Captive European Starlings (*Sturnus vulgaris*) in Breeding Condition Show an Increased Cardiovascular Stress Response to Intruders

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ABSTRACT

European starlings (*Sturnus vulgaris*) alter their physiology and behavior between seasons, becoming territorial during the spring/summer and flocking during the fall/winter. We used captive male starlings in breeding (photostimulated to 18L : 6D) and nonbreeding (11L : 13D) conditions to determine whether changing physiology and behavior alters their reaction to crowding. One or five intruders entered a resident's cage without human disturbance. A subcutaneous heart rate transmitter recorded cardiovascular output in residents. Corticosterone and testosterone were measured in plasma samples taken before and after the intrusion. While corticosterone concentrations did not change, heart rate changed significantly, indicating that these responses can be regulated independently. Long-day birds showed a significantly elevated heart rate response to the single-bird intrusion compared to short-day birds. Whereas five intruders elicited an identical peak response in both groups, long-day birds also demonstrated an equivalent response to one intruder. In addition, one intruder induced longer elevation in heart rate for long-day birds. Male starlings in breeding condition, therefore, demonstrate an increased sensitivity to additional conspecifics. This seasonal shift in response suggests that a higher tolerance for intrusion (i.e., considering a nearby starling as less stressful) may facilitate flocking behavior, while a lower tolerance may aid in territoriality.

Introduction

As seasons change in temperate zones, priorities shift for many birds. The fall and winter present the challenges of foraging for

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food and predator avoidance as resources become increasingly scarce. In these seasons, survival becomes the priority, and many avian species join large flocks capable of finding food and decreasing predation risk. Spring and summer present different challenges of mating, breeding, and raising young. In these seasons, reproduction becomes the priority and flocking behavior is replaced by territorial behavior. Birds therefore adjust their behavioral and physiological response in order to maximize survival and reproductive fitness depending on fluctuating seasonal situations (Wingfield and Silverin 2002).

These behavioral changes are often hormonally mediated. In the spring, males regrow their testes and increase secretion of testosterone, which is believed to be responsible for regulating territorial behavior during the breeding season (Wingfield and Silverin 2002). Castration at this point results in a decrease in territory establishment, and injection of testosterone will cause resumption of this behavior (Collias et al. 2002). Testosterone levels peak as territories are being established and decrease rapidly thereafter (Wingfield 1984).

Despite the seasonal shifts in behavioral priorities, animals face dangerous situations (e.g., predators) and must react appropriately in order to survive throughout the year. Mounting a stress response enables the animal to return to or maintain a state of physiological balance after exposure to an acute stressor, and the ability to initiate a proper response is crucial for survival (Sapolsky et al. 2000). There are two major pathways of the stress response: the immediate release of epinephrine leading to the fight-or-flight response and the subsequent release of glucocorticosteroids (corticosterone in birds). Heart rate can be used as an index of the catecholamine release during the fight-or-flight response, and it has been shown to operate independently from the hormonal response during stress (Nephew et al. 2003). Although corticosterone is the primary hormone released during the slower endocrine response to an acute stress, basal and stress-induced concentrations of corticosterone change seasonally and across different physiological states. Seasonal alterations in the stress response may allow for changes in behavior as the importance of adult survival versus reproduction shifts (Ricklefs and Wikelski 2002).

In this study, we exposed male European starlings (*Sturnus vulgaris*) to acute increases in conspecific density (crowding) in order to determine whether the cardiovascular and/or corticosterone responses to this stressor vary seasonally. Male European starlings show distinctly different behavioral characteristics throughout the year. They join massive flocks while in nonbreeding condition (fall/winter) but become strictly terri-

torial while in breeding condition (spring/summer; Feare 1984). By investigating both the endocrine and the cardiovascular responses to crowding, we can determine whether changes in the stress response may aid in modifying these seasonal changes in behavior. When observed during a photoperiod in which free-living birds would be flocking, captive birds on a short-day light cycle demonstrate a graded response to one, three, and five intruders (Nephew and Romero 2003). However, this response has yet to be examined in birds held on a long-day cycle, when free-living birds have high testosterone concentrations and are territorial. Our hypothesis was that male starlings in breeding condition (recently shifted to a long-day photoperiod) would show less tolerance to intruders and, therefore, mount a greater stress response than males that are in nonbreeding condition (held on a short-day photoperiod).

