

Peter P. Marra · Rebecca L. Holberton

Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season

Received: 14 November 1997 / Accepted: 9 March 1998

Abstract During the non-breeding season, many species of territorial migratory birds exhibit a non-random pattern of habitat distribution, with males and females occupying different habitats. In this study, we examined possible physiological consequences arising from such habitat segregation in one migrant passerine species, the American redstart (*Setophaga ruticilla*), on its non-breeding grounds in Jamaica, West Indies. For 2 years, we measured concentrations of corticosterone, at the time of capture (baseline) and 30 min after capture (profile of acute corticosterone secretion), in redstarts in two distinct habitats, one occupied predominately by males and one mostly by females. All redstarts in both habitat types exhibited similar concentrations of baseline corticosterone levels in fall (October), whereas in spring (March–April), redstarts in female-biased habitat exhibited significantly higher baseline levels regardless of age or sex. In fall, all individuals in both habitats exhibited significant increases in corticosterone concentration with capture and handling, but in spring only redstarts (both sexes) in male-biased habitat continued to exhibit acute corticosterone secretion. Redstarts in female-biased habitat had elevated baseline corticosterone levels and reduced acute corticosterone secretion. In spring, baseline corticosterone concentration was negatively correlated with body mass, suggesting muscle catabolism associated with high corticosterone concentrations or possibly that birds are leaner as a result of increased foraging effort. These results indicate that redstarts (primarily females) in female-biased habitats suffered a decline in physiological condition, which could in turn influence their departure schedules, migration

patterns and even their condition and arrival schedules on the breeding grounds. Thus, segregation of populations into habitats of different quality during the non-breeding period may have ramifications throughout the annual cycle of such migratory species. Furthermore, these results show the usefulness of plasma corticosterone levels as indicators of physiological condition and thus habitat quality for birds during the non-breeding period.

Key words Corticosterone · Non-breeding season · American redstart · *Setophaga ruticilla* · Habitat quality

Introduction

Many species of migratory songbirds are distributed non-randomly during the non-breeding season (e.g. Lynch 1989; Lopez Ornat and Greenberg 1990; Sliwa 1991; Hutto 1992; Wunderle and Waide 1993). These patterns include sex and/or age classes occurring in different proportions, either at different latitudes (Ketterson and Nolan 1976, 1983) or, as is the case with many long-distance migrants, at the same latitude but in different habitat types (Nisbet and Medway 1972; Lynch et al. 1985; Lopez and Greenberg 1990; Wunderle 1992). Sexual habitat segregation is particularly evident in the Neotropical-Nearctic migrant the American redstart (*Setophaga ruticilla*) throughout most of its non-breeding range, including Mexico (Lopez Ornat and Greenberg 1990), Belize (S. Baird, personal communication), D. Petit, personal communication), Jamaica (Sliwa 1991; Parrish and Sherry 1994; Sherry and Holmes 1996; P.P. Marra, this study), Puerto Rico (C. Stacier, personal communication) and Cuba (G. Wallace, personal communication). Despite the pervasiveness of sexual habitat segregation as a spacing pattern in this and other migratory species during the non-breeding period, the proximate factors influencing it, its consequences on the individual, and its effects on population dynamics are not known.

P.P. Marra (✉)
Department of Biological Sciences, Dartmouth College,
Hanover, NH 03755, USA
e-mail: peter.p.marra@dartmouth.edu, Fax: +1-603-6461347

R.L. Holberton
Department of Biology, University of Mississippi,
University, MS 38677, USA

One explanation of this observed pattern is that interference behavior by dominant individuals (e.g., older males) leads to the exclusion of subordinate individuals (e.g., females and young males) from the most suitable habitats (Gauthreaux 1978; Marra et al. 1993). Marra et al. (1993) showed that when male redstarts were removed from male-biased habitat, they were always replaced, and disproportionately so by females. These experiments suggest behavioral dominance to be a proximate mechanism underlying sexual habitat segregation in American redstarts. The questions then arise whether these habitats differ in suitability and whether individuals forced into female-biased habitat survive less well or suffer a decline in physiological condition over the non-breeding period. The objective of this study was to determine if there are habitat-specific physiological consequences arising from differential patterns of habitat occupancy in the American redstart in Jamaica, West Indies, during the non-breeding season.

Since direct measures of survival of migratory birds are nearly impossible to obtain (e.g., dead or dying birds are rarely found), indirect methods, such as indices of physiological condition must be used as indicators of a compromised physiological state. We assessed the levels of corticosterone, a hormone associated with behavioral and physiological changes in energy demand in birds (Harvey et al. 1984), as an indicator of physiological condition that result from differences in the quality of habitat the birds occupy. Corticosterone is the major glucocorticoid in birds (Holmes and Phillips 1976) and is usually released rapidly into the bloodstream from adrenal tissue in response to a variety of perturbations such as storms and/or predation pressure that increase energy demand or decrease food availability (Wingfield et al. 1983; Wingfield 1994). An increase in corticosterone in response to stressors may promote gluconeogenesis, resulting in a source of glucose substrates from non-carbohydrate sources such as skeletal muscle that can be used until conditions ameliorate (Holmes and Phillips 1976; Harvey et al. 1984). Increases in plasma corticosterone are also believed to alter an individual's behavior, such as increasing foraging activity and food intake rate to meet increased energy demand (Nagra et al. 1963; Wingfield and Silverin 1986; Gray et al. 1990; Astheimer et al. 1992; Wingfield 1994).

