Aggressive displays by male House Wrens are composed of multiple components that predict attack

Craig A. Barnett,[1,2,3] Scott K. Sakaluk,[1] and Charles F. Thompson[1]

[1] *Behavior, Ecology, Evolution and Systematics Section, School of Biological Sciences, Illinois State University, Normal, Illinois 61790-4120, USA*
[2] *Department of Life Science, Rikkyo University, Tokyo, Japan*

ABSTRACT. Aggressive signals should predict whether the sender of the signal will attack the receiver, yet this criterion has been little studied. We conducted experiments with male House Wrens (*Troglodytes aedon*) in north-central Illinois in 2009 to test the hypothesis that rates of song delivery and wing-quivering (putative aggressive signals) signal aggressive intent. We simulated a conspecific territorial intrusion by combining playback of male song with a male taxidermic mount, predicting that these signals would be related to a male's likelihood of attacking a conspecific. All males ($N = 37$) sang in response to the intrusion. Males attacking the mount sang at significantly higher rates and performed significantly more wing quivers than males that did not attack. In addition, all males that attacked the mount performed wing quivers (9/9), whereas only 53.6% (15/28) of males that did not attack did so ($P = 0.011$). Our results are consistent with the hypothesis that both song and wing quivering indicate a signaler's aggressive intent and that these signals are likely components of a multi-component, hierarchical display.

RESUMEN. **Los despliegues agresivos de la Ratona Común están compuestos por múltiples componentes que predicen el ataque**
Las señales de agresividad deberían predecir si el emisor de la señal atacará al receptor, aún así este criterio ha sido poco estudiado. Realizamos experimentos en la Ratona Común (*Troglodytes aedon*) en el centro norte de Illinois en 2009 a fin de poner a prueba la hipótesis de que la tasa de emisión del canto y de temblor de alas (señales putativas de agresividad) señalizan la intención agresiva. Simulamos la intrusión territorial de un conespecífico al combinar playback de un macho con un ejemplar taxidermizado, prediciendo que estas señales estarían relacionadas a la probabilidad de un macho de atacar a un conespecífico. Todos los macho ($N = 37$) cantaron en respuesta a la intrusión. Los machos que atacaron el ejemplar taxidermizado realizaron más temblores de alas que los machos que no atacaron. Adicionalmente, todos los machos que atacaron realizaron temblores de alas (9/9), mientras que solo el 53.6% (15/28) de los machos que no atacaron lo realizó. Nuestros resultados son consistentes con la hipótesis que tanto el canto como el temblor de alas indican la intención agresiva del emisor, y que estas señales probablemente sean componentes de un despliegue jerárquico y de múltiples componentes.

Key words: aggression, bird song, escalation, signal evolution, *Troglodytes aedon*, wing quivering

Searcy and Beecher (2009) outlined three criteria that signals should meet to be considered aggressive: (i) signal production should increase in aggressive contexts (the context criterion), (ii) the signal should predict the aggressive escalation of conflicts (the predictive criterion), and (iii) receivers should respond to the signal (the response criterion). Therefore, if song is an aggressive signal and encodes information about a male's motivation to attack a conspecific rival, then males that attack conspecific rivals might sing at higher rates compared with males that do not attack. The predictive criterion has been tested by comparing the song properties of males that attack a conspecific male (or a taxidermic mount of a male in concert with song playback) to those that do not. This approach has been employed to assess whether various song characteristics can be used to predict that males will subsequently attack a territorial intruder (e.g., Searcy et al. 2006).

At least three aspects of avian singing behavior have been suggested to signal intention to attack a rival. First, rates of song matching may signal a male's aggressive intent, with more-aggressive males matching a greater number of their rivals' songs than less-aggressive males (Vehrencamp et al. 2007). However, evidence for song-type matching as a putative signal of aggressiveness is at best mixed (Searcy and Beecher 2009, but see Akçay et al. 2013). Second, in several species, low-amplitude "soft song" signals an individual's propensity to attack a conspecific rival (Searcy et al. 2006, Ballentine et al. 2008, Hof and

[3] Corresponding author. Email: optimalforager@ hotmail.com

Hazlett 2010, Ręk and Osiejuk 2011, Xia et al. 2013). Finally, male Black-capped Chickadees (*Poecile atricapillus*) that attacked a taxidermic mount attached to a speaker broadcasting songs of another male sang at higher rates than males that did not attack (Baker et al. 2012). Therefore, it appears that different species use different aspects of their songs to signal intention to attack. However, aggressive displays may also consist of more than a single behavior (Hurd and Enquist 2001, Hebets and Papaj 2005).

