

Seasonal Variation in Response to Neighbors and Strangers by a Territorial Songbird

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Abstract

Reduced aggression toward territorial neighbors, termed the ‘dear-enemy’ effect, is thought to arise because territorial animals benefit by avoiding contests with neighbors with whom they have already established relationships. The dear-enemy effect has been described in many taxa, but few studies have considered whether or not neighbors’ relationships are affected by changes in the social environment. In this study, I tested whether Carolina wrens, *Thryothorus ludovicianus*, behaviorally discriminate between neighbors and strangers in two different social environments: in spring when territories have been established for several months, and in fall when an influx of new birds claiming territories might de-stabilize wren neighborhoods. Comparisons of responses of territorial males to playbacks of songs from neighbors and strangers showed that Carolina wrens show the dear-enemy effect in spring, but not in fall in this design. The apparent lack of a differential response to neighbors and strangers in fall might be due to a reduction in aggression toward strangers. This study provides evidence that seasonal changes in the dear-enemy effect coincide with seasonal changes in the social environment.

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Introduction

Reduced aggression toward territorial neighbors, termed the ‘dear-enemy’ effect (Fisher 1954), is thought to arise because recognition of neighbors benefits a territorial animal by allowing it to avoid territorial contests with neighbors with whom it has already established relationships. Reduced aggression toward established neighbors could result in mutual benefits for the neighbors by allowing them to reduce the time and energy spent defending a shared territorial boundary.

Recognition of territorial neighbors has been documented in many taxa, including amphibians (Davis 1987), reptiles (Fox & Baird 1992), mammals

(Cheney & Seyfarth 1982), and songbirds (Falls 1982; Stoddard 1996). Although the dear-enemy effect is widespread, few studies have examined how dear-enemy relationships, once established, change over time. Presumably, all territorial dear enemies were once unfamiliar rivals with unsettled boundaries at the time of their initial encounter. Through time these unfamiliar rivals settle territorial boundaries, learn to recognize one another, and achieve a cooperative relationship. Accepting neighbors as dear enemies is a conditional strategy, which ceases when neighbors fail to respect mutual territorial boundaries (Godard 1993). Altered social conditions that cause neighbors in general to become more threatening might result in a loss of dear-enemy cooperation.

The Carolina wren (*Thryothorus ludovicianus*) provides a model system for examining the effect of altered social conditions on dear-enemy cooperation. Male and female Carolina wrens defend territories throughout the year. First-year Carolina wrens pair and begin to set up territories in their first fall, and these territories are often located alongside or between the territories of established older birds (Simpson 1982; C. Hogan and J. Hyman, unpubl. data). An influx of new birds and new territories might destabilize wren neighborhoods in several ways. A constant onslaught of intruders could result in increased levels of overall aggressiveness of territory holders, as has been noted in other species with year-round territoriality and fall territory settlement by first-year birds (Logan & Wingfield 1990). Neighborhoods could also become destabilized due to cascading shifts of territory boundaries as new individuals gain space at the expense of established individuals. Territory owners are known to increase aggression toward displaced neighbors (Husak & Fox 2003), and a territory owner can take advantage of the presence of intruders to expand a territory at the expense of an established neighbor (Itzkowitz 1977). These mechanisms may result in instability of territorial boundaries not only between established residents and young birds, but also between previously established territory owners. With territorial boundaries in flux, male Carolina wrens might fail to show dear-enemy cooperation with neighbors.

In this study, I tested whether Carolina wrens behaviorally discriminate between neighbors and strangers in two different social environments: in spring when territories have been established for several months, and in fall when new territories are settled by the young of the year. I presented territorial males with playbacks of neighbors' and strangers' songs. Responses of territorial males allowed me to determine whether or not Carolina wrens showed the dear-enemy effect. Comparing response to playbacks in spring and fall allowed me to address whether or not their behavior changed in response to different seasonal and social situations.

Methods

I conducted this study at the Mason Farm Biological Reserve in Chapel Hill, NC, USA, where Carolina wrens occupy oak-hickory and riparian forest. All methods were approved by the University of North Carolina IACUC (proposal no. 99-098.0-B).