The rapid increase in plasma concentrations of corticosterone in response to the acute stress of capture and handling has been demonstrated in a variety of bird species (Dawson and Howe 1983; Wingfield et al. 1992, 1994a,b, 1995; Smith et al. 1994; Holberton et al. 1996 a,b; Dufty and Belthoff 1997). As corticosterone is released, the protocol of sampling an individual immediately after capture and at prescribed intervals thereafter has become the accepted paradigm for measuring the sensitivity of the hypothalamic-pituitary-adrenal axis and, therefore, an individual's adrenocortical response to stress (Schwabl et al. 1991; Wingfield et al. 1992, 1994 a,b; Holberton et al. 1996 a,b; Silverin 1997).

While rapid short-term increases in corticosterone may help an individual through brief perturbations, chronic high levels may have negative consequences on reproduction (Greenberg and Wingfield 1987; Wingfield 1988, 1994; O'Reilly and Wingfield 1995; R.L. Holberton and J.C. Wingfield, submitted) or physical condition (e.g., Harvey et al. 1984; Wingfield 1994). If an individual is unable to meet its energy demand, the gluconeogenic activity of corticosterone may result in catabolism of skeletal muscle as a source of glucose substrates (Holmes and Phillips 1976; Harvey et al. 1984). Several studies have shown, however, that acute corticosterone secretion may be suppressed if higher corticosterone levels have inhibitory effects on certain activities such as breeding (Wingfield et al. 1992, 1995; Wingfield 1994; R.L. Holberton and J.C. Wingfield, submitted) or when skeletal muscle must be spared, e.g., during fasting (Cherel 1988a,b) or during migration (Holberton et al. 1996b, Holberton, submitted).

Redstarts begin arriving in Jamaica and settling on territories in mid-September, and remain on those territories for 6–7 months until they depart on spring migration in April and May (P.P. Marra, in preparation). During the arrival period, the rainy season is just starting and habitats occupied by redstarts are typically lush and in some cases have standing water. By January and February, however, precipitation in Jamaica declines steadily and the dry season begins. Some habitats (e.g., logwood scrub, acacia) change dramatically and lose most of their foliage, while others (e.g., mangrove swamps, wet limestone forest) keep much of their vegetation and still retain small pools of standing water. For redstarts, sexual habitat segregation occurs on this wet to dry moisture gradient, with male-biased habitat characterized by tall-canopied mesic forest while female-biased habitats are shrubbier, more open, mostly deciduous, and xeric (Parrish and Sherry 1994; P.P. Marra, unpublished data). Similar habitat associations have been described for redstarts in other parts of their range (e.g., Lopez Ornat and Greenberg 1990). Food availability for insectivorous birds such as redstarts may decline along this wet to dry gradient, which could be important in determining the suitability of these habitats for redstarts.

Based on these observations, we proposed that differences in habitat suitability in October (hereafter fall) during the rainy season are slight, but that as the dry season progressed toward March and early April (hereafter spring), habitat suitability diverges markedly with some habitats becoming significantly drier and of lower suitability (i.e., habitats predominately occupied by females), while other habitats which remain fairly wet are of higher suitability (i.e., those occupied mostly by males). We predicted that the effects of this declining habitat quality would be greater for those redstarts occupying the less suitable, female-biased habitats. The effect of habitat quality should be greatest in spring as evidenced by divergent patterns of corticosterone secretion, with birds in female-biased habitat exhibiting

(1) higher levels of corticosterone at the time of capture, perhaps to facilitate an increase in foraging effort to meet energy demand, and (2) a reduction in the rate of corticosterone secretion as a way to spare muscle protein (Cherel et al. 1988b; Holberton et al. 1996). We also predicted that birds which show a loss in body mass from fall to spring should show high baseline corticosterone levels as an indicator of the mass loss, compared to birds with low baseline corticosterone levels which maintain body mass. Given the apparent lushness of all habitats in the fall, we predicted no such relationship to occur in that season.

Materials and methods

Our research was conducted on the southwestern portion of Jamaica at the Font Hill Nature Preserve, 13 km west of Black River, St. Elizabeth Parish and 5 km east of Whitehouse, Westmoreland Parish. In Jamaica, the proportion of males and females in a given habitat type ranged from 0 to 100%, with many sites containing a majority (70–80%) of one or other sex (Sliwa 1991; P.P. Marra, unpublished observations). For this study we established three gridded 5-ha black mangrove (*Avicennia germinans*) study sites which we predicted would be male-biased habitat and two gridded 5-ha sites in logwood scrub (*Haematoxylon campechianum*) adjacent to the mangrove sites which we predicted would be female-biased habitat. One extra site was necessary in black mangrove habitat to obtain larger sample sizes of females in that habitat type. These two habitat types were chosen because they were extremely biased in their male or female composition, but still had sufficient numbers of the less frequent sex to test for the effects of habitat and sex. Over the 2 years of this study, the black mangrove sites contained on average of 61% male and 39% female redstarts, whereas the logwood sites contained 25% male and 75% female redstarts (P.P. Marra, in preparation).