Another candidate component of aggressive displays is wing quivering, a behavior noted in aggressive contexts in other passerine species (Andrew 1961, Lanyon and Thompson 1984, Kikkawa et al. 1986, Akçay et al. 2013). However, the association between wing quivering and other aggressive signals is poorly understood. Although Andrew (1961) stated that wing quivering was not related to likelihood of attack in passerines, the results of other studies indicate that wing quivering regularly occurs in situations that often lead to attacks (Lanyon and Thompson 1984, Kikkawa et al. 1986, Akçay et al. 2013). Recently, Ballentine et al. (2008) found that wing-waving displays (where individuals raise and wave their wings) of Swamp Sparrows (*Melospiza georgiana*) and soft song (low-amplitude songs) together are redundant signals that predicted physical attack. Therefore, although it (and wing movements in general) may be a component of the aggressive displays in many passerines, wing quivering may also be combined with vocal signals.

The predictive criterion of Searcy and Beecher (2009) posits that to be considered aggressive, a signal must be predictive of aggressive escalation by the sender. We examined the predictive criterion in relation to rates of singing and wing quivering by male House Wrens (*Troglodytes aedon*). If singing and wing quivering act as putative signals of aggressiveness, we predicted that males that attack taxidermic mounts associated with playback of male song should sing and wing quiver at higher rates prior to attacks than non-attacking males. Although aggressiveness is a well-studied behavioral trait, there are still few data that link putative aggressive signals with escalation (Searcy and Beecher 2009). Therefore, more studies of putative aggressive signals and whether they actually predict escalation of aggressive interactions are needed.

METHODS

Study species and site. House Wrens are small (10–12 g) insectivorous passerines that breed throughout much of temperate North America. Near the end of April, males, and then females, return to our study area from their wintering grounds. Upon arrival, males immediately begin placing twigs in nest boxes and singing to attract a mate. Pairs typically raise two, occasionally three, broods of between four and eight nestlings each breeding season at our study site (for additional information, see Johnson 1998). Both sexes provision nestlings, but only females incubate eggs and brood nestlings. Our study was conducted at the Mackinaw study site in McLean County, Illinois (40° 40′N, 88°53′W), where 700 nest boxes were distributed in a grid pattern (density = 5.4 boxes/ha) in secondary deciduous forest surrounded by cultivated fields (see Appendix 1 of Lambrechts et al. 2010 for dimensions and other details about nest boxes).

Assessment of male singing behavior and wing quivering. Aggressiveness in an evolutionary context can be thought of as all behavior directed at increasing an attacker's reproductive prospects at the expense of the attacked or threatened rival (Huber and Kravitz 2010). In an earlier study, we conducted a quantitative analysis of the aggressive behavior (consisting of six behavioral traits) of male House Wrens in association with other behaviors (Barnett et al. 2012). In this study, we used rates of singing and wing quivering (referred to as "wing flutters" in Barnett et al. 2012) collected in these assays (and data from another six males) to determine if these behaviors could be used to predict whether or not males attack conspecifics. Throughout the 2009 breeding season (1 June to 3 August), we measured rates of singing and wing quivering by males during these presentations by counting the number of these behaviors per minute before observations ended, either when an attack occurred or after 7 min of observation. We defined an attack as when a male approached and flew at the mount (see below) and made physical contact with it. Songs were counted when a bird sang a continuous burst of song that typically lasted 3–6 s and were separated by intervals of 5–15 s. Wing quivers were defined as when birds extended their wings from their bodies with the tips pointed to the ground and vibrated them

rapidly in a manner similar to that described for Painted Buntings (*Passerina ciris*; Lanyon and Thompson 1984). Wing quivers typically lasted 3–6 s. Occasionally, wing quivers continued for up to 30 s. On these occasions, we counted each 10-s period as a single wing quiver (e.g., a 30-s wing quiver was counted as three wing quivers).