The first set of playbacks was performed at the beginning of the breeding season in Apr. and May 1998 (spring). All territorial birds included in this study had been present since the previous fall, as had all of their neighbors. No fledged young were observed during this period, although some pairs had nests. The second set of experiments was conducted in Sep. and Oct. 1998 and 1999 (fall), at the time of year when young birds settle territories. I surveyed the population regularly and was able to note the appearance of new territorial individuals in the population. During the course of this study, I observed only one territory established from Feb. to Aug., and 20 territories established from Sep. to Jan.

I color banded all the experimental subjects for individual identification throughout 1998 and 1999 and mapped territories by plotting the locations of singing males with reference to a 25-m grid of stakes over much of the study site. Twelve territorial males served as subjects in the spring of 1998. Six of these birds were tested again in fall 1998. Seven more birds, not used in the 1998 experiments, acted as subjects in the fall of 1999, for a total of 13 subjects in fall. Neighbors were birds whose territories adjoined the subject's. Strangers were territorial males recorded elsewhere on the study site, anywhere from five territory diameters to 2 km away from the subjects' territories. Subjects and neighbors had interacted with each other for several months prior to the experiments. The subjects in the spring experiments had been neighbors for several months. The males used as subjects in the fall experiments had been on their territories since the previous spring, as had most of their neighbors.

I recorded singing Carolina wrens with a Marantz PMD221 (Aurora, Illinois, USA) recorder and a Sennheiser K3U/ME88 (Old Lyme, Connecticut, USA) ultradirectional microphone. I used songs recorded from males in 1998 and 1999 to construct playback tapes. Clear examples of songs were chosen after examination with a Uniscan II real-time spectrum analyzer. I digitized the songs at 16 kHz and 16-bit accuracy on a 68030 Macintosh computer using Audiomedia hardware and software (Digidesign, Palo Alto, CA, USA). All songs were adjusted to the same maximum amplitude and re-recorded on a Marantz PMD221 recorder. Each tape was approximately 45 s long and consisted of seven songs of the same song type, delivered at a rate of approximately 10 songs per minute (intervals varied slightly to match natural singing). This playback was within the natural range of song rate, song type switching, and overall song bout length (Haggerty & Morton 1995). I chose short playback durations to minimize the possibility that subjects would reach a speaker while the tape was still playing. Playback tapes were played from a Marantz PMD221 recorder connected to an Amplivox amplifier and a Realistic horn speaker (frequency response 1.5–2.5 kHz \pm 3 dB, 2.5–8 kHz \pm 2.5 dB) placed in a location approximately 5 m inside the subjects' territory and clamped to a sapling 1.5–2 m above ground.

In all trials, I used different song types for neighbor and stranger on the playback tapes. I did not determine whether the stranger song types were present in the repertoires of the subjects or any adjacent neighbor. Males in this population have a song repertoire of 25–43 songs, and on average neighboring males share 80% of their songs (Simpson 1982). Because the strangers were

usually <1 km from the subjects, the songs of the strangers were likely to be represented in the repertoire of the subject or adjacent neighbors (Simpson 1982; Morton 1987). Each male received two playback treatments: (1) neighbor song played near a correct boundary (N) and (2) stranger song played from the same place (S). I presented each subject with recordings from a different neighbor or stranger, such that the number of exemplars used equaled the number of subjects. The order of presentation was randomized such that half of the subjects received a neighbor's song first, and half heard the stranger's song first. All playbacks were conducted between 06:00 and 09:00 EST. All playbacks began when the subject and all neighbors were silent and out of sight. Treatments were separated by 4–5 d.