Black mangrove sites were predominantly monospecific stands but also contained small amounts of white (*Laguncularia racemosa*) and red (*Rhizophora mangle*) mangrove. The mangrove stands had dense canopies, averaged about 12 m in height, and had almost no ground or shrub level vegetation. Ground vegetation consisted only of black mangrove pneumatophores, most of which were submerged by up to 1 m of water in October but became progressively more exposed as the dry season approached. Standing water in black mangroves cycled seasonally, rather than daily, but some standing water was always present. The mangroves also retained the majority of their leaves throughout the year, keeping this habitat shady and humid relative to logwood.

Logwood stands ranged from 2 to 8 m in height and had well-developed understory and ground layer vegetation. Despite the fact that these logwood sites were part of a larger sanctuary, trees were often cut for charcoal and fence posts, and cattle roamed freely, creating a heterogeneous spatial dispersion of vegetation, with some areas being very open, and others dense with almost impenetrable vine tangles. Less common tree species within these study sites included *Bursera simarubra*, *Terminalia latifolia*, and *Crescentia alata* (see Holmes et al. 1989). In contrast to the mangrove sites, the vegetation in the logwood stands dropped most of its leaves as the dry season approached, and no standing water was ever present.

Redstarts were captured from early October to early November using song playbacks (Holmes et al. 1989) and in mid-March to mid-April with intensive mist netting. Use of playbacks has been shown not to influence plasma levels of corticosterone (Wingfield 1985). In spring, redstarts do not show aggressive responses to playbacks, so capture required intensive mist netting and the frequent checking of nets (0 to 10-min intervals) to minimize corticosterone secretion due to the effect of capture. The

same capture technique was used in both habitats in spring, to avoid biasing samples toward one habitat type. To further insure that intensive mist netting in spring did not influence baseline corticosterone levels, we captured a sample of redstarts in spring with song playbacks and compared these values to those of birds captured with intensive netting. We found no effect of capture technique on baseline corticosterone levels within a habitat in spring ($F = 0.633$, $P < 0.433$, $df = 1,25$, power = 0.88, effect size = 5 ng/ml).

Within 1–2 min of capture (or discovery), between 50–100 μ l of whole blood was collected from the brachial vein into heparinized microcapillary tubes. This sample provided the baseline level of plasma corticosterone. A second blood sample was collected 30 min after capture to provide the profile of acute corticosterone secretion. Because American redstarts are relatively small birds (6–7 g), no additional blood samples were collected, to reduce the amount of imposed stress.

Between blood sampling times, birds were ringed with unique color combinations, measured (unflattened wing chord and tarsus length to nearest 0.1 mm), and weighed to the nearest 0.1 g with an Ohaus scale. Subcutaneous fat in the furcular region was scored using techniques described by Holmes et al. (1989). All individuals were aged and sexed, using plumage characteristics and degree of skull ossification (fall samples only) as either HY (hatching year or <1 year old) or AHY (after hatching year or >1 year old) following Holmes et al. (1989) and Pyle et al. (1987). The amount of handling for each bird during the 30 min of captivity was held as constant as possible. Birds were held in cloth bags when not being handled. Blood samples were stored at 4°C for up to 8 h until centrifuged at 10,000 rpm (10,000 rcf) for 10 min. Hematocrit was measured on each time 0 sample with electronic calipers. Plasma was then recovered from each sample with a 50- μ l Hamilton syringe and kept frozen in microcentrifuge tubes until assayed for corticosterone by radioimmunoassay (as described by Wingfield et al. 1992). The sensitivity of the assay was 7.8 pg/ml, interassay variation 14.6%, and within-assay variation 1.1%.

Data on baseline corticosterone levels were of two types: (1) a recapture sample composed of individuals caught in the fall period and then recaptured in the spring, and (2) a population sample based on all individuals caught in fall or in spring (recaptures were included, but only spring data). The effects of Sex (male vs female), Habitat (logwood vs mangrove), and Season (fall vs spring) and a random effect (i.e., Individual) to control for repeated sampling of individuals were analyzed for the recaptured sample of redstarts with a mixed-model ANOVA using JMP (SAS 1997). All data met assumptions of normality and equal variances. The effect of Age was included in the analyses involving population samples, but not in the recaptured sample because of missing values for some treatment groups. Separate mixed-model ANOVAs were conducted for fall and spring to examine the acute corticosterone secretion. The effect of Age was included in the analysis of the fall data but not spring data because of small sample sizes for some treatment groups. Sample sizes in the spring only allowed a test for effects of Age on females in female-biased habitat.

Correlation coefficients were calculated between spring baseline corticosterone concentrations and (1) % mass change from fall to spring for recaptured birds and (2) mass corrected for body size for birds comprising the population sample. A similar test was performed between fall baseline corticosterone concentrations and mass corrected for body size for birds captured in the fall. To calculate mass corrected for body size, we first calculated the scores of a principal-component analysis (PCA) based on unflattened wing chord and tarsus length of all birds in the spring sample. The scores from the first principal component were used as an estimate of skeletal body size. We then regressed body mass against these PCA scores and used the residuals from this regression as an estimate of mass corrected for body size. To investigate the possibility that mass change was due to dehydration (Sherwood 1993), we correlated the change in hematocrit (i.e., packed red blood cell volume) levels from fall to spring against the change in body mass from fall to spring in recaptured redstarts.