Males were captured the day before (i.e., on brood-day 2, with brood-day 0 being the day the first egg hatched) simulated conspecific territorial intrusions took place using a sample of conspecific male song played back with an mp3 player with a built-in speaker (Aiwa AZ-BS32) to draw them into a mist-net placed near nest boxes. Males were caught within 5 min of starting playback and banded with a numbered U.S.G.S. aluminum band and three color bands to aid in individual identification. Although we cannot rule out that males may have remembered the properties of the song between days, all males were treated the same.

Songs were recorded using a cassette-recorder (Model TC 150A, Sony, Tokyo, Japan) and an electronic parabolic microphone (Dan Gibson P-650, RD Systems of Canada, Toronto). Our song recording consisted of an ∼3-min sample of song taken from a longer recording recorded by C.F.T. at the study site over 20 yr prior to our study. Given that the record lifespan reported for House Wrens is at least 7 yr and 1 mo (Johnson 1998), the songs in the recording would not have been familiar to the males in our study. Although we did not conduct spectrographic analysis of the songs, they sounded like normal songs from the local population to the human ear (C.A.B., pers. obs.), and always elicited a response from males when played near their nests. The song sample was compressed into mp3 file format (sampling rate of 48 kHz, sample size of 16 bits) and loaded onto the mp3 player. Although mp3 files compress songs to fit human hearing perception and we were unsure as to how birds respond, if at all, to the compression, we were attempting to provide the same stimulus to all males to elicit a behavioral response from them. Therefore, we think it unlikely that the compressed mp3 format affected our results because the same recording was played back to all individuals and it elicited responses from all males in our study. The song was played on a continuous loop from the start of each observation. Each playback repetition was separated by a pause of ∼30 s. The speaker always faced toward the nest box in the focal bird's territory and the song was broadcast at 75 dB (peak output) measured 1 m from the speaker (using SPL meter app for Iphone [version 1.2]). A comparison of body sizes to song amplitudes confirms that birds of similar size to House Wrens produce song amplitude peaks between 60 and 80 dB (Anderson et al. 2008, Brumm 2009).

To assess male aggressiveness, we simulated a conspecific territorial intrusion by a male using a taxidermic mount in concert with playback of male song on brood-day 3. On brood-day 3, nestlings are still vulnerable to being killed by intruding conspecifics (White and Kennedy 1997), so intrusion by a conspecific male represents a significant danger to nestlings. Moreover, conducting trials on brood-day 3 also controlled for differences in nestling age among nests, which might account for differences in aggressive response among males (Montgomerie and Weatherhead 1988). Our simulated intrusions normally elicited a territorial response from territorial pairs and sometimes the females responded before males. Although we realize that the behavior of females could affect male responses, we were only considering the behavior of males and so only collected data from males.

The day of a trial, but prior to a trial's initiation, we entered the subject's territory (when both parents were away from the nest) and tethered the taxidermic mount to a branch stripped of obstructing leaves. Branches were 5–7 m from nest boxes and at a height of 1.2–2 m. We fastened the mount to the branch using fine, galvanized steel wires attached to the mount's tarsi. We also hung the mp3 player from a branch within 1 m of the mount and broadcast a sample of song (the same one used the day before to capture the male [see below for our justification of this protocol]). We conducted trials between 07:00 and 12:00 CDT. When playback was initiated, the observer (C.A.B.) moved 10–15 m further from the nest box to observe the male's response (placing the observer 15–23 m from the nest box). When the focal male was spotted, the time was noted and the male was identified using binoculars. The response time (the time when the male was first observed) was normally within 2 min of starting playback (mean = 53.0 ± 8.0 [SE] s). The male was then observed through binoculars until he either attacked the taxidermic mount or until 7 min had elapsed without

attack (whichever came first). Observations of males were stopped after 7 min because responses declined noticeably after this time (C.A.B., pers. obs.). Although we attempted to watch all birds for similar amounts of time, this was not always possible, so we calculated the number of songs and wing quivers per minute.