I recorded subjects' responses for 15 min beginning at the start of the playback tape. Response variables recorded were latency to approach (time from the start of the playback tape to an approach closer than 15 m to the speaker), closest approach (closest the subject came to the speaker in 15 min following the initiation of the trial), time close (time spent within 15 m of the speaker), latency to sing (time elapsed between the initiation of the trial and the first songs sung by the subject), number of songs (total number of songs sung by the subject in 15 min following the initiation of the playback), and time calling (minutes during a trial when calling activity occurred). Male Carolina wrens have a repertoire of calls, described as 'chirt', 'cheer', and 'rasp', and these calls are used more frequently in fall than in spring (Haggerty & Morton 1995). These calls are often used in combination, and are difficult to quantify individually, so 'time calling' reflects number of minutes during a playback trial when a subject male was giving any of these calls. These response measures are likely to be correlated, so I used principal components analysis (PCA) to create a composite score. To compare treatments I used the scores on the first and second principal components in a two-tailed Wilcoxon matched-pairs signed-ranks test. The scores from the first and second principal component were analyzed, as they appeared to reflect different aspects of a response (see Results). Power analyses were performed using StudySize 1.0.8. By comparing responses to the neighbor and stranger trials, I determined whether the subjects behaviorally discriminated between familiar and unfamiliar birds on the basis of song.

I made seasonal comparisons to determine whether birds respond differently to playback in spring and fall. I compared responses of subjects to playbacks of neighbors at correct boundaries in both seasons. Comparing subjects' responses to similar stimuli in spring and fall allowed me to determine whether playback responses differed with season. Natural mortality of subjects over the course of the year made it impossible to test all subjects in both seasons. Therefore, the comparisons of spring and fall behavior were not paired, and I used the scores on the first principal components in a two-tailed Mann–Whitney U-test. It is unlikely that habituation had any effect on the outcome of the fall experiments. First, 7 of 13 birds used in the fall experiments had not previously been used in this experiment. Second, previous experiments demonstrated that Carolina wrens do

not habituate to a single song type being played for 2 h outside their territory (Simpson 1984). Finally, given the short duration of the playbacks used in the present experiment (45 s), many subjects did not approach the playback until after the song had stopped, and the total exposure to playback was exceedingly small compared with the number of natural vocal interactions a territorial male would have over the course of several months.

To test whether levels of aggression differed between the breeding season and fall, I performed a set of playbacks in combination with taxidermic mounts in order to elicit attacks. These trials were conducted in Jun. and Jul. 2000 and again with different males in Oct. 2000. Attack rates in these two seasons were compared using a two-tailed Fisher's exact test. In these experiments each subject received 5 min of a stranger's song from a speaker attached to a 1.5-m pole. The mount was attached to the top of this pole. The only responses analyzed were attacks, defined as trials in which the subject physically struck the mount.

Results

The subjects' responses to playbacks of neighbors and strangers in spring are shown in Fig. 1a. The first principal component (PC1) explained 43.8% of the variance in the response measures and the second principal component (PC2) explained a further 27.7% (see Table 1 for the principal component loadings). Examining the component loadings reveals that approach variables load highly on PC1, while vocal variables load highly on PC2. A comparison of PC1 scores showed that subjects showed significantly stronger responses to strangers' songs than to neighbors' (Fig. 2a, Wilcoxon matched-pairs signed-ranks test, $Z = -2.353$, $n = 12$, $p = 0.019$), while there was no statistically significant difference in PC2 (Fig. 2b, Wilcoxon matched-pairs signed-ranks test $Z = 1.098$, $n = 12$, $p = 0.272$).

The subjects' responses to playbacks of neighbors and strangers in fall are shown in Fig. 1b. A comparison of the PCA response scores showed that responses to strangers' songs did not statistically differ from responses to neighbors' for either PC1 or PC2 (Fig. 2a, PC1 Wilcoxon matched-pairs signed-ranks test $Z = -0.734$, $n = 13$, $p = 0.463$; Fig. 2b, PC2 Wilcoxon matched-pairs signed-ranks test $Z = -0.664$, $n = 13$, $p = 0.507$). I also checked for differences in response to neighbors and strangers in fall using a PCA on the fall playbacks alone and discriminant function analysis (DFA) with all variables included, but these analyses failed to find a significant difference as well (PCA Wilcoxon matched-pairs signed-ranks test $Z = -1.223$, $n = 13$, $p = 0.221$; DFA $F_{5,20} = 0.761$, $p = 0.588$).