Results

Differences in baseline corticosterone

In a three-way ANOVA on baseline corticosterone levels for individuals captured in fall and recaptured in spring, only Habitat, Season and their interaction were significant (Table 1). Thus, sex differences within or between habitats were not significant. Baseline (time 0) mean corticosterone concentration during the fall did not differ between individuals in male-biased and female-biased habitat [14.10 ± 1.8 (SE) vs 16.15 ± 1.7 ng/ml; Table 1, Fig. 1]. However, for those same individuals recaptured in spring, baseline corticosterone levels diverged significantly, with birds in female-biased habitat exhibiting baseline levels twice as high as those in the same habitat in fall (16.15 ± 1.7 vs 32.55 ± 4.16 ng/ml; Table 1, Fig. 1) and significantly higher than those in male-biased habitat (16.15 ± 1.7 vs 17.40 ± 2.15 ng/ml; Table 1, Fig. 1). In contrast, redstarts in male-biased habitat in spring exhibited only a slight increase in baseline levels compared to those from the same habitat in fall (14.10 ± 1.8 vs 17.40 ± 2.15 ng/ml; Table 1, Fig. 1).

In a four-way ANOVA of the data from the population sample, Habitat ($F = 23.62$, $P < 0.0001$), Season ($F = 35.42$, $P < 0.0001$) and the Habitat \times Season interaction ($F = 7.84$, $P < 0.006$) were significant, while neither Age ($F = 0.26$, $P = 0.61$), Sex ($F = 0.49$, $P = 0.48$), nor any of their interactions were significant.

Baseline corticosterone and mass change

In recaptured redstarts, % mass change was negatively correlated with spring baseline corticosterone concen-

Table 1 ANOVA of baseline corticosterone levels in American redstarts (*Setophaga ruticilla*) captured in fall and then recaptured in spring during the non-breeding period in Jamaica, West Indies (1994 and 1995). F -test denominator = $MS_{\text{Bird}[\text{Sex}, \text{Habitat}]}$ for all source effects except season which was tested over MS_{Error} . Sex = male or female. Habitat = male-biased (i.e., black mangrove) or female-biased (i.e., logwood) habitat. Season = fall or spring. Data are shown in Fig. 1

Source	df	Mean squares	F-statistic	Prob > F
Sex	1	476.4	3.46	0.07
Habitat	1	1261.7	9.17	0.004
Season	1	1,606.8	9.66	0.004
Sex \times Habitat	1	25.9	0.18	0.66
Sex \times Season	1	132.7	0.80	0.38
Habitat \times Season	1	725.6	4.36	0.04
Sex \times Habitat \times Season	1	139.0	0.84	0.37
Individual	36	133.7	0.80	0.74
[Sex, Habitat]				
Error	34			
Mean square error = 166.307				

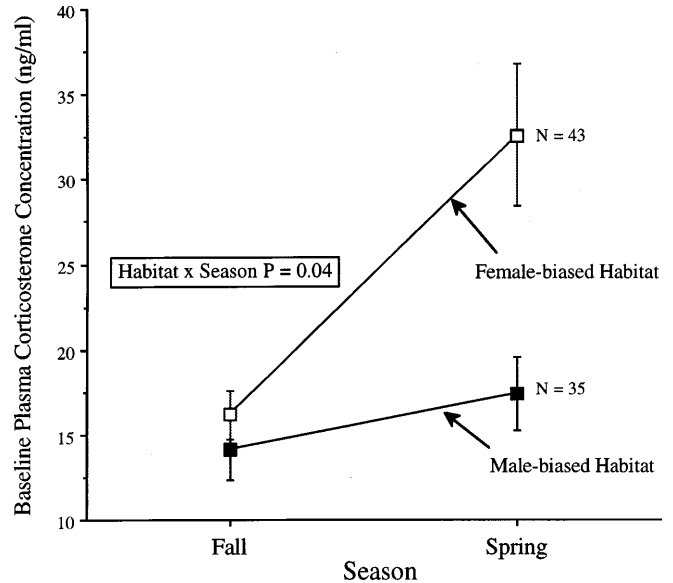


Fig. 1 Plasma baseline levels (mean \pm 1 SE) of corticosterone in American redstarts (*Setophaga ruticilla*) at time of capture (baseline) in male- and female-biased habitat types in fall (October) and spring (late March/early April) on the non-breeding grounds in Jamaica, West Indies. Sexes combined due to non-significant effects of sex in ANOVA (see Table 1)

trations from fall to spring ($r = -0.35$, $P < 0.03$; Table 2, Fig. 2a). Redstarts losing mass over the non-breeding period also had high baseline concentrations of corticosterone when measured in spring, and these were predominantly birds in female-biased habitat (Fig. 2a). A similar relationship was found in the population sample ($r = -0.32$, $P < 0.002$; Fig. 2b). Individuals with low mass given their body size (i.e., in poor energetic condition) had high baseline levels of corticosterone, whereas individuals that were heavier or at a sufficient mass given their body size had lower concentrations of corticosterone. The low correlation coefficients reported for the population sample may be attributable to the range in discovery times of birds captured in mist nets in spring. Similar to the analysis of recaptured redstarts, most of the birds in poor energetic condition were from female-biased habitat (Fig. 2b). No such relationship was found between fall baseline corticosterone concentrations and mass corrected for body size for birds captured in the fall ($r = 0.08$, $P > 0.25$). Furthermore, we found no correlation between the seasonal change in hematocrit and change in body mass from fall to spring in recaptured redstarts ($r = 0.16$, $P = 0.33$). Few, if any redstarts had visible subcutaneous fat stores in either season.