Data handling and statistical analysis. Use of a single mount and song exemplar for multiple playbacks could be considered a form of pseudoreplication (see Kroodsma et al. 2001). This concern, although applicable to some experimental designs, is misplaced here. Pseudoreplication becomes a problem when individuals are asked to choose between single exemplars used to represent different populations (Kroodsma et al. 2001). However, we were only interested in whether certain behaviors were predictive of an aggressive response to a standardized stimulus. In this situation, we wanted the threat posed by the mount and song stimulus to be the same for each subject. Changing songs and mounts would have introduced variation in the stimulus between individuals that could potentially have confounded the observation of behavioral variation among individuals that was the focus of our study (see Hurlbert 1984 and Sandoval 2011 for a fuller discussion of this point).

We recorded the times when focal males first sang and wing quivered in response to the simulated territorial intrusion. We calculated the rates of song and wing-quiver delivery per minute from when males were first identified until the observation was censored (see below). We did not include in the analysis periods when the male was not in view to remove the possibility of mistakenly counting another individual's behavior as that of the focal male. If birds attacked the mount, we recorded the singing and wing-quivering rates up until the bird made contact with the mount for the first time. In nine instances that males attacked the mount, we calculated the mean time to attack (mean = 326.4 s). For birds that did not attack, we generated 28 times randomly drawn from a normal distribution with the same mean and standard deviation as the attacking birds. Although the mean did not match the attacking group because of random sampling (mean = 334.6 s), they were similar. We used these times to censor the observation periods for non-attackers, thereby scoring the behaviors

of non-attacking birds over comparable time periods as attacking birds.

We compared the times when focal males first sang and wing quivered in response to the simulated territorial intrusion using a Cox's proportional hazards model. We used generalized additive mixed models (GAMMs) to determine if rates of singing and wing quivering predicted whether or not males attacked the mount. GAMMs are a powerful mixed-modeling technique that allow continuous variables to be included in models as factors expressed as smoothed terms (similar to splines) along with categorical fixed-factors and random factors. We ran one model with incidence of attack (i.e., whether the focal bird attacked the mount or not) as the dependent variable and song rate as a smoothed term and clutch size and day number (1 January = day 1) as random variables. In the second model, we substituted wing-quivering rate for song rate and maintained all other parameters as in the previous model. We used a binomial model with log link function and log-likelihood tests to generate P values. All models were run using the MGCV package (Wood 2013) running in R (R Development Core Team 2013, version 3.0.1).

RESULTS

We conducted simulated territorial intrusions with 37 different males (attackers: $N = 9$, non-attackers: $N = 28$). All males sang in response to the simulated intrusion irrespective of whether they attacked. However, we found a significant difference between males that attacked and did not attack the mount in the proportion that wing quivered (proportion wing quivering: attackers = 100% [9/9]; non-attackers = 53.6% [15/28]; $\chi_1^2 = 6.4$, $P = 0.011$).

Males that attacked the taxidermic mount also sang at significantly higher rates than males that did not attack (Wald $\chi_1^2 = 5.0$, $P = 0.026$, Fig. 1a). Additionally, attackers wing quivered at a higher rate than males that did not attack ($\chi_1^2 = 8.4$, $P = 0.0037$, Fig. 1b).

There was a significant difference in the time at which males first sang in response to the territorial intrusion and the time males first wing quivered (Cox's proportional hazards model: Wald $\chi_1^2 = 43.4$, $P < 0.0001$, Fig. 2). Specifically, males started singing significantly
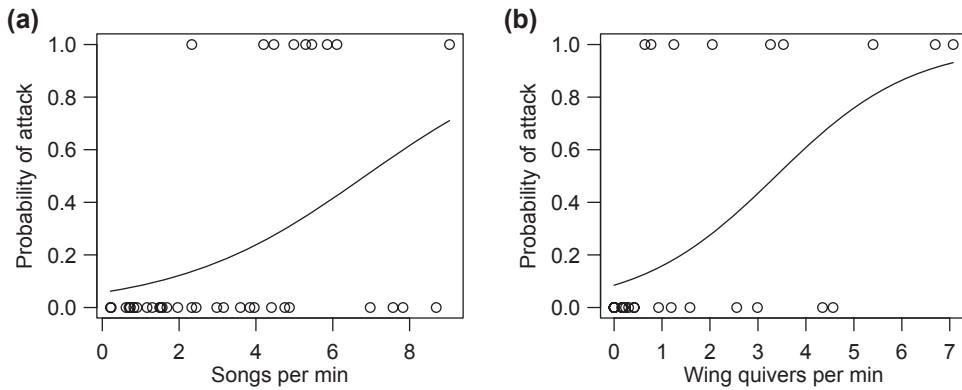
Fig. 1. Components of the aggressive behavior of male House Wrens predicted whether or not they attacked models. Males with (a) higher singing rates and (b) higher rates of wing quivering were more likely to attack the mount. Curves were derived from estimators taken from the generalized additive mixed models.

earlier in the aggressive interaction than when they started wing quivering.