Comparing response to playbacks of neighbors in spring and fall showed no significant difference for either PC1 or PC2 (Fig. 2a, PC1 Mann-Whitney U-test: $U = 105$, $n_1 = 12$, $n_2 = 13$, $p = 0.142$; Fig. 2b, PC2 Mann-Whitney U-test: $U = 58.5$, $n_1 = 12$, $n_2 = 13$, $p = 0.142$). Similarly, PC1 response scores to strangers in spring and fall showed no significant difference (Fig. 2a, PC1 Mann-Whitney U-test: $U = 63.0$, $n_1 = 12$, $n_2 = 13$, $p = 0.415$). In contrast, an analysis

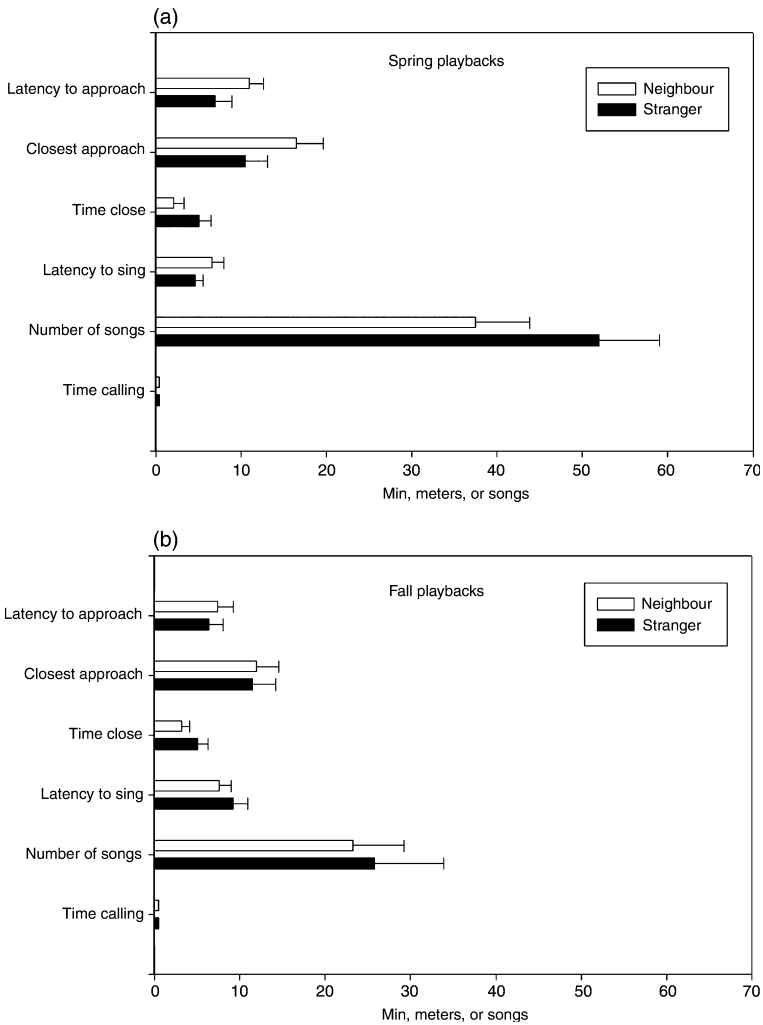


Fig. 1: (a) Mean (\pm SE) of response variables to neighbors and strangers in spring. (b) Mean (\pm SE) of response variables to neighbors and strangers in fall

of PC2 suggests a significant difference in singing responses to strangers in spring and fall (PC2 Mann–Whitney U-test: $U = 115$, $n_1 = 12$, $n_2 = 13$, $p = 0.044$), with a reduced singing response to strangers in fall.

Further evidence of a difference between breeding season and fall territory defense comes from the taxidermic mount experiments, which revealed significantly higher rates of attack in the breeding season than in the fall. In both seasons, most males approached the playback and appeared to investigate the

Table 1: Loadings of the response measures on the first two principal components for responses to neighbors and strangers in spring and fall

Response measures	Loadings	
	PC1	PC2
Latency to approach	0.939	0.132
Closest approach	0.952	0.087
Time close	-0.877	-0.102
Latency to sing	-0.069	-0.899
Number of songs	-0.241	0.859
Time calling	0.094	-0.289

mount, but males in the fall often moved away more quickly. In the breeding season experiments, 8 of 15 males eventually attacked the taxidermic mount, while in the fall, 1 of 12 attacked the mount (Fisher's exact test: $p = 0.019$).