Material and Methods

Birds

All starlings were captured in the wild in eastern Massachusetts and brought into captivity. Male starlings used in the short-day (SD) group were placed in a communal aviary and maintained on a light cycle of 11L : 13D to mimic the fall and winter months. Testosterone concentrations and testicular development were not evaluated, but birds' dark beaks indicated low levels of testosterone and general nonbreeding condition (Ball and Wingfield 1987). Male starlings used in the long-day (LD) group were put on a 10L : 14D light cycle in a communal aviary and allowed to undergo a complete molt before photostimulation to an 18L : 6D light cycle that mimicked spring and summer months. Experiments were performed at the previously reported peak in testosterone concentrations on days 13 and 15 after photostimulation (Young et al. 2001), and individual testosterone concentrations as well as testes size were evaluated.

Both groups (SD and LD) were subsequently housed in identical specially designed crowding cages with an upper and a lower chamber connected by a trapdoor that could be operated remotely to prevent human disturbance (see Nephew and Romero 2003). Residents were placed in the top chamber, which also contained the food, water, perch, and receiver for the implanted heart rate monitor. Two experiments were conducted simultaneously with cages next to each other. All resident birds were male, but intruders were a mix of male and female and were randomly selected from our captive population (30 birds) on the day of the experiment. All experiments complied with Association for Assessment of Laboratory Animal Care guidelines, and the Tufts Institutional Animal Care and Use Committee approved the protocol.

Transmitter Implantation

Implantation of the heart rate transmitters followed the protocol presented by Nephew et al. (2003). Briefly, residents were implanted with a 4.0-g, 20 × 10 × 10-mm Data Sciences International (DSI, St. Paul, MN) transmitter (model TA10EA-F20). Each bird was anesthetized via either a beak cone infused with Metofane (Pitman-Moore, Mundelein, IL) or an injection of Ketamine (30 mg/kg) and Xylazine (10 mg/kg) into the pectoral muscle. The two electrocardiogram (ECG) leads with exposed ends were secured at either the neck region or the back region with a suture in the muscle using coated Vicryl braided suture (Ethicon, Somerville, NJ). The body of the transmitter was placed in the abdominal cavity by opening up enough space in the right side to accommodate the transmitter, and extra lead and sutures were used to close the muscle wall followed by the skin. Antibiotic ointment was applied to all areas where incisions had been made. Some birds were given Ketophen to relieve any pain associated with the surgery. SD birds were allowed 2 d for recovery and LD birds were allowed up to 1 wk for recovery in individual cages. All birds were observed to have fully recovered from the surgery before the experiments and demonstrated a full range of motion and flight ability.

Crowding Protocol

The protocol for resident crowding was followed according to Nephew and Romero (2003). All experiments were conducted between 0900 and 1200 hours to limit daytime fluctuations in corticosterone (CORT) and stress responses (Romero and Remage-Healey 2000). Residents were acclimated to the cage arrangement before the trials. They were fed ad lib. as the top chamber contained the food and water. The top chamber also contained the receiver to transfer the data from the implanted heart rate monitor to a computer outside the room. Either one or five intruders were placed in the bottom chamber of the cage, which contained water and a perch but no food. All birds were allowed 2 h to acclimate after the initial move; no human entered or exited the room during this time. At the time of the experiment, the trap door, equipped for remote operation, was opened, and all intruders entered the upper resident's chamber in less than 3 min. Once all intruders had flown up, the trap door was shut. This protocol removed any human disturbance during the intrusion. All birds were allowed to interact for 30 min, and continuous heart rate data were collected. Thirty minutes after intrusion, the resident was removed and bled within 3 min of entering the room. All the birds were then returned to their individual cages or flight aviary. Each resident was exposed to one and five intruders in a repeated-measures design, with heart rate recordings taken 30 min before intrusion serving as the control. For LD birds, these experiments were conducted 1 d apart during peak testosterone levels. Experiments with SD birds were also conducted in series. The order of the treatments was randomly chosen for each resident.

