Received: 20 December 2018 | Revised: 8 April 2019 | Accepted: 10 April 2019
DOI: 10.1111/eth.12881

RESEARCH PAPER

ethology International journal of behavioural biology WILEY

Evaluating seasonal patterns of female aggression: Case study in a cavity-nesting bird with intense female–female competition

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Funding information
National Science Foundation, Grant/Award Number: IOS-1656109; Indiana University Department of Biology

Editor: Walter D. Koenig

Abstract

Seasonal plasticity in aggression is likely to be shaped by the contexts in which aggression is beneficial, as well as the constraints inherent in its underlying mechanisms. In males, seasonal plasticity in testosterone (T) secretion is thought to underlie seasonal plasticity in conspecific aggression, but it is less clear how and why female aggression may vary across different breeding stages. Here, we integrate functional and mechanistic perspectives to begin to explore seasonal patterns of conspecific aggression in female tree swallows (*Tachycineta bicolor*), a songbird with intense female–female competition and T-mediated aggression. Female tree swallows elevate T levels during early breeding stages, coinciding with competition for nest boxes, after which time T levels are roughly halved. However, females need to defend ownership of their nesting territory throughout the breeding season, suggesting it may be adaptive to maintain aggressive capabilities, despite low T levels. We performed simulated territorial intrusions using 3D-printed decoys of female tree swallows to determine how their aggressive response to a simulated intrusion changes across the breeding season. First, we found that 3D-printed decoys produce data comparable to stage-matched studies using live decoys, providing researchers with a new, more economical method of decoy construction. Further, female aggressiveness remained relatively high through incubation, a period of time when T levels are quite low, suggesting that other mechanisms may regulate conspecific female aggression during parental periods. By showing that seasonal patterns of female aggression do not mirror the established patterns of T levels in this highly competitive bird, our findings provide a unique glimpse into how behavioural mechanisms and functions may interact across breeding stages to regulate plasticity.

KEYWORDS
3D-printed decoy, behavioural plasticity, breeding season, female, simulated territorial intrusions, *Tachycineta bicolor*

1 | INTRODUCTION

Male–male competition for limited breeding resources has been the focus of research for decades (Andersson, 1994; West-Eberhard, 1983), while female–female competition has remained comparatively less studied (Hrdy, 2013). Nevertheless, competition among females occurs in many of the same contexts as males (Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011), and females express a variety of competitive traits that give them an advantage in female–female competition (Tobias, Montgomerie, & Lyon, 2012). For instance, females that are more aggressive towards conspecifics may be better able to acquire breeding territories, maintain monogamy, secure paternal investment, or have higher reproductive success (Cain & Ketterson, 2012; Dunn & Hannon, 1991; Gowaty & Wagner, 1988; Jawor, Young, & Ketterson, 2006; Langmore, Cockrem, & Candy, 2002; Rosvall, 2008, 2011a; Sandell, 1998; Stockley & Bro-Jørgensen, 2011). However, aggression can also be costly due to increased risk of injury and demands on time and energy (Brown, 1964), which contribute to trade-offs with other behaviours, like parental care (Cain & Ketterson, 2013; Stiver & Alonzo, 2009). Cost–benefit perspectives like this are common in animal behaviour (Johnstone, 1997), although they are less frequently applied to questions of competitive traits in females (Cain & Rosvall, 2014).

The costs and benefits of conspecific aggression can vary seasonally depending on mating system, parental care systems, and other life history traits or ecological factors. As such, females may be expected to also seasonally modulate aggressive behaviours, at least to the degree that plasticity allows (Sih, Bell, Johnson, & Ziemba, 2004). For example, females of territorial species might benefit by displaying heightened aggression towards conspecifics during territory acquisition, followed by reduced aggression as territories become more established (Gowaty, 1981). On the other hand, females of species with biparental care may increase conspecific aggression as parental roles develop later in the breeding season to secure exclusive paternal investment (Gowaty, 1981; Slagsvold & Lifjeld, 1994). These patterns of aggression have been most thoroughly studied in birds, in which all these life history traits and ecological factors are relevant. However, studies often find that female aggression peaks prior to egg laying and decreases during incubation and nestling rearing, with only a handful of studies reporting sustained aggression across the season or peak aggression during parental phases (reviewed in Slagsvold & Lifjeld, 1994). These findings suggest there could be a species or sampling bias (such as fewer studies during parental periods) or that behavioural flexibility is ultimately constrained by its underlying mechanisms, which may not always be congruent with optimal functioning (Duckworth, 2010; Lessells, 2008; McNamara & Houston, 2009).

Mechanistic explanations for seasonal plasticity in aggression are well studied in temperate-breeding males, where conspecific aggression typically peaks during the period of territory and mate acquisition, and declines during parental phases (Wingfield, Hegner, Dufty, & Ball, 1990). This pattern is thought to stem from trade-offs between aggression and parental care that may be mediated by the sex steroid testosterone (T) (Lynn, 2008, 2016; Wingfield et al., 1990). Levels of T in circulation often parallel seasonal changes in male aggression, peaking early in the breeding season when male–male competition for mates and territories is at its highest, and then declining during parental care (Goymann, Landys, & Wingfield, 2007; Hirschenhauser & Oliveira, 2006; Lynn, 2008, 2016; Wingfield et al., 1990). Whether this mechanistic constraint applies to and would therefore shape seasonal patterns of aggression in females is less clear (Goymann & Wingfield, 2014; Ketterson, Nolan, & Sandell, 2005).

Tree swallows (*Tachycineta bicolor*) are uniquely positioned to bring together these functional and mechanistic perspectives for a greater understanding of how female–female aggression varies across the breeding season. Tree swallows are single-brooded, obligate secondary cavity-nesting songbirds, meaning that they require a cavity for nesting but lack the ability to excavate one themselves (Winkler et al., 2011). Females play an important role in competition for these often-limited sites, with more aggressive females outcompeting less aggressive females (Rosvall, 2008). This female–female competition is thought to relate to the female-biased delayed plumage maturation observed in this system, which is otherwise quite rare (Lyon & Montgomerie, 1986). Specifically, females in their first breeding season exhibit a brown plumage that is distinct from the iridescent blue-green plumage of older females and all males (Hussell, 1983) and potentially serves as a subordinate status signal, thereby mitigating received aggression from conspecifics (Lozano & Handford, 1995; Stutchbury & Robertson, 1987a, 1987b). Recent studies have begun to explore the mechanisms of aggression in this species and show that, at least in part, T mediates female aggression and trade-offs with maternal care (Rosvall, 2013a). Experimentally elevated T enhances female aggression to simulated territorial intruders, but it can reduce incubation behaviours, demonstrating that elevated T levels would be costly via effects on maternal care (Rosvall, 2013a). Unsurprisingly, T levels in female tree swallows decline as the breeding season progresses, with marked T production during territory establishment and nest building, followed by a precipitous decline during incubation and nestling rearing (George & Rosvall, 2018). From a functional perspective, though, the necessity of conspecific aggression may remain high throughout the breeding season, even after territories have been claimed and laying has begun. Most tree swallow populations have numerous non-territorial “floaters” that have not yet acquired a nesting cavity and can evict or even kill females, their eggs, or offspring, while seeking a cavity (Leffelaar & Robertson, 1985; Stutchbury & Robertson, 1987a). Thus, females may need to maintain the ability to be aggressive towards conspecifics during later stages of breeding, even after the decline in systemic T has begun. Past observational work suggests that rates of aggressive interactions between females decline as the breeding season progresses (George & Rosvall, 2018; Robertson, Gibbs, & Stutchbury, 1986), although there are a few exceptions suggesting that rates of aggressive interactions can remain relatively high during parental periods (Harris, 1979; Stutchbury & Robertson, 1987a). Rates of naturally occurring interactions, however, are sensitive to population-level factors and do not clarify patterning in the *ability* to be aggressive. Usurpations have been observed during both incubation and nestling stages (Leffelaar & Robertson, 1985), suggesting the ability to aggressively defend a territory is still critical. However, we are not aware of any study that has experimentally tested (i.e., with simulated intrusions) how female aggressiveness towards conspecifics changes across multiple breeding stages.