DISCUSSION

Male House Wrens with higher singing and wing-quiver rates were more likely to attack the taxidermic mount during simulated territorial intrusions than males that displayed at lower rates. Therefore, both behaviors predicted the focal bird's attack behavior. Although previous studies have revealed that song rate can predict
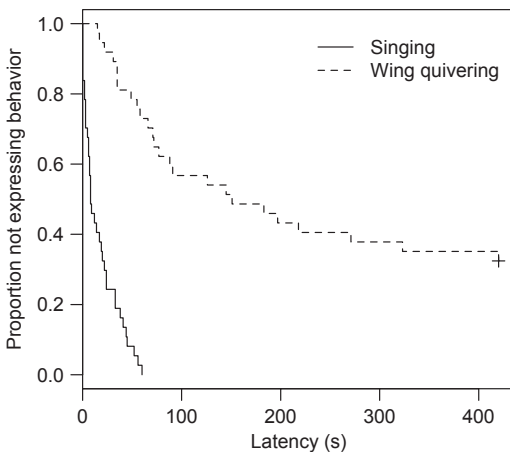

Fig. 2. The proportion of males not performing singing or wing quivering as a function of the time elapsed since the beginning of the simulated territorial intrusion.

attack (Baker et al. 2012), our results suggest that wing quivering also predicts a bird's propensity to attack conspecifics. This result is important because, although the expression of aggressive displays has been extensively studied, relatively few data link aggressiveness displays to the escalation of interactions and this is especially the case with wing-quivering behavior (but see Ballentine et al. 2008).

Despite the wealth of information linking song to male aggressiveness, there are still surprisingly few data that link song properties with escalation of aggressive behavior or fighting ability. However, in several species of songbirds, males that utter soft songs at higher rates are more likely to attack a conspecific (Searcy et al. 2006, Ballentine et al. 2008, Hof and Hazlett 2010, Ręk and Osiejuk 2011, Xia et al. 2013). In addition, Baker et al. (2012) found that male Black-capped Chickadees that sang at higher rates were more likely to attack conspecifics. Therefore, our results are consistent with recent observations that suggest that song in general or specific song properties may predict a bird's likelihood of attacking a conspecific. However, further research is required to examine the generality of these findings and to determine if there are other song properties that conform to the predictive criterion (Searcy and Beecher 2009).

Wing quivering by songbirds has also been observed in aggressive contexts (Andrew 1961, Lanyon and Thompson 1984, Kikkawa et al. 1986). For example, Swamp Sparrows perform a behavior called wing waving, which is an

exaggerated wing movement during which a male raises one or both wings above his back and waves them. This behavior has also been shown to be performed in aggressive contexts (Akçay et al. 2013), and the wing-wave rate combined with soft song has been shown to predict attacks (Ballentine et al. 2008). Our data also show that wing quivering is a putative signal of aggressiveness and predicts a House Wren's probability of attacking rivals.

Singing and wing-quivering behaviors might both have aggressive functions, but may be used in different ways. Songs can be perceived over a wide spatial scale. Therefore, when a territorial male House Wren hears a conspecific sing in his territory, he may first counter-sing (C.A.B., pers. obs.). Indeed, all males in our study sang when first responding to playback. When the intruder (the taxidermic mount) did not retreat, the territorial male then moved toward the intruder and chose whether to escalate the contest (C.A.B., pers. obs.). One way of signaling intent to escalate a dispute might be to incorporate new visual or vocal signals (such as wing quivering) into aggressive displays. These hierarchical multi-component signals may therefore convey more information about the sender's motivational state to the receiver than a single component (Searcy and Beecher 2009). In our study, attackers quivered their wings whereas only about half of the non-attackers wing quivered, suggesting that wing quivering may indicate an increased motivation to attack the mount. Moreover, when wing quivering occurred, it was expressed significantly later in the simulated territorial intrusion than was singing (Fig. 2), in support of the contention that males employ song and wing quivering in a hierarchical fashion.