Heart Rate

Heart rate was recorded 30 min before intruders entered the upper chamber. A mean baseline was calculated for each individual resident from the data 20–25 min into heart rate recording before intrusion. Postintrusion heart rate was recorded for 30 min after all intruders were inside the residents' cage. Heart rate data were processed with Dataquest Advanced Research Technology (ART) Gold (ver. 1.1, St. Paul, MN) software. *R* wave frequency was averaged over 10-s intervals, and a rolling mean was constructed for 30 s. The 30-s intervals were then averaged into 5-min blocks for the 60 min of recording. For each individual, these time points were subtracted from that individual's mean baseline value in order to determine the change in heart rate above baseline.

CORT Analysis

Basal blood samples were taken before arranging the birds in the crowding cage (2 h before the basal heart rate sampling). Postintrusion samples were taken after 30 min of crowding. Both basal and postintrusion samples were drawn within 3 min of entering the room. Blood was collected from the wing vein in capillary tubes. The tubes were centrifuged at 400 *g* for 5–6 min to separate the plasma component; the plasma was immediately frozen. The radioimmunoassay (RIA) for CORT analysis has been described previously (Wingfield et al. 1992). Briefly, samples were spiked with 2,000 cpm of tritiated CORT for later recovery analysis and allowed to equilibrate. CORT was extracted from the protein component of the plasma using redistilled dichloromethane and dried using nitrogen gas. Samples were then reconstituted in phosphate-buffered saline buffer, with an aliquot used to assess recovery. Samples were then assayed in duplicate using tritiated CORT and a CORT antibody (B3-163, Endocrine Sciences). Activated charcoal separated the unbound from the bound steroids. The bound : unbound ratio was fitted to a standard curve and corrected with the recovery percentage and the original amount of plasma in order to determine the CORT concentration for each sample. All samples were measured in a single assay with an intra-assay variability of 2.0% and a detectability of 0.98 ng/mL.

Testosterone Analysis and Gonad Evaluation

Blood was collected from LD males on day 15 after photostimulation. Blood and plasma were handled in the same manner as the samples described above, with an identical RIA except for substitution of tritiated testosterone and a testosterone antibody (T-3003, Endocrine Sciences). All samples were included in one assay with an intra-assay variability of 1.8%. Mean testosterone concentration for the eight residents was 0.55 ± 0.15 ng/mL, which is consistent with the peak testosterone concentrations in photostimulated males at 2 wk after a shift to 18L : 6D light cycles, as published by Young et al. (2001). Testes were removed from each resident after the two treatments and measured. The mean for the paired testes mass was 0.72 ± 0.09 g, which was consistent with the size demonstrated for testes 2 wk after photostimulation, as published by Young et al. (2001).

Statistical Analysis

We compared three heart rate parameters between SD and LD birds in a repeated-measures analysis of one and five intruders. First, peak heart rate in response to the intruders was evaluated in order to compare the initial response between groups and manipulations. Second, heart rate data were integrated for the 30 min after intrusion in order to determine the total sustained increase in heart rate for the length of the intrusion. Third, the amount of time it took each group to resume baseline heart rate was evaluated by assigning a time point at which each individual bird's heart rate returned to within a standard deviation of its own mean baseline value (Nephew et al. 2003). All three parameters and CORT data were analyzed using SAS JMP software (ver. 5.0.1.2) employing a repeated-measures MANOVA comparing day length effects to intruder number.

Results

For all groups there was a clear and significant peak in heart rate (HR) at the 35-min time point, when all intruders were in the resident's cage (Fig. 1). We calculated a change over baseline to control for the high variability that was observed
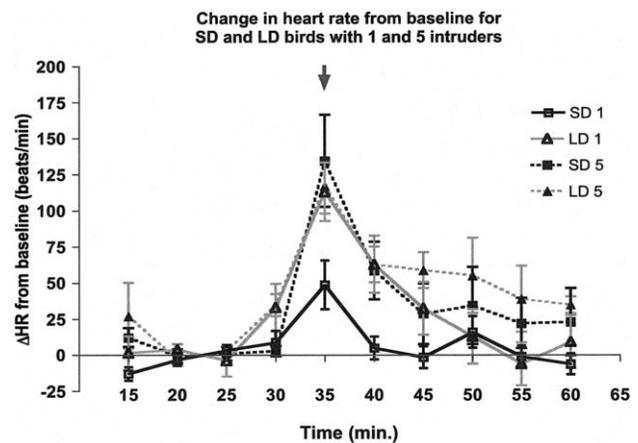