In the present study, our primary goal was to determine how aggressive capabilities change across the breeding season in female tree swallows. We measured aggressive responses to same-sex conspecific simulated territorial intrusions across four breeding stages. If female aggression is constrained by seasonal variation in circulating T levels, as is thought to be the case in temperate-breeding males (Wingfield et al., 1990), then seasonal patterns of female aggression will parallel established seasonal changes in circulating T levels (George & Rosvall, 2018), i.e., with marked aggression until later parental stages when T levels drop. However, if other mechanisms regulate aggression in females or if these mechanisms change across the breeding season, then aggressive capabilities may persist during later breeding stages, beyond the decline in T that occurs at the beginning of incubation. If aggression is decoupled from circulating T, this would allow greater flexibility in its functional use, which might be expected based on the degree of competition for territories in this species. As a secondary goal, we tested the use of novel, 3D-printed decoys in simulated territorial intrusions. Many past studies have used live birds to simulate a territorial intrusion, which have the benefit of providing many of the naturalistic cues associated with a real intrusion, but they pose additional risks too, such as unpredictable behaviour, animal welfare concerns, and they necessitate a protective cage that can interfere with behavioural assays (by obstructing interactions or causing neophobia; Scriba & Goymann, 2008). Taxidermic models have also been used as decoys, but high-quality mounts can be expensive and difficult to find, thus also warranting a protective cage (Scriba & Goymann, 2008). It can also be difficult to have numerous live or taxidermic models, which introduces pseudoreplication into experimental designs. To overcome these issues, we developed a fast and economical method to construct decoys using salvaged animal skins and a 3D printer. We tested the reproducibility of our findings with previously published data obtained from simulated territorial intrusions with live decoys in this same species (Rosvall, 2008, 2010, 2011b, 2013a). Ultimately, this work integrates functional and mechanistic perspectives to explore seasonal plasticity in female aggression using a new method of decoy construction to measure behaviours.

2 | METHODS

2.1 | Study population

We monitored breeding tree swallows located near Bloomington, Indiana (39°9N, 86°31W), between Apr. and Jul. 2016. As part of our population monitoring efforts, birds were captured in their nest boxes and given unique numbered USGS aluminium bands on one leg and a plastic colour band on the other leg. Birds were also individually marked with non-toxic acrylic paint to facilitate identification during flight. Individuals were sexed using a combination of morphology (cloacal protuberance in males or a brood patch in females, and wing chord length), behaviour, and/or plumage coloration (Stutchbury & Robertson, 1987b). Female T concentrations were measured across the breeding season in individuals that were also from this population in the same year and can be found in George and Rosvall (2018). This study was approved by the Bloomington Institutional Animal Care and Use Committee under protocol #15-004.

2.2 | Decoy construction

The 3D model was developed by scanning a taxidermied female tree swallow, which had been posed in an aggressive posture that is characteristic of this species (Figure 1a). See supplementary material for full step-by-step details of decoy construction, including 3D print files (see "3D-printed decoy protocol" and Figure S1). To summarize, decoys were printed with polylactic acid at 0.2 mm layer height with 10% infill using a MakerBot Replicator fifth generation 3D printer (MakerBot Industries). The model was then covered in real tree swallow skin/feathers (Figure 1b,c) collected from after-second year

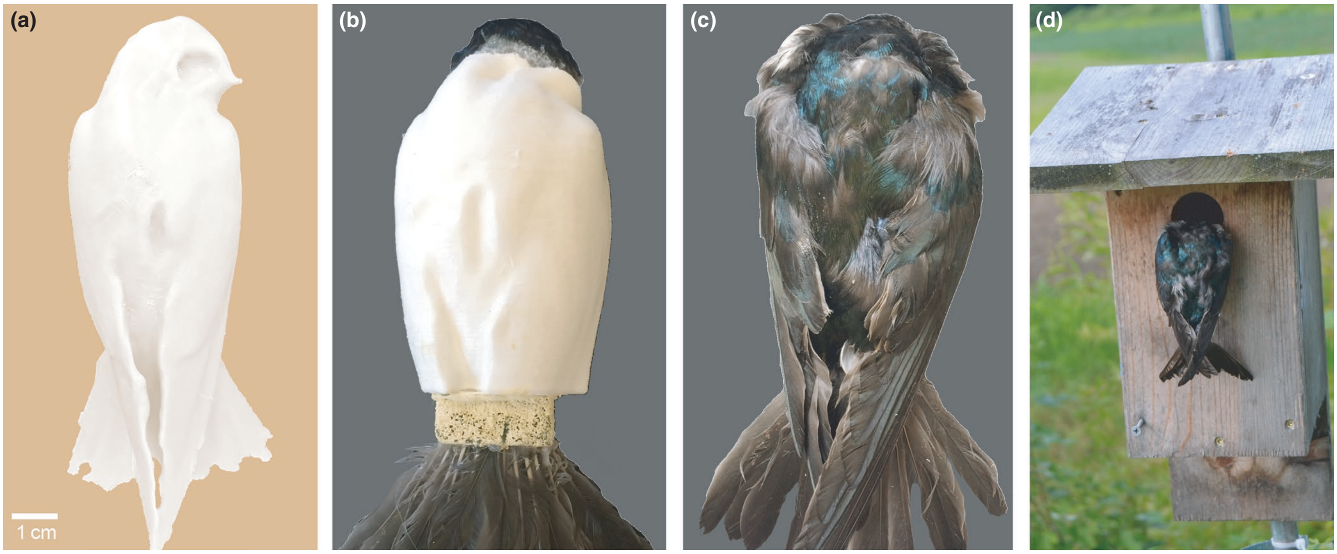

FIGURE 1 (a) Tree swallow 3D-printed decoy, (b) tail and scalp feathers attached to bodice, (c) bodice covered with salvaged tree swallow skin/feathers, and (d) decoy placed at a nest box in a defensive posture [Colour figure can be viewed at wileyonlinelibrary.com]

females in our study population that we euthanized or salvaged. All deceased females were found in nest boxes following natural bouts of competition or inclement weather. We removed the skin/feathers in three pieces: (a) the scalp, (b) tail, and (c) the rest of the dorsal surface of the body, including intact wings. Skins were dried with corn starch in a hood for at least 24 hr, after which the fully feathered dorsal surface was attached to the 3D-printed bodice along with a head, constructed by adhering the scalp to a Styrofoam ball to which the beak (or one constructed from hot glue) and "eyes" (craft beads) had been attached. Tail feathers were arranged in floral foam and adhered to the posterior side of the 3D-printed bodice.