Differences in the profile of acute corticosterone secretion

All redstarts exhibited a significant increase in corticosterone secretion from time of capture to 30 min after capture (i.e., acute corticosterone secretion, hereafter ACS) in both habitats in fall, but in spring

Table 2 ANOVA results of baseline corticosterone levels in a population sample of American redstarts (*S. ruticilla*) captured in fall or spring during the non-breeding period in Jamaica, West Indies (1994 and 1995). *Age* = HY (hatch year or < 1 year old) and AHY (after hatch year or > 1 year old). *Sex* = male or female. *Habitat* = male-biased (i.e., Black Mangrove) or female-biased (i.e., logwood). *Season* = fall or spring

Source	<i>df</i>	Mean squares	<i>F</i> -statistic	Prob > <i>F</i>
Age	1	34.8	0.26	0.61
Sex	1	66.3	0.49	0.48
Habitat	1	3,816.9	23.62	< 0.0001
Season	1	4,779.3	35.42	< 0.0001
Age × Sex	1	36.6	0.27	0.60
Age × Habitat	1	19.5	0.14	0.70
Age × Season	1	29.3	0.22	0.64
Sex × Habitat	1	4.0	0.03	0.86
Sex × Season	1	243.9	1.81	0.18
Habitat × Season	1	1,057.6	7.84	0.006
Age × Sex × Habitat	1	140.2	1.04	0.31
Age × Habitat × Season	1	65.0	0.48	0.49
Sex × Habitat × Season	1	89.2	0.66	0.42
Age × Sex × Habitat × Season	1	389.0	2.88	0.09
Error	224			

Mean square error = 134.93

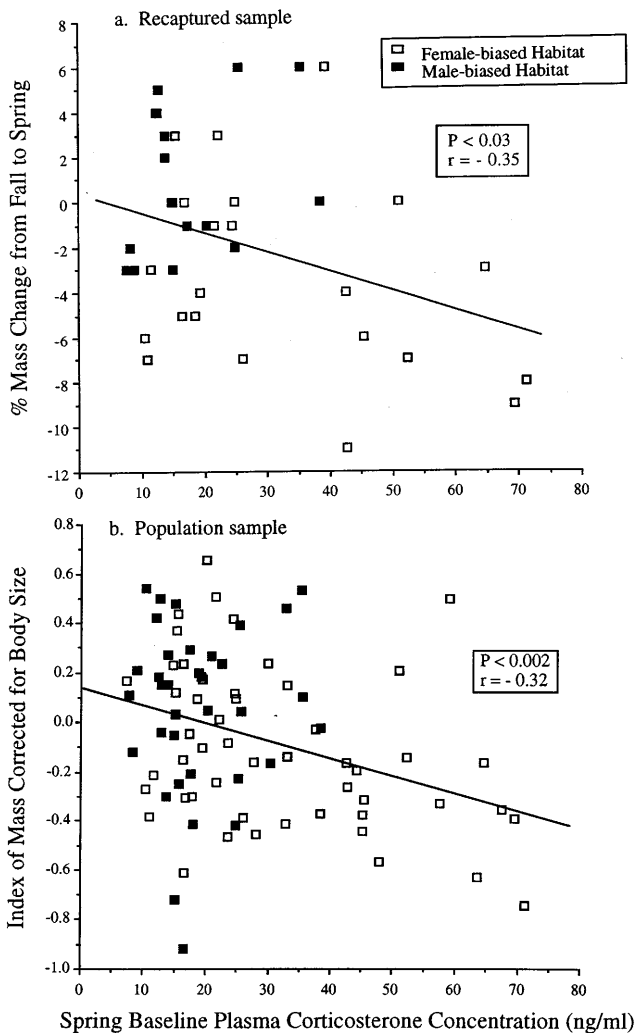


Fig. 2a, b Relationship between % mass change and spring baseline levels of plasma corticosterone in American redstarts (*S. ruticilla*) over the non-breeding period in Jamaica. **b** Each point used as an index of mass has been corrected for body size, based on the residual from a regression between mass in spring against the scores from the first axis of a principal-component analysis involving tarsus and wing length (see text)

following the overwinter period, only individuals (both males and females) in male-biased habitat continued to show ACS (Table 3, Fig. 3). The effect of Individual was significant in both models but contributed little to the overall variance ($F = 1.67$ and 2.37). None of the other main effects, including the effect of Age, nor any interactions were significant in the fall model (Table 3). Redstarts in female-biased habitat in spring (regardless of sex), exhibited reduced, although still significant, acute responses in corticosterone secretion (Fig. 3). Both Habitat and the Habitat ACS interaction were significant (Table 3) in the spring models. To further examine the effects of Age in spring, we did a similar analysis for only females in female-biased habitat, including only the effects of Age and ACS. In this, ACS ($F = 9.78$, $P < 0.004$) and Individual ($F = 2.23$, $P < 0.01$) were the only significant factors, with ACS explaining the majority of the variance. There was no effect of Age ($F = 0.22$, $P < 0.64$).