Figure 1. Mean (±SEM) change in heart rate for short-day (SD) and long-day (LD) residents faced with one and five intruders before and after intrusion at 35 min (*n* = 8 for SD, *n* = 7 for LD). Baseline, as determined before intrusion (between 20 and 25 min), was subtracted from the heart rate for each time point. The peak for SD birds with one intruder was significantly different from the other treatment peaks ($F_{1,13} = 5.19$, $P < 0.05$). The arrow indicates the point of intrusion.

between individual birds. LD and SD groups did not differ in their overall peak response (effect of day length: $F_{1,13} = 0.707$, $P = 0.416$), but five intruders induced a significantly higher HR peak (effect of the number of intruders: $F_{1,13} = 6.28$, $P <$
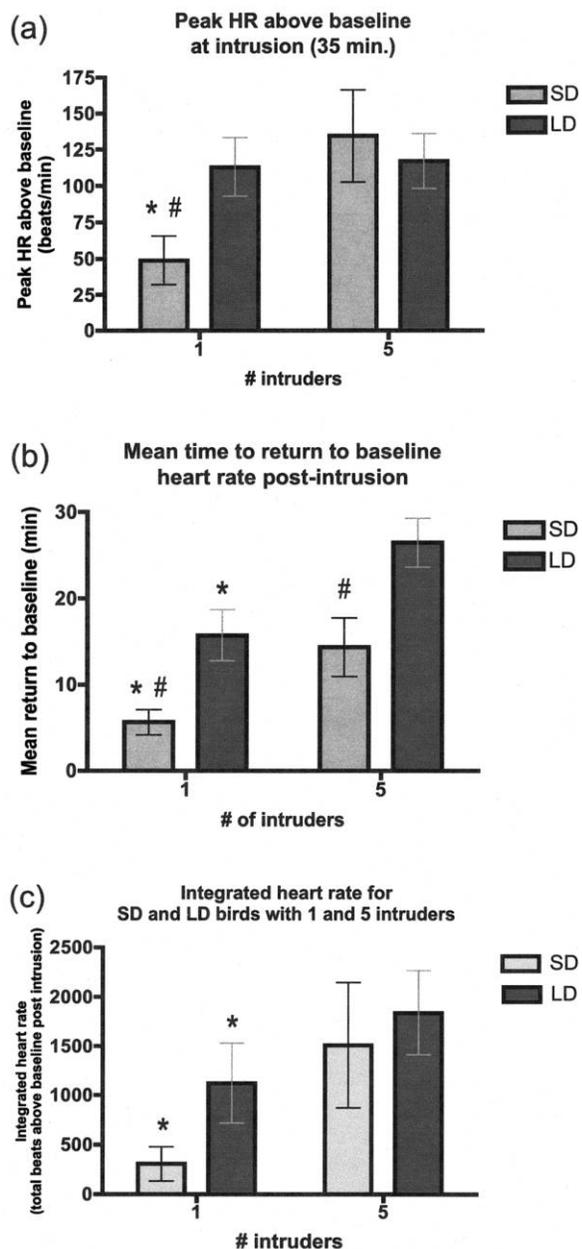

(a) **Peak HR above baseline at intrusion (35 min.)**

(b) **Mean time to return to baseline heart rate post-intrusion**

(c) **Integrated heart rate for SD and LD birds with 1 and 5 intruders**

Figure 2. Analysis of three heart rate parameters: (*a*) peak heart rate (change from baseline) at the point of intrusion, (*b*) mean time for resident to return within 1 SD of baseline, and (*c*) the integrated response evaluating the total area above baseline postintrusion. Bars indicate means ± SEM; *n* = 8 for short day (SD) and *n* = 7 for long day (LD). Significant difference compared to five intruders indicated by an asterisk, and significant difference compared to LD birds indicated by a number sign.