2.3 | Simulated territorial intrusions

We performed simulated territorial intrusions during four breeding stages: territory establishment (females are engaging in aggressive interactions at nest sites to defend territory ownership, but none had a complete nest), nest building (nest material is present but no eggs), incubation (eggs warm), and nestling rearing (nestlings present). We assayed aggression in 50 individual females, 17 of whom were opportunistically measured in multiple breeding stages (14 in two breeding stages and 3 in three breeding stages) for a grand total of 70 trials. The final behavioural assay performed was during the nestling stage on Jun. 6, which was prior to the cessation of laying (birds were continuing to initiate nests until Jun. 13), suggesting late-arriving and floater females still represented a threat to territory-holding females.

Simulated territorial intrusions were modified from Rosvall (2008) to use the 3D-printed decoys. Six unique decoys were created and randomized across trials. Decoys were placed at nest box entrances in a defensive posture (Figure 1d) and paired with audio playback of aggressive conspecific calls for 5 min. Audio playbacks were broadcast via an iPod connected to an Altec iM237 speaker camouflaged on the back of the nest box, a few inches from the decoy. During the 5-min trial, we used a digital voice recorder to document behaviour of the focal female, and we also documented whether her mate was present. Heterospecific competitors were not present during trials. We calculated aggression score as the total number of 5-s intervals during which the female displayed aggressive behaviours, including contact with decoy (pecking, perching, or directly hitting), swooping at, or hovering within 0.75 m of the decoy (Rosvall, 2008). In addition, we recorded whether the focal female escalated to physical contact with the decoy at any time during the trial. Physical contact typically involved perching on and pecking the decoy around the head, neck, or eyes.

2.4 | Statistical analyses

We analysed seasonal changes in aggression score and probability of physical attack in separate generalized linear mixed effects models, with negative binomial and binomial distributions, respectively. Female ID was included as a random effect to account for some females being assayed in multiple breeding stages. In initial testing, we asked whether decoy ID, mate presence, or female age had any influence on aggression or probability of physical attack. As in previous work (Rosvall, 2008), we found no effect of these variables (all $p > 0.28$), and so, we excluded them from the final models. Statistical analyses were performed using R (v. 3.4.3, R Core Team, 2017), and all means are followed by *SE* unless otherwise stated.

An important consideration when measuring how behaviour changes over time is whether the outcome stems from sensitization (aggression increases) or habituation (aggression decreases) over successive simulated territorial intrusions, rather than true biological changes in aggressive capabilities over the course of the breeding season. To evaluate these possibilities, we capitalized on the $n = 9$ females who were exposed to multiple simulated territorial intrusions within a breeding stage and performed a paired Wilcoxon signed-rank test and a McNemar's test on aggression score and probability of physical attack, respectively.

To assess the reproducibility of measuring aggression with 3D-printed decoys, we compared our aggression scores with those obtained from studies using live decoys but otherwise comparable methodology (Rosvall, 2008, 2010, 2011b, 2013a). We combined territory establishment and nest building into a "pre-laying" category because prior studies did not differentiate between these stages and these stages were not statistically different in the current study (see "Results" below). We quantified heterogeneity in stage-matched aggression scores between studies using the R package *metafor* (Viechtbauer, 2010). We fit random effects models (REMs) using restricted maximum likelihood to obtain unbiased estimates of variance in aggression scores within each breeding stage. We present Cochran's Q to indicate the extent of between-study variability in aggression scores; however, because this test has low power when sample sizes are small, we also present I^2 (the proportion of variation in aggression score due to between-study heterogeneity; Higgins & Thompson, 2002).

3 | RESULTS

Aggressive responses to simulated territorial intrusions significantly changed across breeding stages, with lower aggression later in the breeding season (aggression score: $\chi^2 = 21.9$, $p < 0.01$; Figure 2a). In particular, aggression scores during the nestling-rearing stage were significantly lower than all other breeding stages (Tukey test, all $p < 0.001$); all other pairwise comparisons were not significantly different from one another (all $p > 0.16$). The probability of physical attack also changed significantly across breeding stages ($\chi^2 = 8.0$, $p = 0.04$; Figure 2b). Females were significantly more likely to physically attack the decoy during nest building (61.1%, 11 of 18 trials) than during nestling rearing (7.1%, 1 of 14 trials; Tukey test, $p = 0.04$); all other pairwise comparisons were not significantly different from one another (territory establishment: 47.1%, 8 of 17 females; incubation: 33.3%, 7 of 21; all $p > 0.14$).

For females whose aggression was assayed more than once within a breeding stage, neither aggression score ($V = 22$, $p = 0.62$)

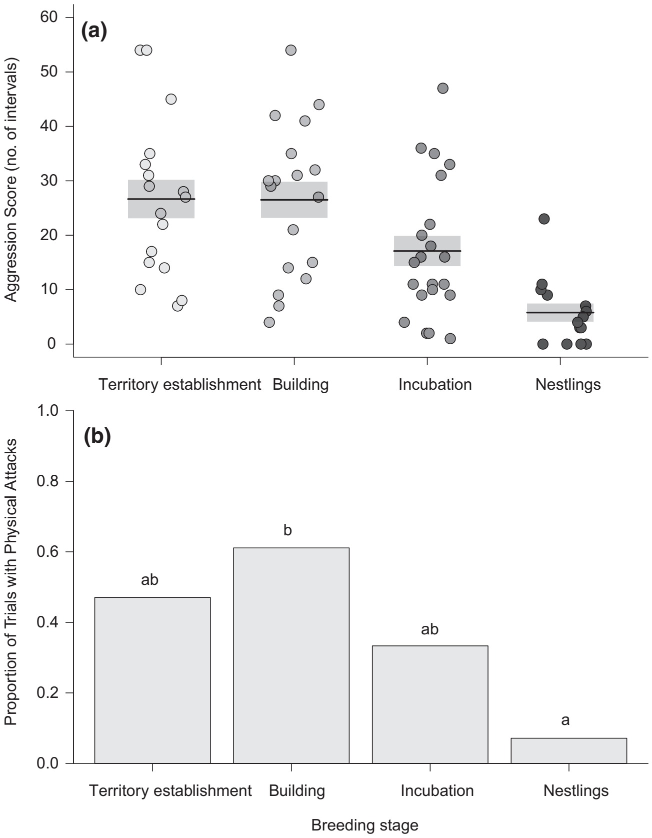

FIGURE 2 (a) Aggression score (number of 5-s intervals spent attacking) from 5-min simulated territorial intrusion trials performed across breeding stages. The black line is the mean, shading denotes standard error, and each circle is one simulated territorial intrusion trial (territory establishment, *n* = 17; building, *n* = 18; incubation, *n* = 21; nestling, *n* = 14). (b) Proportion of trials that escalated to physical attacks in each breeding stage. Letters denote significant differences between breeding stages ($p < 0.05$)

nor probability of physical attack ($\chi^2_1 = 1.0$, $p = 0.32$) was significantly different between the first and second simulated territorial intrusions. Average aggression scores of females that were assayed more than once (incubation: 14.89 ± 4.55 *SE*; nestlings: 4.36 ± 1.11 *SE*) did not differ from females only assayed once (incubation: 18.75 ± 3.56 *SE*; nestlings: 11.00 ± 6.66 *SE*), and the range of aggression seen in females assayed multiple times (incubation: 2–47; nestlings: 0–11) was largely overlapping with those measured only once (incubation: 1–36; nestlings: 0–23).