Discussion

In this study, we found that American redstarts occupying different habitats during the non-breeding season exhibited different patterns of corticosterone secretion. Regardless of age or sex, redstarts that occupied female-biased habitat had higher levels of baseline corticosterone and lost more body mass (up to 11% of overall body mass). This occurred in spring when the habitats appeared to be most different in quality. In addition, these same birds showed a less intense corticosterone increase to handling stress than birds (males and females) occupying male-biased habitats. Taken together, these changes in corticosterone secretion over the non-breeding season most likely reflect differences in habitat suitability for redstarts. Furthermore, these findings are supported by two types of samples: the recapture and population.

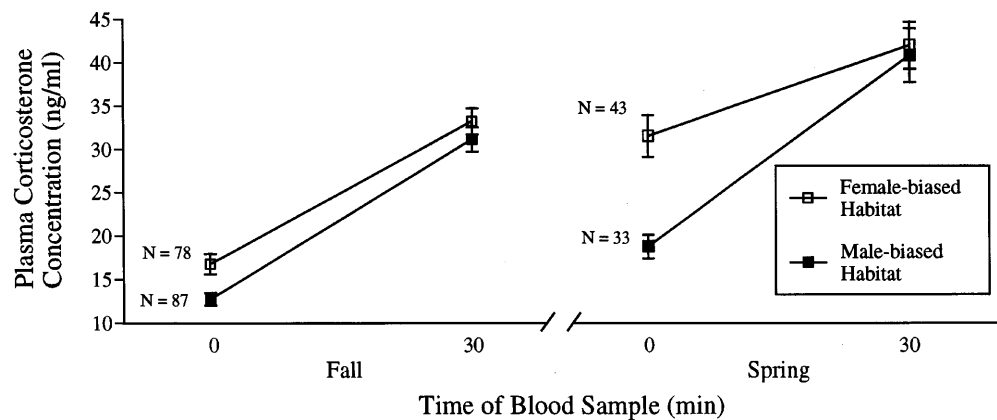
The higher baseline plasma corticosterone levels in redstarts in female-biased habitats may serve to facilitate

Table 3 ANOVA of the profiles of acute corticosterone secretion (ACS change in plasma corticosterone concentration from time of capture to 30 min after capture) in fall and spring samples of American redstarts (*S. ruticilla*) during the non-breeding period in Jamaica, West Indies. Only individuals with both a time 0 and time 30 estimate of corticosterone secretion were included in the analysis. F -test denominator = $MS_{\text{Bird}} [Age, Sex, Habitat]$ and $MS_{\text{Bird}} [Sex, Habitat]$ for all source effects except ACS which was tested over

$MS_{\text{error}} \cdot Age = HY$ (hatch year or <1 year old) and AHY (after hatch year or >1 year old). Age was only included in the fall sample. $Sex =$ male or female. $Habitat =$ male-biased (i.e., black mangrove) or female-biased (i.e., logwood). $Individual$ is nested within Age, Habitat, and Sex (fall model) or Habitat and Sex (spring model.) Mean square errors = 102.214 and 156.743 for the two ANOVA models. Data shown in Fig. 3

Source	Fall			Spring		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Age	1	1.92	0.17			
Sex	1	0.90	0.34	1	0.01	0.90
Habitat	1	2.14	0.14	1	5.01	0.03
ACS	1	230.07	0.0001	1	43.8	<0.0001
Sex × Habitat	1	0.00	0.97	1	0.14	0.71
Sex × ACS	1	0.02	0.88	1	0.07	0.80
Age × Sex	1	0.04	0.85			
Age × Habitat	1	0.68	0.41			
Age × ACS	1	0.04	0.84			
Habitat × ACS	1	0.31	0.57	1	4.87	0.03
Sex × Habitat × ACS	1	1.02	0.31	1	0.29	0.59
Age × Habitat × ACS	1	1.12	0.29			
Age × Habitat × Sex	1	3.48	0.06			
Age × Sex × ACS	1	0.50	0.48			
Age × Habitat × Sex × ACS	1	1.07	0.30			
Individual	157	1.67	0.001	72	2.37	0.0002

Fig. 3 Profiles of corticosterone secretion at the time of capture (0) and 30 min after capture (30) in American redstarts (*S. ruticilla*) in female- and male-dominated habitat types in fall (October) and spring (late March/early April) on the non-breeding grounds in Jamaica. Sexes and ages combined due to non-significant effects of both in ANOVA (see Table 3)



both behavioral and physiological responses that help them meet energy demands when environmental conditions deteriorate. In this study, redstarts in female-biased habitats may increase foraging effort in response to greater corticosterone secretion to compensate for lower food availability. Increased foraging effort accompanied by mobilization of energy reserves together may help an individual through periods of low food availability or when opportunities to forage become limited (Wingfield 1994). The fact that they exhibited greater mass loss implies that they are unable to compensate fully. If corticosterone remains elevated, gluconeogenesis will occur, thereby redirecting intermediary metabolism in such a way as to use non-carbohydrate sources such as lipids and proteins as glucose substrates when dietary carbohydrates are unavailable (Holmes and Phillips 1976). Because we found no relationship between mass

change and hematocrit, it is unlikely that decreases in body mass are due to dehydration. Also, few of the birds in either season had subcutaneous fat, further suggesting that the decline in mass in both habitats combined was at the expense of muscle protein catabolized under the influence of corticosterone over the non-breeding period. However, as we do not know how long these birds had experienced higher levels of corticosterone before being captured, we cannot determine the precise relationship between mass loss and corticosterone.