0.03). SD residents with one intruder had a significantly lower HR peak than the other treatments (interaction between day length and the number of intruders: $F_{1,13} = 5.19$, $P < 0.05$; Fig. 2*a*). In addition, overall, LD residents took longer to return to baseline (effect of day length: $F_{1,13} = 13.65$, $P < 0.003$), and residents with five intruders took longer than residents with one intruder (effect of the number of intruders: $F_{1,13} = 14.61$, $P < .003$). The interaction between day length and number of intruders was the same ($F_{1,13} = 0.1487$, $P = 0.7060$; Fig. 2*b*). The integrated values for heart rate indicated that residents with five intruders had a significantly higher sustained elevation during the intrusion (effect of number of intruders: $F_{1,13} = 5.43$, $P < 0.04$), but there was no significant difference in the elevation between the SD and LD groups (effect of day length: $F_{1,13} = 1.414$, $P = 0.2556$), and the change observed for each group was the same (interaction between day length and number of intruders: $F_{1,13} = 0.349$, $P = 0.565$; Fig. 2*c*).

The CORT levels did not significantly rise above baseline levels after the intrusion for any treatment ($P > 0.14$ for all comparisons; Fig. 3).

Discussion

While both SD and LD residents reacted to five intruders with similar cardiovascular responses, they differed markedly when faced with one intruder. In the SD birds, a one-bird intrusion caused a brief, minor rise in heart rate and a return to baseline almost immediately. In contrast, LD residents' heart rate peak was the same regardless of the number of intruders. Peak sympathetic response was also identical for SD with five intruders and LD residents with one or five intruders. These data suggest that LD birds consider one intruder as immediately stressful as five intruders. However, LD residents do respond differently overall to the number of intruders. With five intruders, LD birds had a higher elevation in heart rate throughout the intrusion and took 10 min longer, on average, to return to baseline, as compared to their return with one intruder.

These data suggest that six birds (five intruders plus the resident) in this size cage is simply a "crowding" situation. For the SD group, this number can be interpreted as beyond the optimal group size. In nature, a larger group size outside of the breeding season enables individuals to decrease predation risk (Powell 1974), but a group will reach an optimal size when resources are not limited (Yamaguchi and Yahara 2002; Pride 2005). Since resources were not limited in this study, SD birds that would naturally form groups will prefer an optimal size; six birds appears to surpass this density. In contrast, even one intruder seems to surpass the tolerance for additional birds for LD residents, despite the lack of physical crowding.

While LD residents retained an elevated heart rate for over 15 min during the one-bird intrusion, the heart rate of SD residents returned immediately to baseline. The different response in SD birds may be an indicator of tolerance for ad-
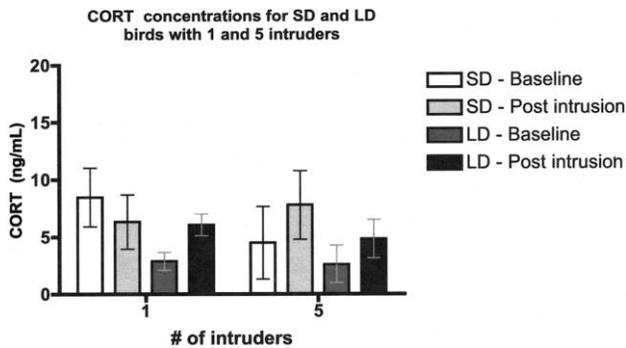
Figure 3. Mean ($\pm$ SEM) corticosterone concentrations for short-day (SD) and long-day (LD) birds before and after intrusion ($n = 8$ for SD, $n = 7$ for LD).

ditional birds close by, or it may be a consequence of starlings' social behavior during the fall and winter months. In social rodents, pair housing can contribute to stress relief such that stress hormones decrease (Westenbroek et al. 2005) and elevated heart rates return to baseline or even below baseline (Sharp et al. 2003). Although similar data are lacking in birds, the quick return to baseline in SD residents with one intruder may reflect calming effects of companionship.