Discussion

The results indicate that in spring, Carolina wrens recognize neighbors and have a dear-enemy relationship with them. Subjects consistently responded more strongly to strangers than to neighbors, as has been found in many other studies of songbirds (Stoddard 1996). In fall, Carolina wrens showed no consistent difference in response to strangers or neighbors. Thus, although Carolina wrens are capable of recognizing and responding less aggressively toward neighbors, as indicated by the experiments in spring, they do not show a differential response to neighbors and strangers in fall. It is important to note that the sample size in fall was larger than that in spring, and the power of this test to detect an effect of the size seen in the spring trials is reasonably high (power = 0.72). Thus the failure to detect a difference of the magnitude seen in spring trials is not due to a smaller sample size. Although it remains possible that looking at other response variables or using a different analysis would reveal a differential response to neighbors and strangers in fall, either the wrens did not behaviorally discriminate between neighbors and strangers in fall, or they discriminated to a much lesser degree than in spring. However, the failure to discriminate between neighbors and strangers in fall occurred for reasons contrary to my initial hypothesis.

I hypothesized that responses to neighbors and strangers might differ between spring and fall because an influx of young birds establishing territories in fall would upset territorial boundaries and increase aggression between established neighbors. However, I detected no increase in aggression toward neighbors in fall. Instead, the failure to find the dear-enemy effect in fall may be the result of a decrease in territorial aggression, and perhaps specifically, a decrease in response to strangers. A decrease in territorial aggression in fall was suggested by the results of the taxidermic mount playback experiment

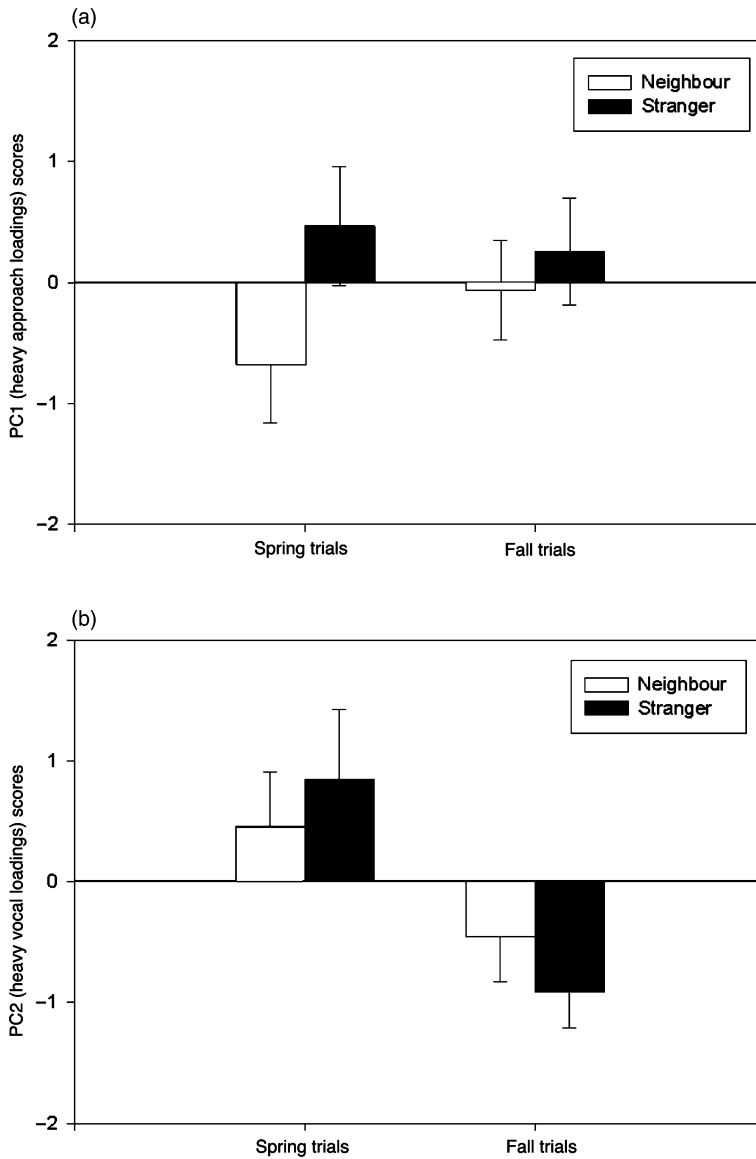


Fig. 2: (a) Mean (\pm SE) first principal component scores for responses to neighbors and strangers in spring and fall. (b) Mean (\pm SE) second principal component scores for responses to neighbors and strangers in spring and fall