Redstarts in female-biased habitats exhibited different profiles of corticosterone secretion in fall and spring. Not only were baseline levels significantly higher in spring, but the magnitude of increase in corticosterone in response to capture and handling was significantly reduced. Although the actual maximum levels of corticosterone are unknown, the rate at which it was being

secreted was significantly slower in birds during spring, indicating a reduction in the responsiveness of the hypothalamic-pituitary-adrenal axis, either through the relative inhibition of the hypothalamic-releasing hormone, or adrenocorticotropin from the pituitary, or both, and possibly accompanied by reduced capacity of the adrenocortical tissue to respond to these signals. Whatever the cause, the reduced adrenocortical response to stress may be a way for an individual to deter the deleterious effects that high corticosterone can have on the immune system, nerve cell function, and muscle catabolism (e.g., Holmes and Phillips 1976; Siegel 1980; Axelrod and Reisine 1984; Harvey et al. 1984). Such modulation of the corticosterone stress response has been observed during the breeding season and migration, activities often associated with extremely high levels of corticosterone (Wingfield et al. 1983; Wingfield and Silverin 1986; Wingfield 1994; O'Reilly and Wingfield 1995; Holberton et al. 1996, Holberton, submitted). Chérel et al. (1988a,b) have shown that a reduction in corticosterone secretion results in significant protein sparing, a strategy demonstrated in penguins that must make energy reserves last through long periods of fasting. Redstarts forced to forage in suboptimal habitats may similarly avoid using skeletal muscle protein by reducing their responsiveness to acute stress.

Sudden inclement weather, such as snowstorms, drops in temperature, and heavy rains (Rohwer and Wingfield 1981; Wingfield et al. 1983; Rogers 1987; Rogers et al. 1993) have all been shown to elicit acute "emergency responses" (Rogers et al. 1993) in plasma corticosterone secretion, possibly due to reduced access to food. For these migratory birds at a tropical latitude, food availability is most likely the major limiting factor (Lovette and Holmes 1995). In our study system in Jamaica, food may be declining gradually from fall to spring due to decreasing precipitation. The gradual loss of leaves in the deciduous vegetation of the female-biased habitat from October to May probably contributes to the declining suitability of this habitat to insectivorous birds by decreasing food substrates for phytophagous insects as well as affecting microclimatic conditions that could influence insect availability. Therefore, the decline in vegetation and ultimately food abundance over the winter season is probably the environmental stressor affecting these birds and their insect prey in Jamaica. The responses we report, however, do not appear to be acute emergency responses, but rather may be chronic levels needed for coping with deteriorating environmental conditions.

These findings suggest that redstarts in female-biased habitat are in a compromised physiological condition. Combined with the results of earlier removal experiments (Marra et al. 1993), this poorer physical condition is probably the indirect consequence of behavioral dominance by individuals in male-biased habitat. Elevated baseline levels and the absence of ACS may then be a mechanism allowing for the persistence and survival of birds in habitats of lower suitability over the

non-breeding period. Despite this apparent functional response of corticosterone secretion, the chronic elevated concentrations and resulting mass loss reported in this paper may have negative consequences on overall fitness. For example, departure from Jamaica on spring migration was significantly later for redstarts occupying female-biased habitat relative to those in male-biased habitat, regardless of age or sex (P.P. Marra and R.T. Holmes, in preparation). Delays in departure could be due to inadequate energy reserves and reduced physiological condition at the end of the non-breeding period. Such delays in departure from the non-breeding grounds may have severe consequences for events during migration or on the breeding grounds, and thus negatively impact the fitness of these birds. Furthermore, if sexual habitat segregation in winter regularly results in lower physiological condition for certain sex or age groups (particularly young females), and possibly lower survival because of behavioral dominance, then the winter period may be a potentially limiting season for that sex. Events in winter, therefore, might contribute to the apparent male-biased sex ratio observed in this species and others during the breeding season.