In contrast, males are territorial during the breeding season. In these months, tolerating a neighbor may cost the resident not only his resources but also his mate. In the breeding season, the increase in testosterone concentrations has been correlated with increased territorial aggression (see review in Wingfield 2005), and castration of breeding birds eliminates male-male aggression typical of territorial defense (Wingfield and Ramenofsky 1985; Soma et al. 2002). However, there are additional factors, which were not used in this study, that induce breeding condition and behavior observed in nature. These factors include male-male interactions (Wingfield et al. 1990), the availability of nest boxes (Gwinner et al. 2002), and the presence of females (Pinxten et al. 2003). For starlings in captivity, there is little evidence that the elevated basal testosterone concentration, due to photostimulation alone, increases aggressive behavior. Therefore, in our study we assumed that increasing the number of birds in the same-size cage mimicked natural acute increases in density, but we did not directly measure changes in aggression. Although a previous study on crowding stress demonstrates that aggression increases with a larger number of birds in one cage (Nephew and Romero 2003), the cage size in which the animals are constrained appears to be more important in evaluating crowding stress than the number of animals interacting (Brown and Grunberg 1995). Male LD residents responded to one intruder with a physiological response similar to the one they had when physically crowded by five intruders. Therefore, the presence of an intruding bird seems to be a more important component of the stressor for LD birds than the number of interactions or density of animals.

Although the cardiovascular response was pronounced, birds in this study did not show a significant corticosterone response to increases in density. In the context of the stressor of a territorial invasion, in species in which testosterone concentrations remain constant throughout the year, an intrusion causes a corticosterone response in the resident only if eggs are present (Van Duyse et al. 2004). In tropical stonechats, a species in which the females are also highly territorial, the female responds aggressively toward a male intruder but does not exhibit an increase in corticosterone (Canoine and Gwinner 2005). In addition, it is unlikely that the male residents would have interpreted the crowding cage as their "territory" such that their territorial behavior would have initiated a stress response. In lizards, a corticosterone response in an intrusion situation depended on the duration and dominance of the individual (Knapp and Moore 1995). In birds transitioning from flocking to territoriality, dominance is decided by prior residence (Snell-Rood and Cristol 2005). Because the males in this study had only been placed in the crowding cage before the experiment, they might not have established dominance over their "territory." Therefore, an intrusion simulation during different seasons in the field might have a more dramatic response than one observed in captivity. Perhaps a field-based study could address the effects of natural territorial conditions on heart rate and corticosterone response to intrusion.

The observation that the sympathetic stress response can be dissociated from the endocrine stress response is also quite important. Previous work has already indicated that heart rate and corticosterone can be regulated independently, depending on the severity of the stressor (Nephew et al. 2003), and results from this study contribute to this observation. Our study demonstrates that the stressors (crowding and intrusion) merit a fight-or-flight response, but these stressors are not perceived as dire enough to require a corticosterone release typical of more severe stressors such as restraint. This ability to separate aspects of the response may be an adaptive function of having the two types of physiological reactions to an acute stressor. On the spectrum of perceiving severity of a stressor, a seemingly less harmful stressor, such as a strange noise, may warrant preparedness activated by the sympathetic response, while a potentially life-threatening stressor, such as being chased by a predator, would require both the quick escape phase from the sympathetic response and the slower recovery phase from the corticosterone response. Both situations are very different, and the dissociation between the responses would allow the animal in the first example to mount a sympathetic cardiovascular response to be alert and ready without having the consequences of activating the rise in corticosterone unnecessarily.

In conclusion, the stressor of intrusion for LD males was not severe enough to elicit a corticosterone response, perhaps because of the captive setting. However, considering that "breeding condition" had been simplified with only photostimulation, elevated testosterone concentration, and increase in

testes size, the observation that LD birds demonstrate a difference in their cardiovascular reaction to an intruder, as compared to their SD counterparts, indicates a basic seasonal shift in the male starling's physiological response to a conspecific in its proximity. The seasonal peak in response, during long days, may help males repel a challenger in their territory during the breeding season, whereas the nadir in the response to crowding, during short days, may facilitate flocking behavior in the nonbreeding season. Thus, the changing stress response, allowing the starling to either tolerate its neighbor or be on intrusion alert, may be an important underlying component of the social behavior differences observed as the seasons change.

Acknowledgments

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