indicating that males are more likely to attack an intruder in the breeding season than in the fall. The decreased response to strangers was suggested by the fact that Carolina wrens sang less overall in fall than in spring, and the seasonal difference in song was greatest when responding to strangers. It is worth noting that my ability to detect a decrease in response to strangers was

dependent on the fact that there was a trend toward a higher response to strangers than neighbors in the spring, which is typical of the dear-enemy effect, but a trend toward a lower response to strangers than neighbors in the fall. Although these trends are not statistically significant in my sample, the latter trend raises the possibility that strangers in fall are viewed as less of a threat than established neighbors.

There remains a question of why strangers in fall would be viewed as less of a threat at the time of year when there is an influx of new birds prospecting for territories. The lower aggression toward strangers in fall could occur because most of the strangers in fall are young birds, and it is possible that territory owners view them as less of a long-term threat. Young birds are often subordinate to older birds (Arcese & Smith 1985; Arcese 1987; Piper & Wiley 1989), and most of the young intruders are likely to disperse or die without ever establishing a territory.

Lower aggression in fall could also occur if males are more aggressive during the breeding season because they are defending both their territory and paternity, but only defending a territory in fall. Carolina wrens remain paired year-round and appear not to engage in extra-pair mating behavior (Haggerty et al. 2001), suggesting that there is little need for paternity defense. It is possible, however, that rare incidences of mate switching or extra-pair fertilizations are enough to select for higher aggression during the breeding season and that monogamy in Carolina wrens is a result of effective paternity defense. Another possible explanation for higher aggression during the breeding season is high testosterone levels in spring and summer are related to reproductive activity, resulting in a correlated increase in territorial aggression. If testosterone levels decrease in fall, territorial aggression may decrease as well, although one might expect the decrease in response to be similar to neighbors and strangers. It is not known how Carolina wren hormone levels change seasonally. In other species with year-round territoriality, however, testosterone levels vary seasonally, but song production and territorial aggression appear to be independent of testosterone levels (Wingfield et al. 1999). Interestingly, in studies of year-round territoriality in song sparrows, the intensity of territoriality decreases during the pre-basic molt in early fall, and at this same time, young males are settling territories (Wingfield & Hahn 1994). This pattern may hold true for Carolina wrens as well, as the timing of pre-basic molt also corresponds with the timing of territory settlement by young males (Haggerty & Morton 1995). Despite these possible proximate explanations, there remains an interesting question of why territorial aggression in Carolina wrens would be lowest at the time of year when they face the largest number of intruders.

This study thus documents a seasonal change in the dear-enemy effect associated with seasonal changes in the birds' social environment. Stoddard (1996) reported another case in which the dear-enemy effect depended on the social environment. Song sparrows failed to show the dear-enemy effect in an area where predation by cats created territory vacancies so that boundaries were in

constant flux (Stoddard 1996). This case more closely resembles a situation in which territory settlement is never completed. For Carolina wrens, dear-enemy cooperation might be lost annually, during the seasonal influx of young birds attempting to establish territories, because dear-enemy cooperation becomes irrelevant, as strangers encountered in this season appear to elicit no more alarm than neighbors.

Acknowledgements

I thank Haven Wiley, Helmut Mueller, Steve Nowicki, Ken Lohmann, Alan Feduccia, Cindy Hogan, Will Mackin, Amy Skypala, Joanna Vondrasek and Barbara Ballentine for their help on this manuscript. I also thank Dr Chris Hill and Dr David Spector for their thorough and helpful reviews. This study was conducted at the Mason Farm biological Reserve, Chapel Hill, NC. This work was supported in part by a Wilson Award from the Department of Biology, UNC-Chapel Hill.

