age classes of males at territory sites (50-76% of males occupied the same territory in consecutive years; Lanyon & Thompson, 1986). Further investigation of the function and behavioral implications of DPM in painted buntings are relevant both forming a more complete understanding of this species' life history and to a general understanding of the selective mechanisms behind female-like subadult plumages.

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Table 1: P-values from Mann-Whitney U tests comparing responses by territorial adult males to adult and subadult caged intruders. Significant p-values are indicated with an asterisk (*). Results are shown for the complete dataset and a conservative version; the latter was defined by removing trials with potential confounding factors, such as the presence of a singing male in a neighboring territory (see methods).

	Dataset			
	Complete		**Conservative**	
n Adult trials	11		10	
n Subadult trials	9		8	
Statistic				
	p	U	p	U
Song count	1.000	50	0.965	39
Call count	0.690	55	0.739	44
Approach count	0.042 *	23	0.065	19.5
Attack count	0.007 *	22	0.017 *	20
Attack duration (sec)	0.013 *	22	0.017 *	20
Wing quiver count	1.000	39.5	1.000	36

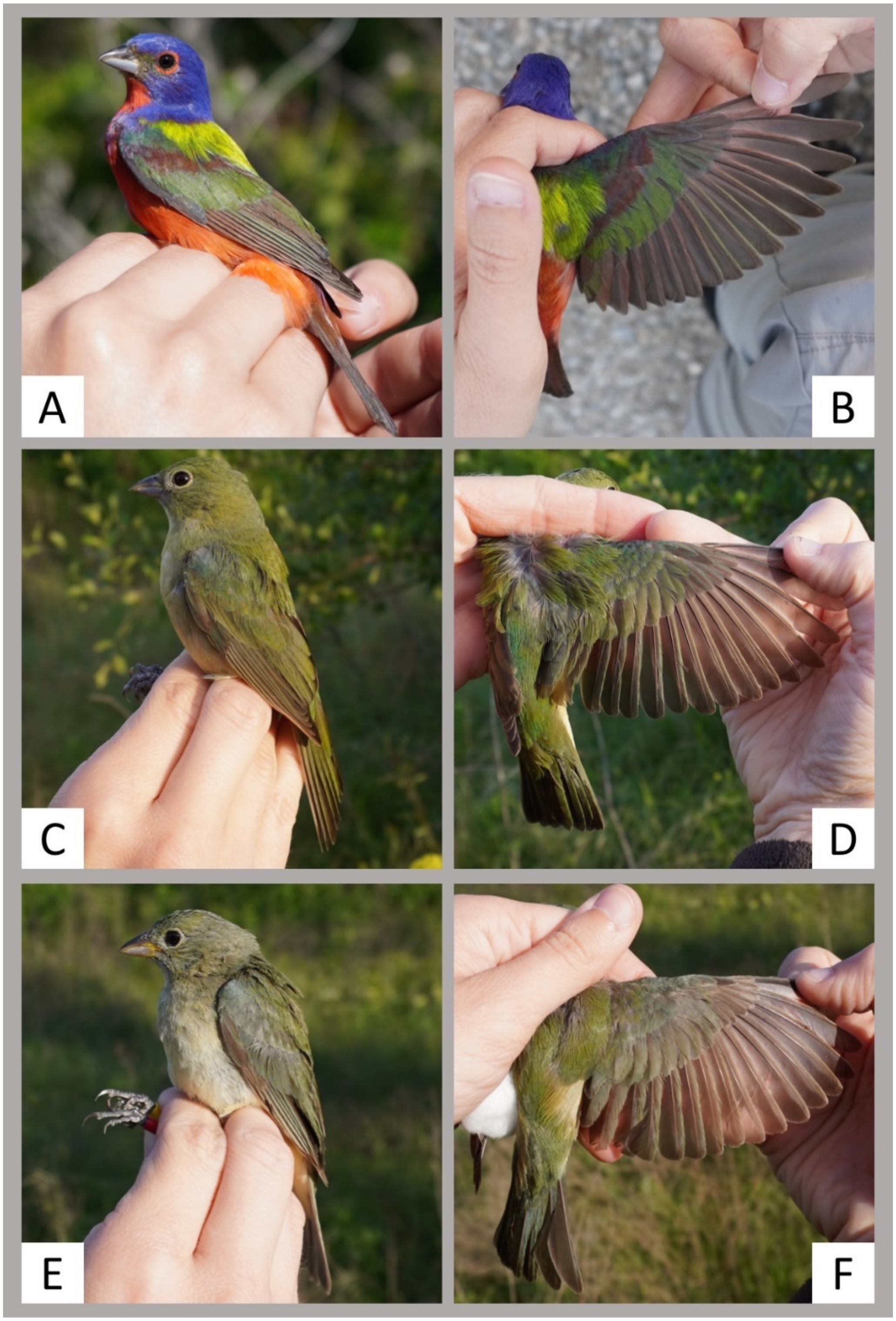

Figure 2: Typical summer plumage of painted buntings (*Passerina ciris*): adult male (A - B), adult female (C - D), and subadult male (E - F). Each pair of images are different views of the same individual.