Overall, there was significant heterogeneity between studies of female aggression in this species ($I^2 = 90.46\%$, $Q = 105.36$, $p < 0.0001$), which is not surprising considering that we found that aggression significantly declines across successive breeding stages and each study was conducted during a single stage, in different populations and years. When studies were stage-matched, however, heterogeneity declined (Figure 3). Variation due to between-study heterogeneity was not significant during the pre-laying period (territory establishment and building; $I^2 = 47.49\%$, $Q = 5.68$, $p = 0.13$) or incubation ($I^2 = 0.00\%$, $Q = 0.11$, $p = 0.74$), suggesting similarity in the aggression scores obtained with live and 3D-printed decoys. During nestling rearing, however, there was significant between-study heterogeneity ($I^2 = 85.71\%$, $Q = 7.00$, $p = 0.01$), with lower aggression scores obtained in the current study.

4 | DISCUSSION

Females responded with robust aggression to simulated intrusions by our 3D-printed decoys. Specifically, total aggression was quite high during territory establishment and nest building, followed by a marginal, but non-significant, decrease in aggression during incubation and a precipitous decline during nestling rearing. Similarly, the probability of attack also remained relatively high through incubation, with nearly 50% of females physically attacking the decoy, until a significant drop during nestling rearing. Repeated measures on a subset of females suggest that these declines in aggression across the breeding season are not likely to stem from habituation, but may instead reflect biologically relevant changes in how females respond to same-sex intruders. Consistent with this view, our data are also comparable to stage-matched aggression scores obtained by exposing female tree swallows to live decoys. These findings suggest female tree swallows are capable of relatively high levels of conspecific aggression through multiple breeding stages (from territory establishment, to nest building and incubation) until nestling rearing, a period when rates of naturally occurring aggressive interactions among tree swallows are also declining (George & Rosvall, 2018; Robertson et al., 1986). Importantly, this pattern of aggression does not fully correspond with seasonal changes in T levels, which are already quite low during incubation in this population (territory establishment & nest building: 0.32 ng/ml [95% CI: 0.28–0.38] vs. incubation: 0.18 ng/ml [95% CI: 0.14–0.21]; George & Rosvall, 2018), despite evidence that female aggression is mediated by T to some degree (Rosvall, 2013a). Thus, our data suggest that females have the mechanistic flexibility to extend aggressive responses beyond the seasonal decline in circulating T levels, perhaps in relation to the function of female aggression in this nest-site-limited species. Below we discuss these patterns as they relate to our understanding of the functional use and mechanistic underpinnings of female aggression.

By and large, patterns of aggression that decline as the breeding season progresses are consistent with aggression serving to acquire and defend a breeding territory (Gowaty, 1981; Wingfield et al., 1990). Our observation that aggressive responses to a conspecific intruder were higher during earlier breeding stages suggests that aggression has a territorial function. In support of this, only the most aggressive females in this system are able to obtain a nesting cavity during competition (Rosvall, 2008), demonstrating a clear benefit of being aggressive during territory establishment. However, why then do females maintain relatively high aggressive capabilities after territories have been established and breeding has begun? One explanation is that competition for nesting cavities is so intense in this species that sustained aggressiveness during incubation is needed to repel floater females who are still trying to secure a nesting site (Stutchbury & Robertson, 1985, 1987a). While

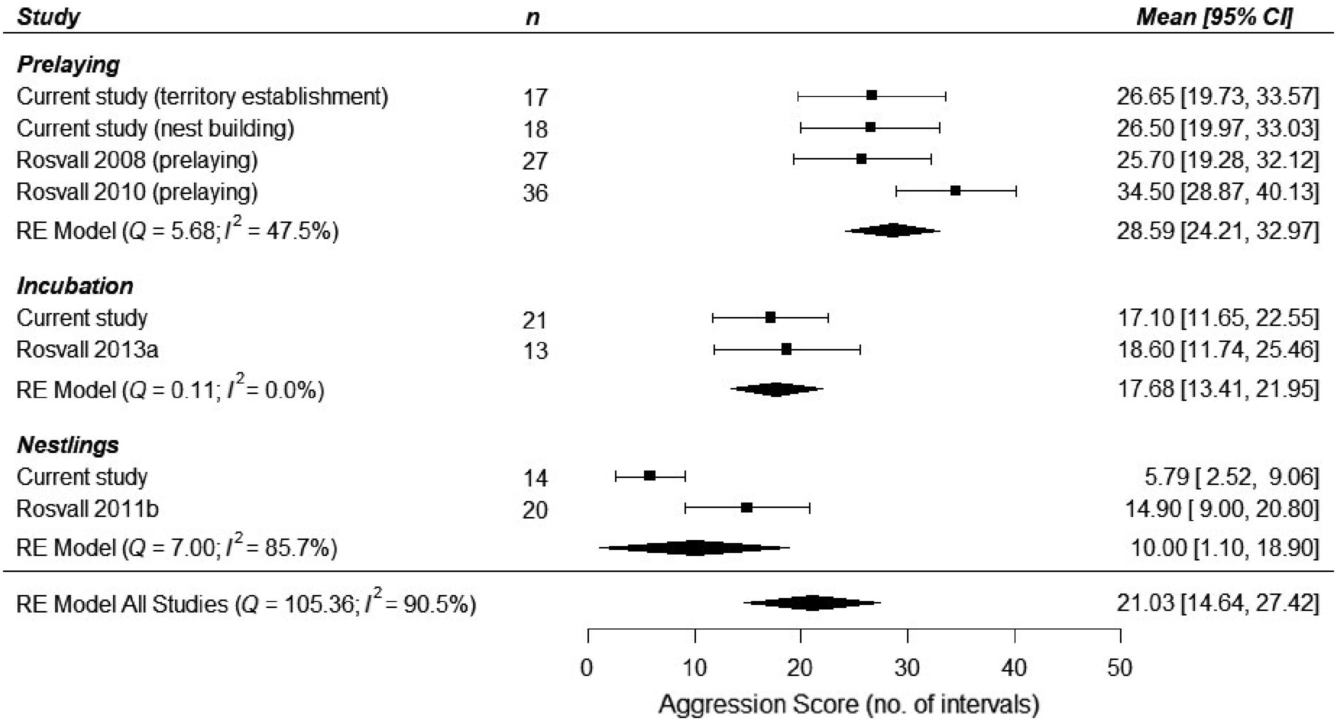

FIGURE 3 Distribution of mean aggression scores (± 95% CI) within pre-laying (territory establishment and nest building), incubation, and nestling-rearing breeding stages across studies using live caged decoys and the current study using 3D-printed decoys. The diamonds display the estimated mean from the random effects model (REM) fit with restricted maximum likelihood overall and within each breeding stage