Literature Cited

- Arcese, P. 1987: Age, intrusion pressure and defense against floaters by territorial male song sparrows. *Anim. Behav.* **35**, 773–784.
- Arcese, P. & Smith, J. N. M. 1985: Phenotypic correlates and ecological consequences of dominance in song sparrows. *J. Anim. Ecol.* **54**, 817–830.
- Cheney, D. L. & Seyfarth, R. M. 1982: Recognition of individuals within and between groups of free-ranging vervet monkeys. *Am. Zool.* **22**, 519–529.
- Davis, M. S. 1987: Acoustically mediated neighbour recognition in the North American bullfrog, *Rana catesbeiana*. *Behav. Ecol. Sociobiol.* **21**, 185–190.
- Falls, J. B. 1982: Individual recognition by sound in birds. In: *Acoustic Communication in Birds*, Vol. 2 (Kroodsma, D. E. & Miller, E. H., eds). Academic Press, New York, pp. 237–278.
- Fisher, J. 1954: Evolution and bird sociality. In: *Evolution as a Process* (Huxley, J., Hardy, A. C. & Ford, E. B., eds). Allen and Unwin, London, pp. 71–83.
- Fox, S. F. & Baird, T. A. 1992: The dear enemy effect in the collared lizard, *Crotaphytus collaris*, with a cautionary note on experimental methodology. *Anim. Behav.* **44**, 780–782.
- Godard, R. 1993: Tit for tat among neighbouring hooded warblers. *Behav. Ecol. Sociobiol.* **33**, 45–50.
- Haggerty, T. M. & Morton, E. S. 1995: Carolina wren (*Thryothorus ludovicianus*). In: *The Birds of North America*, No. 188 (Poole, A. & Gill, F., eds). The Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, DC. pp. 1–20.
- Haggerty, T. M., Morton, E. S. & Fleischer, R. C. 2001: Genetic monogamy in Carolina wrens (*Thryothorus ludovicianus*). *Auk* **118**, 215–219.
- Husak, J. F. & Fox, S. F. 2003: Adult male collared lizards, *Crotaphytus collaris*, increase aggression toward displaced neighbours. *Anim. Behav.* **65**, 391–396.
- Itzkowitz, M. 1977: Interrelationships of dominance and territorial behaviour in the pupfish, *Cyprinodon variegatus*. *Behav. Processes* **2**, 383–391.
- Logan, C. A. & Wingfield, J. C. 1990: Autumnal territorial aggression is independent of plasma testosterone in mockingbirds. *Horm. Behav.* **24**, 568–581.
- Morton, E. S. 1987: The effects of distance and isolation on song type sharing in the Carolina wren. *Wilson Bull.* **99**, 601–610.
- Piper, W. & Wiley, R. H. 1989: Correlates of dominance in wintering white-throated sparrows: age, sex, and location. *Anim. Behav.* **37**, 298–310.
- Simpson, B. S. 1982: Communication with complex vocal repertoires by a territorial passerine, the Carolina Wren. PhD Thesis, Univ. North Carolina, Chapel Hill.
- Simpson, B. S. 1984: Tests of habituation to song repertoires by Carolina wrens. *Auk* **101**, 244–254.
- Stoddard, P. K. 1996: Vocal recognition of neighbours by territorial passerines. In: *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D. E. & Miller, E. H., eds). Cornell Univ. Press, Ithaca, NY, pp. 356–374.

- Wingfield, J. C. & Hahn, T. P. 1994: Testosterone and territorial behavior in sedentary and migratory sparrows. *Anim. Behav.* **47**, 77—89.
- Wingfield, J. C., Jacobs, J. D., Soma, K., Maney, D. L., Hunt, K., Wisti-Peterson, D., Meddle, S., Ramenofsky, M. & Sullivan, K. 1999: Testosterone, aggression, and communication: ecological bases of endocrine phenomena. In: *The Design of Animal Communication* (Hauser, M. D. & Konishi, M., eds). MIT Press, Cambridge, pp. 255—284.

Received: August 4, 2004

Initial acceptance: October 2, 2004

Final acceptance: February 13, 2005 (S. Foster)