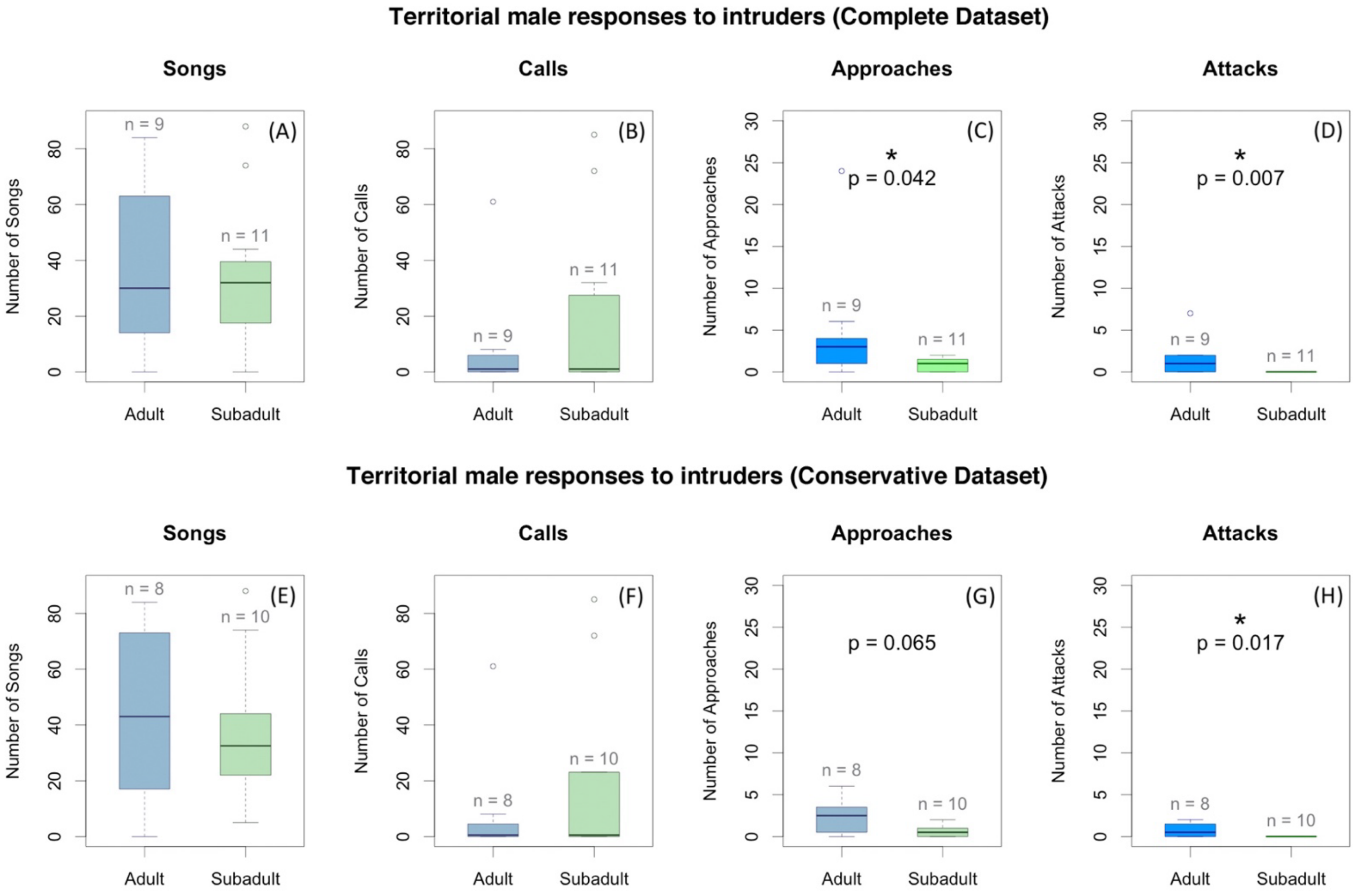

Figure 3: Comparison of resident adult male responses to adult and subadult male intruders for two datasets (complete, A-D, and conservative, E-H). Measured responses included number of songs, calls, approaches within 3 m of the intruder, and attacks (i.e., dive within 0.5 m of intruder). A total of 2 trials were excluded in the conservative dataset due to potential confounding factors (see methods).

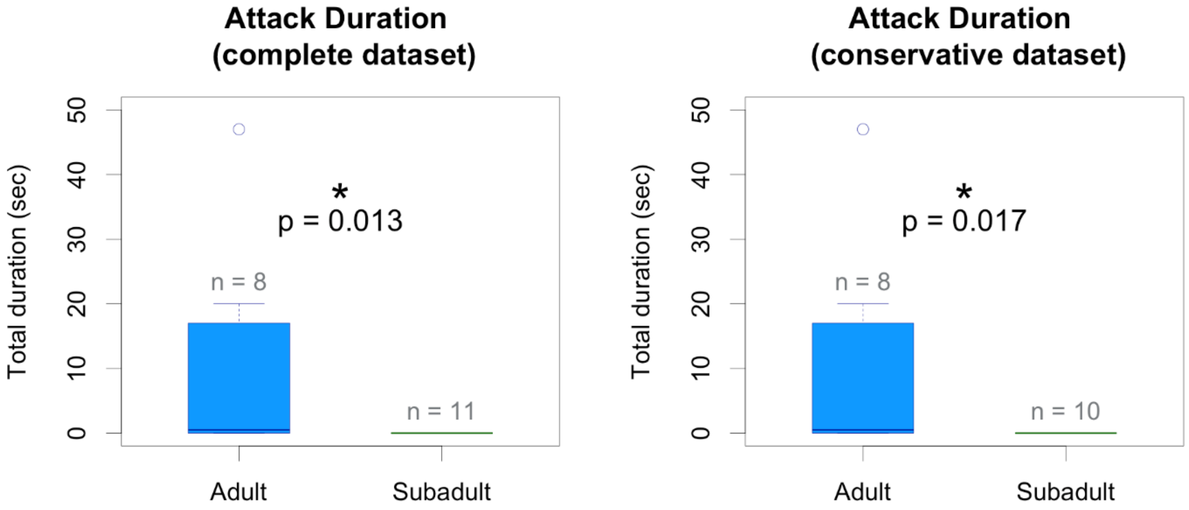

Figure 4: Comparison of total duration of attacks (seconds spent diving at or landing on cage containing intruder) by resident males in response to adult and subadult male intruders. Two trials were excluded in the conservative dataset due to potential confounding factors; because attack duration data was not available for one trial, however, effectively only one trial was excluded for comparison of this measure (see methods).

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