some studies suggest that the rate of intrusions by these floater females declines as the breeding season progresses (George & Rosvall, 2018; Lombardo, 1987; Robertson et al., 1986), usurpations have been observed during both incubation and nestling-rearing periods (Leffelaar & Robertson, 1985). In the current study, females were still initiating nests during the period when early-breeding females had begun nestling care, further suggesting that late-arriving or floater females could represent a threat to territory-holding females beyond the initial period of territory establishment. Yet, this does not explain the decline in aggressiveness observed during nestling rearing. It is possible that a natural decrease in the rate of conspecific intrusions (George & Rosvall, 2018; Lombardo, 1987; Robertson et al., 1986), coupled with higher costs of aggression, could lead to stronger selection *against* high levels of conspecific aggression during the nestling-rearing stage. Aggression and parental care are often negatively correlated (Duckworth, 2006; Sih et al., 2004), indicating these behaviours may constrain one another via underlying trade-offs (such as those with energy expenditure; Williams, 1988). Thus, the diminished behavioural responsiveness to conspecific intrusions that we observed during nestling rearing may represent an adaptation to maximize fitness, balancing territorial defence with parental care. This hypothesis would ideally be tested by examining individual-level flexibility as reaction norms across the breeding season (Duckworth, 2009). Nevertheless, our population-level analysis demonstrates that females are capable of robust aggressive responses towards conspecifics well into incubation, but that there may be constraints on aggressiveness during nestling rearing, despite the functional benefits that could be gained by defending against floaters.

Seasonal trade-offs between aggression and parental care have historically been thought to be mediated by T in temperate-breeding male vertebrates, where levels of circulating T often parallel seasonal changes in aggression (Goymann et al., 2007; Hirschenhauser & Oliveira, 2006; Lynn, 2008, 2016; Wingfield et al., 1990). While we know far less about these patterns in females, it is becoming clear that, at least in some systems, females may experience similar T-mediated trade-offs between aggression and parental care (de Jong et al., 2016; Ketterson et al., 2005; Rosvall, 2013a, 2013b). Critically, female tree swallows demonstrate T-mediated trade-offs between territorial aggression and incubation behaviours (Rosvall, 2013a) along with declines in circulating T that occur during incubation (George & Rosvall, 2018). Gene expression analyses further demonstrate that incubating females have diminished steroidogenic capabilities in the ovary (Bentz, Dossey, & Rosvall, 2018). Thus, considering these potential mechanistic constraints, females might be expected to display low conspecific aggressiveness during both incubation and nestling rearing. While we did find that aggression is somewhat lower during incubation, it is certainly not eliminated or as low as levels observed during nestling rearing, which lies in contrast to the exceedingly low T production capabilities seen during incubation. These seemingly contradictory observations suggest the intriguing possibility that mechanisms of female aggression may change throughout the breeding season. Natural selection may favour mechanisms that enhance aggression but minimize its costs, leading to circulating T levels and aggression becoming mechanistically uncoupled, particularly during parental periods when females may still benefit from aggression (Ketterson, Atwell, & McGlothlin, 2009; Rosvall, 2013b). High circulating T can be detrimental for many females, including tree swallows, during incubation and/or nestling rearing, as experimentally elevated T has been shown to reduce maternal care, for example (O'Neal, Reichard, Pavilis, & Ketterson, 2008; Rosvall, 2013a; Veiga & Polo, 2008). Thus, it is feasible that mechanisms of female aggression would be shaped by these costs, particularly during later breeding stages.

The regulation of conspecific aggression in females is still not well understood, but there are several potential mechanisms that are not wholly dependent on circulating T levels and may therefore be adaptive for females. For example, aggression could be mediated by tissue level processing of T or its metabolites (Rosvall et al., 2012). The adrenal prohormone dehydroepiandrosterone can also promote steroid processing in the brain to facilitate aggression during periods of low T (Rendon, Rudolph, Sengelaub, & Demas, 2015; Soma, Scotti, Newman, Charlier, & Demas, 2008; Soma & Wingfield, 2001). Notably, seasonal variation in these alternative endocrine mechanisms has been observed in males and females of tropical-breeding species (Canoine, Fusani, Schlinger, & Hau, 2007; Goymann, Wittenzellner, Schwabl, & Makomba, 2008; Hau, Stoddard, & Soma, 2004; Voigt & Goymann, 2007). While far less research has occurred in tropical species, parallels can be drawn between the findings here and with tropical species that display year-round territorial aggression but have relatively low circulating T (compared to temperate-breeding species), potentially as a means to avoid the costs of constantly elevated T (Goymann et al., 2004; Wikelski, Hau, Robinson, & Wingfield, 2003). Other mechanisms that are independent of circulating T include neuropeptides, like oxytocin and vasopressin, that are strongly associated with aggression during periods of parental care in mammals (Bosch, 2013; Duque-Wilckens & Trainor, 2017; Kelly & Vitousek, 2017; Lonstein & Gammie, 2002) and some studies have found a link between mesotocin and vasotocin and territorial aggression in birds (Goodson, Kelly, & Kingsbury, 2012; Kelly & Goodson, 2014; Kelly & Vitousek, 2017; Maney, Erwin, & Goode, 2005). Alternatively, the relatively high aggressive responses to simulated intruders that we observed during incubation could be a lingering effect of previously elevated T. Prior T elevations can have lasting effects on later aggression in male vertebrates (Gleason, Fuxjager, Oyegbile, & Marler, 2009; Hsu, Earley, & Wolf, 2006; Wingfield et al., 1990), but these long-term social priming effects of T are not well established in females, except in a few studies in captive rodents (Albert, Jonik, & Walsh, 1990; Silva, Fry, Sweeney, & Trainor, 2010). Furthermore, experimental manipulations that remove the gonads and by extension, eliminate gonadal sex steroid secretion, suggest that aggression declines rapidly thereafter (Arnold, 1975; Francis, Jacobson, Wingfield, & Fernali, 1992; Selinger & Bermant, 1967), indicating that any lingering behavioural effects of T are short-lived and would not necessarily account for relatively high levels of aggression seen in incubating females. Future work is certainly needed to clarify the mechanistic underpinnings of aggression in females, but considering the distinct shift in physiology and behaviour that females undergo during the breeding season as they transition to parental stages, there may be a concomitant seasonal shift in the regulation of aggression.