Our results suggest that both singing and wing quivering are components of House Wren aggressiveness displays. Aggressiveness displays with multiple components (i.e., multi-modal) may be advantageous for signalers in a number of ways (Hurd and Enquist 2001, Hebets and Papaj 2005). First, displays with multiple components might allow information to be encoded in a hierarchical manner to convey information about a signaler's motivational state (Searcy and Beecher 2009). Second, multi-component aggressive signals may allow both sexes to perform aggressive displays toward rivals. For species of songbirds in which females do not sing or

sing infrequently (Catchpole and Slater 2008), multi-component signals might allow females to signal aggressive intent to conspecific rivals and participate in territory defense. Third, signals composed of multiple components may evoke stronger responses (e.g., flight responses) from receivers (Calvert et al. 2004). Therefore, aggressive signals that include vocal signals (i.e., songs and calls) as well as movements (e.g., wing quivering and tail raising) may be more effective at transmitting the signaler's motivational state to receivers than single-component signals.

In conclusion, our results confirm that male House Wrens transmit their intention to attack a conspecific rival using information encoded in their aggressive displays. Our results add to the growing amount of data showing that various aspects of song displays are putative aggressive signals. We also show that wing quivering predicts a male's likelihood of attacking a conspecific according to Searcy and Beecher's (2009) predictive criterion. These signals may also be hierarchical in their expression with song being used initially. We encourage further research to examine the use of different signals in aggressive interactions and whether they are hierarchical in their expression

LITERATURE CITED

AKÇAY, C., M. E. TOM, E. CAMPBELL, AND M. D. BEECHER. 2013. Song type matching is an honest early threat signal in a hierarchical animal communication system. Proceedings of the Royal Society B 280: 1–8.

ANDERSON, R. C., W. A. SEARCY, S. PETERS, AND S. NOWICKI. 2008. Soft song in Song Sparrows: acoustic structure and implications for signal function. Ethology 114: 662–676.

ANDREW, R. J. 1961. The displays given by passerines in courtship and reproductive fighting: a review. Ibis 103a: 315–348.

BAKER, T. M., D. R. WILSON, AND D. J. MENNILL. 2012. Vocal signals predict attack during aggressive interactions in Black-capped Chickadees. Animal Behaviour 84: 965–974.

BALLENTINE, B., W. A. SEARCY, AND S. NOWICKI. 2008. Reliable aggressive signalling in Swamp Sparrows. Animal Behaviour 75: 693–703.

BARNETT, C. A., C. F. THOMPSON, AND S. K. SAKALUK. 2012. Aggressiveness, boldness and parental food provisioning in House Wrens (*Troglodytes aedon*). Ethology 118: 984–993.

BRUMM, H. 2009. Song amplitude and body size in birds. Behavioral Ecology and Sociobiology 63: 1157–1165.

CALVERT, G., C. SPENCE, AND B. E. STEIN. 2004. The handbook of multisensory processes. MIT Press, Cambridge, MA.

CATCHPOLE, C. K., AND P. J. SLATER. 2008. Bird song: biological themes and variations, 2nd edition. Cambridge University Press, Cambridge, UK.

HEBETS, E. A., AND D. R. PAPAJ. 2005. Complex signal function: developing a framework of testable hypotheses. Behavioral Ecology and Sociobiology 57: 197–214.

HOF, D., AND N. HAZLETT. 2010. Low-amplitude song predicts attack in a North American wood warbler. Animal Behaviour 80: 821–828.

HUBER, R., AND E. A. KRAVITZ. 2010. Aggression: towards an integration of gene, brain and behaviour. In: Social behaviour: genes, ecology and evolution (T. Székely, A. J. Moore, and J. Komdeur, eds.), pp. 185–199. Cambridge University Press, Cambridge, UK.

HURD, P. L., AND M. ENQUIST. 2001. Threat display in birds. Canadian Journal of Zoology 79: 931–942.