One exciting practical implication of our findings is that 3D-printed decoys elicited strong responses that were comparable in magnitude to stage-matched studies using live decoys, despite these studies being conducted in different populations and years. In addition, Lombardo (1987) found that the mean response (hover/dive/contact) of parents towards a taxidermic mount decoy within a 5-min time period during nestling rearing roughly fit within the margin of error found in the current study, but we did not include this in our analysis due to differences in methodologies. In the past, there have generally been two variants of how simulated territorial intrusions are performed, with a live conspecific or a taxidermic mount. Live birds, while more natural in evoking aggressive responses, can pose animal welfare risks and behave unpredictably, inhibiting a researcher's ability to conduct a standardized test of behaviour (Scriba & Goymann, 2008). Taxidermic mounts are more standardized, but they are also expensive, and investigators often opt to protect them with cages, which can obstruct key visual cues at best and induce neophobia from focal animals, at worst (Scriba & Goymann, 2008). Our 3D-printed decoys offer a way to standardize behavioural testing, affordably and without the need for a protective cage. New decoys can be readily made with access to a 3D printer, some basic craft supplies, a salvaged skin, and rudimentary dissection skills. Because these decoys can be so easily made, researchers can cheaply create numerous mounts that are almost disposable, minimize pseudoreplication, and enhance reliability in ethological studies (Parker, Greig, Nakagawa, Parra, & Dalisio, 2018). 3D printing is revolutionizing many different disciplines within ecology and evolution (Behm, Waite, Hsieh, & Helmus, 2018; Domingue et al., 2015; Igic et al., 2015; Porter, Adriaens, Hatton, Meyers, & McKittrick, 2015; Qing & Bert, 2018), and in the future, advanced modifications, such as iridescent or UV-matched paint colours, instead of animal skins, could remove the need to use live animals in a range of behavioural tests.

ACKNOWLEDGEMENTS

This work was supported by the National Science Foundation [grant IOS-1656109] and the Indiana University Department of Biology. We would like to thank SD Myers, EM George, EK Dossey, and MS Izzo for help in the field and lab. We would also like to acknowledge Indiana University Research and Teaching Preserve and Indiana Department of Natural Resources for access to field sites and the 3D-printing facility at Indiana University's Wells Library.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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REFERENCES

Albert, D. J., Jonik, R. H., & Walsh, M. L. (1990). Aggression by ovariectomized female rats with testosterone implants: Competitive experience activates aggression toward unfamiliar females. *Physiology & Behavior*, *47*, 699–703. https://doi.org/10.1016/0031-9384(90)90080-N

Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton Univ. Press.

Arnold, A. P. (1975). The effects of castration and androgen replacement on song, courtship, and aggression in zebra finches (*Poephila guttata*). *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, *191*, 309–325. https://doi.org/10.1002/jez.1401910302

Behm, J., Waite, B. R., Hsieh, S. T., & Helmus, M. R. (2018). Benefits and limitations of three-dimensional printing technology for ecological research. *bioRxiv*, 283895. https://doi.org/10.1186/s12898-018-0190-z

Bentz, A. B., Dossey, E. K., & Rosvall, K. A. (2018). Tissue-specific gene regulation corresponds with seasonal plasticity in female testosterone. *General and Comparative Endocrinology*, *270*, 26–34.

Bosch, O. J. (2013). Maternal aggression in rodents: Brain oxytocin and vasopressin mediate pup defence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*, 20130085.

Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *Wilson Bulletin*, *76*, 160–169.

Cain, K. E., & Ketterson, E. D. (2012). Competitive females are successful females; phenotype, mechanism, and selection in a common songbird. *Behavioral Ecology and Sociobiology*, *66*, 241–252. https://doi.org/10.1007/s00265-011-1272-5

Cain, K. E., & Ketterson, E. D. (2013). Costs and benefits of competitive traits in females: Aggression, maternal care and reproductive success. *PLoS ONE*, *8*, e77816. https://doi.org/10.1371/journal.pone.0077816

Cain, K. E., & Rosvall, K. A. (2014). Next steps for understanding the selective relevance of female-female competition. *Frontiers in Ecology and Evolution*, *2*, 32. https://doi.org/10.3389/fevo.2014.00032

Canoine, V., Fusani, L., Schlinger, B., & Hau, M. (2007). Low sex steroids, high steroid receptors: Increasing the sensitivity of the nonreproductive brain. *Developmental Neurobiology*, *67*, 57–67. https://doi.org/10.1002/dneu.20296

Clutton-Brock, T. H., & Huchard, E. (2013). Social competition and selection in males and females. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*, 20130074.

de Jong, B., Lens, L., Amininasab, S. M., van Oers, K., Darras, V. M., Eens, M., … Groothuis, T. G. G. (2016). Effects of experimentally sustained elevated testosterone on incubation behaviour and reproductive success in female great tits (*Parus major*). *General and Comparative Endocrinology*, *230*, 38–47. https://doi.org/10.1016/j.ygcen.2016.02.017

Domingue, M. J., Pulsifer, D. P., Lakhtakia, A., Berkebile, J., Steiner, K. C., Lelito, J. P., … Baker, T. C. (2015). Detecting emerald ash borers (*Agrilus planipennis*) using branch traps baited with 3D-printed beetle decoys. *Journal of Pest Science*, *88*, 267–279. https://doi.org/10.1007/s10340-014-0598-y

Duckworth, R. A. (2006). Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology*, *17*, 1011–1019. https://doi.org/10.1093/beheco/arl035

Duckworth, R. A. (2009). The role of behavior in evolution: A search for mechanism. *Evolutionary Ecology*, *23*, 513–531. https://doi.org/10.1007/s10682-008-9252-6

Duckworth, R. A. (2010). Evolution of personality: Developmental constraints on behavioral flexibility. *The Auk*, *127*, 752–758. https://doi.org/10.1525/auk.2010.127.4.752

Dunn, P. O., & Hannon, S. J. (1991). Intraspecific competition and the maintenance of monogamy in tree swallows. *Behavioral Ecology*, *2*, 258–266. https://doi.org/10.1093/beheco/2.3.258

Duque-Wilckens, N., & Trainor, B. C. (2017). *Behavioral neuroendocrinology of female aggression*. Oxford, UK: Oxford Research Encyclopedia of Neuroscience.

Francis, R. C., Jacobson, B. E. N., Wingfield, J. C., & Fernali, R. D. (1992). Castration lowers aggression. *Ethology*, *93*, 247–255.

George, E. M., & Rosvall, K. A. (2018). Testosterone production and social environment vary with breeding stage in a competitive female songbird. *Hormones and Behavior*, *103*, 28–35. https://doi.org/10.1016/j.yhbeh.2018.05.015

Gleason, E. D., Fuxjager, M. J., Oyegbile, T. O., & Marler, C. A. (2009). Testosterone release and social context: When it occurs and why. *Frontiers in Neuroendocrinology*, *30*, 460–469. https://doi.org/10.1016/j.yfrne.2009.04.009

Goodson, J. L., Kelly, A. M., & Kingsbury, M. A. (2012). Evolving nonapeptide mechanisms of gregariousness and social diversity in birds. *Hormones and Behavior*, *61*, 239–250. https://doi.org/10.1016/j.yhbeh.2012.01.005

Gowaty, P. A. (1981). Aggression of breeding Eastern bluebirds (*Sialia sialis*) toward their mates and models of intra-and interspecific intruders. *Animal Behaviour*, *29*, 1013–1027. https://doi.org/10.1016/S0003-3472(81)80055-3

Gowaty, P. A., & Wagner, S. J. (1988). Breeding season aggression of female and male Eastern bluebirds (*Sialia sialis*) to models of potential conspecific and interspecific egg dumpers. *Ethology*, *78*, 238–250. https://doi.org/10.1111/j.1439-0310.1988.tb00234.x

Goymann, W., Landys, M. M., & Wingfield, J. C. (2007). Distinguishing seasonal androgen responses from male–male androgen responsiveness—Revisiting the challenge hypothesis. *Hormones and Behavior*, *51*, 463–476. https://doi.org/10.1016/j.yhbeh.2007.01.007

Goymann, W., Moore, I. T., Scheuerlein, A., Hirschenhauser, K., Grafen, A., & Wingfield, J. C. (2004). Testosterone in tropical birds: Effects of environmental and social factors. *American Naturalist*, *164*, 327–334. https://doi.org/10.1086/422856

Goymann, W., & Wingfield, J. C. (2014). Male-to-female testosterone ratios, dimorphism, and life history—What does it really tell us? *Behavioral Ecology*, *25*, 685–699.