HURLBERT, S. H. 1984. Pseudoreplication and design of ecological field experiments. Ecological Monographs 54: 187–211.

JOHNSON, L. S. 1998. House Wren (*Troglodytes aedon*). In: The Birds of North America, No. 380 (A. Poole and F. Gill, eds.). The Birds of North America, Philadelphia, PA.

KIKKAWA, J., J. N. M. SMITH, R. PRYS-JONES, P. FISK, AND C. CATTERALL. 1986. Determinants of social dominance and inheritance of agonistic behavior in an island population of Silvereyes, *Zosterops lateralis*. Behavioral Ecology and Sociobiology 19: 165–169.

KROODSMA, D. E., B. E. BYERS, E. GOODALE, S. JOHNSON, AND W.-C. LIU. 2001. Pseudoreplication in playback experiments, revisited a decade later. Animal Behaviour 61: 1029–1033.

LAMBRECHTS, M. M., F. ADRIAENSEN, D. R. ARDIA, A. V. ARTEMYEV, F. ATIÉNZAR, J. BAŃBURA, E. BARBA, J.-C. BOUVIER, J. CAMPRODON, C. B. COOPER, R. D. DAWSON, M. EENS, T. EEVA, B. FAIVRE, L. Z. GARAMSZEGI, A. E. GOODENOUGH, A. G. GOSLER, A. GRÉGOIRE, S. C. GRIFFITH, L. GUSTAFSSON, L. S. JOHNSON, W. KANIA, O. KEIŠ, P. E. LLAMBIAS, M. C. MAINWARING, R. MÄND, B. MASSA, T. D. MAZGAJSKI, A. P. MØLLER, J. MORENO, B. NAEF-DAENZER, J.-Á. NILSSON, A. C. NORTE, M. ORELL, K. A. OTTER, C. R. PARK, C. M. PERRINS, J. PINOWSKI, J. PORKERT, J. POTTI, V. REMES, H. RICHNER, S. RYTKÖNEN, M.-T. SHIAO, B. SILVERIN, T. SLAGSVOLD, H. G. SMITH, A. SORACE, M. J. STENNING, I. STEWARD, C. F. THOMPSON, P. TRY-JANOWSKI, J. TÖRÖK, A. J. VAN NOORDWIJK, D. W. WINKLER, AND N. ZIANE. 2010. The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. Acta Ornithologica 45: 1–26.

LANYON, S. M., AND C. F. THOMPSON. 1984. Visual displays and their context in the Painted Bunting. Wilson Bulletin 96: 396–407.

MONTGOMERIE, R. D., AND P. J. WEATHERHEAD. 1988. Risks and rewards of nest defence by parent birds. Quarterly Review of Biology 63: 167–187.

R DEVELOPMENT CORE TEAM [online]. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.Rproject.org> (Accessed 25 May 2013).

RĘK, P., AND T. S. OSIEJUK. 2011. Nonpasserine bird produces soft calls and pays a retaliation cost. Behavioral Ecology 22: 657–662.

SANDOVAL, L. 2011. Male–male vocal interactions in a territorial quail: which song characteristics predict a territorial male's response? Behaviour 148: 1103–1120.

SEARCY, W. A., R. C. ANDERSON, AND S. NOWICKI. 2006. Bird song as a signal of aggressive intent. Behavioral Ecology and Sociobiology 60: 234–241.

———, AND M. D. BEECHER. 2009. Song as an aggressive signal in songbirds. Animal Behaviour 78: 1281–1292.

VEHRENCAMP, S. L., M. L. HALL, E. R. BOHMAN, C. D. DEPEINE, AND A. H. DALZIELL. 2007. Song matching, overlapping and switching in the Banded Wren: the sender's perspective. Behavioral Ecology 18: 849–859.

WHITE, D. W., AND E. D. KENNEDY. 1997. Effect of egg covering and habitat on nest destruction by House Wrens. Condor 99: 873–879.

WOOD, S. [online]. 2013. Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation. R package version: 1.7–24. <http://CRAN.R-project.org/package=mgcv> (Accessed 6 June 2013).

XIA, C., J. LIU, P. ALSTRÖM, Q. WU, AND Y. ZHANG. 2013. Is the soft song of the Brownish-flanked Bush Warbler an aggressive signal? Ethology 119: 653–661.