Goymann, W., Wittenzellner, A., Schwabl, I., & Makomba, M. (2008). Progesterone modulates aggression in sex-role reversed female African black coucals. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 1053–1060. https://doi.org/10.1098/rspb.2007.1707

Harris, R. N. (1979). Aggression, superterritories, and reproductive success in tree swallows. *Canadian Journal of Zoology*, *57*, 2072–2078. https://doi.org/10.1139/z79-273

Hau, M., Stoddard, S. T., & Soma, K. K. (2004). Territorial aggression and hormones during the non-breeding season in a tropical bird. *Hormones and Behavior*, *45*, 40–49. https://doi.org/10.1016/j.yhbeh.2003.08.002

Higgins, J. P., & Thompson, S. G. (2002). Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine*, *21*, 1539–1558. https://doi.org/10.1002/sim.1186

Hirschenhauser, K., & Oliveira, R. F. (2006). Social modulation of androgens in male vertebrates: Meta-analyses of the challenge hypothesis. *Animal Behaviour*, *71*, 265–277. https://doi.org/10.1016/j.anbehav.2005.04.014

Hrdy, S. B. (2013). The 'one animal in all creation about which man knows the least'. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*, 20130072. https://doi.org/10.1098/rstb.2013.0072

Hsu, Y., Earley, R. L., & Wolf, L. L. (2006). Modulation of aggressive behaviour by fighting experience: Mechanisms and contest outcomes. *Biological Reviews*, *81*, 33–74. https://doi.org/10.1017/S146479310500686X

Hussell, D. J. T. (1983). Age and plumage color in female tree swallows. *Journal of Field Ornithology*, *54*, 312–318.

Igic, B., Nunez, V., Voss, H. U., Croston, R., Aidala, Z., López, A. V., … Hauber, M. E. (2015). Using 3D printed eggs to examine the egg-rejection behaviour of wild birds. *PeerJ*, *3*, e965. https://doi.org/10.7717/peerj.965

Jawor, J. M., Young, R., & Ketterson, E. D. (2006). Females competing to reproduce: Dominance matters but testosterone may not. *Hormones and Behavior*, *49*, 362–368. https://doi.org/10.1016/j.yhbeh.2005.08.009

Johnstone, R. A. (1997). The evolution of animal signals. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (pp. 155–178). Oxford, UK: Blackwell Science.

Kelly, A. M., & Goodson, J. L. (2014). Social functions of individual vasopressin–oxytocin cell groups in vertebrates: What do we really know? *Frontiers in Neuroendocrinology*, *35*, 512–529.

Kelly, A. M., & Vitousek, M. N. (2017). Dynamic modulation of sociality and aggression: An examination of plasticity within endocrine and neuroendocrine systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*, 20160243.

Ketterson, E. D., Atwell, J. W., & McGlothlin, J. W. (2009). Phenotypic integration and independence: Hormones, performance, and response to environmental change. *Integrative and Comparative Biology*, *49*, 365–379. https://doi.org/10.1093/icb/icp057

Ketterson, E. D., Nolan, V., & Sandell, M. (2005). Testosterone in females: Mediator of adaptive traits, constraint on sexual dimorphism, or both? *American Naturalist*, *166*, S85–S98.

Langmore, N. E., Cockrem, J. F., & Candy, E. J. (2002). Competition for male reproductive investment elevates testosterone levels in female dunnocks, *Prunella modularis*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*, 2473–2478.

Leffelaar, D., & Robertson, R. J. (1985). Nest usurpation and female competition for breeding opportunities by tree swallows. *Wilson Bulletin*, *97*, 221–224.

Lessells, C. K. (2008). Neuroendocrine control of life histories: What do we need to know to understand the evolution of phenotypic plasticity? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*, 1589–1598. https://doi.org/10.1098/rstb.2007.0008

Lombardo, M. P. (1987). Attendants at tree swallow nests. III. Parental responses to live and stuffed-model attendants. *Condor*, *89*, 768–778. https://doi.org/10.2307/1368524

Lonstein, J. S., & Gammie, S. C. (2002). Sensory, hormonal, and neural control of maternal aggression in laboratory rodents. *Neuroscience & Biobehavioral Reviews*, *26*, 869–888. https://doi.org/10.1016/S0149-7634(02)00087-8

Lozano, G. A., & Handford, P. T. (1995). A test of an assumption of delayed plumage maturation hypotheses using female tree swallows. *Wilson Bulletin*, *107*, 153–164.

Lynn, S. E. (2008). Behavioral insensitivity to testosterone: Why and how does testosterone alter paternal and aggressive behavior in some avian species but not others? *General and Comparative Endocrinology*, *157*, 233–240.

Lynn, S. E. (2016). Endocrine and neuroendocrine regulation of fathering behavior in birds. *Hormones and Behavior*, *77*, 237–248. https://doi.org/10.1016/j.yhbeh.2015.04.005

Lyon, B. E., & Montgomerie, R. D. (1986). Delayed plumage maturation in passerine birds: Reliable signaling by subordinate males? *Evolution*, *40*, 605–615.

Maney, D. L., Erwin, K. L., & Goode, C. T. (2005). Neuroendocrine correlates of behavioral polymorphism in white-throated sparrows. *Hormones and Behavior*, *48*, 196–206. https://doi.org/10.1016/j.yhbeh.2005.03.004

McNamara, J. M., & Houston, A. I. (2009). Integrating function and mechanism. *Trends in Ecology & Evolution*, *24*, 670–675. https://doi.org/10.1016/j.tree.2009.05.011

O'Neal, D. M., Reichard, D. G., Pavilis, K., & Ketterson, E. D. (2008). Experimentally-elevated testosterone, female parental care, and reproductive success in a songbird, the dark-eyed junco (*Junco hyemalis*). *Hormones and Behavior*, *54*, 571–578. https://doi.org/10.1016/j.yhbeh.2008.05.017

Parker, T. H., Greig, E. I., Nakagawa, S., Parra, M., & Dalisio, A. C. (2018). Subspecies status and methods explain strength of response to local versus foreign song by oscine birds in meta-analysis. *Animal Behaviour*, *142*, 1–17. https://doi.org/10.1016/j.anbehav.2018.05.023

Porter, M. M., Adriaens, D., Hatton, R. L., Meyers, M. A., & McKittrick, J. (2015). Why the seahorse tail is square. *Science*, *349*, aaa6683. https://doi.org/10.1126/science.aaa6683

Qing, X., & Bert, W. (2018). 3D printing in zoological systematics: Integrative taxonomy of *Labrys chinensis* gen. nov., sp. nov. (Nematoda: Tylenchomorpha). *Journal of Zoological Systematics and Evolutionary Research*, *56*, 35–47.

R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rendon, N. M., Rudolph, L. M., Sengelaub, D. R., & Demas, G. E. (2015). The agonistic adrenal: Melatonin elicits female aggression via regulation of adrenal androgens. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20152080.

Robertson, R. J., Gibbs, H. L., & Stutchbury, B. J. (1986). Spitefulness, altruism, and the cost of aggression: Evidence against superterritoriality in tree swallows. *Condor*, *88*, 104–105. https://doi.org/10.2307/1367767

Rosvall, K. A. (2008). Sexual selection on aggressiveness in females: Evidence from an experimental test with tree swallows. *Animal Behaviour*, *75*, 1603–1610. https://doi.org/10.1016/j.anbehav.2007.09.038

Rosvall, K. A. (2010). Do males offset the cost of female aggression? An experimental test in a biparental songbird. *Behavioral Ecology*, *21*, 161–168. https://doi.org/10.1093/beheco/arp167

Rosvall, K. A. (2011a). Intrasexual competition in females: Evidence for sexual selection? *Behavioural Ecology*, *22*, 1131–1140.

Rosvall, K. A. (2011b). Maintenance of variation in sexually selected traits in females: A case study using intrasexual aggression in tree swallows *Tachycineta bicolor*. *Journal of Avian Biology*, *42*, 454–462.

Rosvall, K. A. (2013a). Life history trade-offs and behavioral sensitivity to testosterone: An experimental test when female aggression and maternal care co-occur. *PLoS ONE*, *8*, e54120.

Rosvall, K. A. (2013b). Proximate perspectives on the evolution of female aggression: Good for the gander, good for the goose? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *368*, 20130083.

Rosvall, K. A., Burns, C. B., Barske, J., Goodson, J. L., Schlinger, B. A., Sengelaub, D. R., & Ketterson, E. D. (2012). Neural sensitivity to sex steroids predicts individual differences in aggression: Implications for behavioural evolution. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 3547–3555.

Sandell, M. I. (1998). Female aggression and the maintenance of monogamy: Female behaviour predicts male mating status in European starlings. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*, 1307–1311.

Scriba, M., & Goymann, W. (2008). The decoy matters! Hormonal and behavioural differences in the reaction of territorial European robins towards stuffed and live decoys. *General and Comparative Endocrinology*, *155*, 511–516. https://doi.org/10.1016/j.ygcen.2007.08.001

Selinger, H. E., & Bermant, G. (1967). Hormonal control of aggressive behavior in Japanese quail. *Behaviour*, *28*, 255–268. https://doi.org/10.1163/156853967X00037

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology*, *79*, 241–277. https://doi.org/10.1086/422893

Silva, A. L., Fry, W. H. D., Sweeney, C., & Trainor, B. C. (2010). Effects of photoperiod and experience on aggressive behavior in female California mice. *Behavioural Brain Research*, *208*, 528–534. https://doi.org/10.1016/j.bbr.2009.12.038

Slagsvold, T., & Lifjeld, J. T. (1994). Polygyny in birds: The role of competition between females for male parental care. *American Naturalist*, *143*, 59–94. https://doi.org/10.1086/285596

Soma, K. K., Scotti, M. A. L., Newman, A. E., Charlier, T. D., & Demas, G. E. (2008). Novel mechanisms for neuroendocrine regulation of aggression. *Frontiers in Neuroendocrinology*, *29*, 476–489. https://doi.org/10.1016/j.yfrne.2007.12.003

Soma, K. K., & Wingfield, J. C. (2001). Dehydroepiandrosterone in songbird plasma: Seasonal regulation and relationship to territorial aggression. *General and Comparative Endocrinology*, *123*, 144–155. https://doi.org/10.1006/gcen.2001.7657

Stiver, K. A., & Alonzo, S. H. (2009). Parental and mating effort: Is there necessarily a trade-off? *Ethology*, *115*, 1101–1126.

Stockley, P., & Bro-Jørgensen, J. (2011). Female competition and its evolutionary consequences in mammals. *Biological Reviews*, *86*, 341–366. https://doi.org/10.1111/j.1469-185X.2010.00149.x

Stutchbury, B. J., & Robertson, R. J. (1985). Floating populations of female tree swallows. *The Auk*, *102*, 651–654.

Stutchbury, B. J., & Robertson, R. J. (1987a). Behavioral tactics of subadult female floaters in the tree swallow. *Behavioral Ecology and Sociobiology*, *20*, 413–419.

Stutchbury, B. J., & Robertson, R. J. (1987b). Signaling subordinate and female status: Two hypotheses for the adaptive significance of subadult plumage in female tree swallows. *The Auk*, *104*, 717–723.

Tobias, J. A., Montgomerie, R., & Lyon, B. E. (2012). The evolution of female ornaments and weaponry: Social selection, sexual selection and ecological competition. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*, 2274–2293. https://doi.org/10.1098/rstb.2011.0280

Veiga, J. P., & Polo, V. (2008). Fitness consequences of increased testosterone levels in female spotless starlings. *American Naturalist*, *172*, 42–53. https://doi.org/10.1086/587850

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*, 1–48.

Voigt, C., & Goymann, W. (2007). Sex-role reversal is reflected in the brain of African black coucals (*Centropus grillii*). *Developmental Neurobiology*, *67*, 1560–1573. https://doi.org/10.1002/dneu.20528

West-Eberhard, M. J. (1983). Sexual selection, social competition, and speciation. *Quarterly Review of Biology*, *58*, 155–183. https://doi.org/10.1086/413215

Wikelski, M., Hau, M., Robinson, W. D., & Wingfield, J. C. (2003). Reproductive seasonality of seven neotropical passerine species. *Condor*, *105*, 683–695. https://doi.org/10.1650/7251

Williams, J. B. (1988). Field metabolism of tree swallows during the breeding season. *The Auk*, *105*, 706–714.

Wingfield, J. C., Hegner, R. E., Dufty, A. M., & Ball, G. F. (1990). The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, *136*, 829–846. https://doi.org/10.1086/285134

Winkler, D. W., Hallinger, K. K., Ardia, D. R., Robertson, R. J., Stutchbury, B. J., & Cohen, R. R. (2011). Tree swallow (*Tachycineta bicolor*), version 2.0. In A. F. Poole (Ed.), *The birds of North America*. Ithaca, NY: Cornell Lab of Ornithology.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Bentz AB, Philippi KJ, Rosvall KA. Evaluating seasonal patterns of female aggression: Case study in a cavity-nesting bird with intense female–female competition. *Ethology*. 2019;125:555–564. https://doi.org/10.1111/eth.12881