Corticosterone sampling may provide a powerful tool for assessing bird physiological condition and habitat suitability. Data from our spring population sample of redstarts suggest that measures such as baseline corticosterone concentration and its relationship to mass corrected for body size in spring are useful in detecting the physiological condition of birds in this season. Sampling individuals in spring, prior to the onset of migratory restlessness, across an array of habitats would provide information on a wide range of habitat suitabilities. This coupled with demographic information would provide critical information about the population consequences of occupying different habitat types. Future research on migratory birds during the non-breeding season should focus more on population level questions, such as understanding how various habitat occupancy patterns might influence the physical and energetic condition of individual birds at both spatially and temporally extensive scales. Our research on habitat-specific adrenocortical responses in American redstarts needs replication not only in additional habitats throughout the non-breeding range of redstarts, but also in additional species both in the New and Old World. This approach should be conducted not only on species with territorial spacing patterns in the non-breeding season, but also in species that form dominance hierarchies within conspecific flocks (e.g., Lundberg 1985; Hogstad 1988; Piper and Wiley 1990; Koivula et al. 1996). Furthermore, it will only be through additional studies that measures of habitat suitability such as density, sex ratios and over-winter persistence can become verified as suitable measures directly correlated with the physical condition of individuals and habitat suitability.

Acknowledgements This research was made possible through grants awarded to P.P.M. including a Doctoral Dissertation

Improvement Grant from the National Science Foundation, an Albert Cass Fellowship from Rockefeller University, a Grant-in-Aid of Research from Sigma-Xi, and a Frank M. Chapman Memorial Fund Grant from the American Museum of Natural History. Additional financial support was provided by the National Science Foundation through grants awarded to Richard T. Holmes (Dartmouth College) and Thomas W. Sherry (Tulane University). Financial support to conduct radioimmunoassays at the University of Mississippi was provided by the UM faculty research program. We thank Robb Dobbs, James Goetz, Jason Knight, Richard Holmes, Jenn Barg, Al Strong, John Prather, Scott Sillet, Thomas Sherry, and Peter Hunt for their excellent assistance in the field. Richard Holmes, Matthew Ayres, and Scott Sillet provided substantial amounts of advice on experimental design and statistical analysis throughout various stages of this project. We would especially like to thank Deb and Richard Holmes and Pam (Williams Becay) for providing a car in Jamaica. This paper was greatly improved from comments by Richard T. Holmes, Matthew Ayres, Ken Nagy, and three anonymous reviewers. We are especially grateful to the Petroleum Corporation of Jamaica for allowing us to conduct this research at the Font Hill Nature Preserve, and Yvette Strong and NRC A for their continued support of our research in Jamaica. Finally, Robert Sutton, Anne Haynes-Sutton, Pam (Williams) Becsy, Steve and Sue Callaghan, and Peter Williams have provided limitless support during P.P.M.'s long stays in Jamaica.

References

- Asstheimer LB, Buttemer WA, Wingfield JC (1992) Interactions of corticosterone with feeding, activity and metabolism in passerine birds. *Ornis Scand* 23: 355–365
- Axelrod J, Reisine TD (1984) Stress hormones: their interaction and regulation. *Science* 224: 452–459
- Cherel Y, Robin JP, Walch O, Karmann H, Netchitailo P, Le Maho Y (1988a) Fasting in the King Penguin. I. Hormonal and metabolic changes during breeding. *Am J Physiol* 23: R170–R177
- Cherel Y, Leloup J, Le Maho Y (1988b) Fasting in the King Penguin. II. Hormonal and metabolic changes during molt. *Am J Physiol* 23: R178–R184
- Dawson A, Howe PD (1983) Plasma corticosterone in wild startlings (*Sturnus vulgaris*) immediately following capture and in relation to body weight during the annual cycle. *Gen Comp Endocrinol* 51: 303–308
- Dufty AM, Belthoff JR (1997) Corticosterone and the stress response in young Western Screech Owls: effects of captivity, gender and activity period. *Physiol Zool* 70: 143–149
- Gauthreaux S (1978) The ecological significance of behavioral dominance. *Perspect Ethol* 3: 17–54
- Gray JM, Yarian D, Ramenofsky M (1990) Corticosterone, foraging behavior, and metabolism in Dark-Eyed Juncos, *Junco hyemalis*. *Gen Comp Endocrinol* 79: 375–384
- Greenberg N, Wingfield JC (1987) Stress and reproduction: reciprocal relationships. In: Norris DO, Jones RE (eds) *Hormones and reproduction in fishes, amphibians and reptiles*, Plenum, New York, pp 461–503
- Harvey S, Phillips JG, Rees A, Hall TR (1984) Stress and adrenal function. *J Exp Zool* 232: 633–646
- Hogstad O (1988) Rank-related resource access in winter flocks of Willow Tit *Parus montanus*. *Ornis Scand* 19: 169–174
- Holberton RL, Helmuth B, Wingfield JC (1996a) The corticosterone stress response in Gentoo (*Pygoscelis papua*) and King (*Aptenodytes patagonicus*) Penguins during the non-fasting period. *Condor* 98: 850–854
- Holberton RL, Parrish JD, Wingfield JC (1996b) Modulation of the adrenocortical stress response in Neotropical migrants during autumn migration. *Auk* 113: 558–564
- Holmes WN, Phillips JG (1976) The adrenal cortex in birds. In: Chester-Jones I, Henderson I (eds) *General and comparative endocrinology of the adrenal cortex*. Academic Press, New York, pp 293–420
- Holmes RT, Sherry TW, Reitsma L (1989) Population structure, territoriality, and overwinter survival of two migrant warblers in Jamaica. *Condor* 91: 545–561
- Hutto RL (1992) Habitat distributions of migratory landbird species in western Mexico. In: Hagan JM III, Johnston DW (eds) *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC, pp 221–239
- Ketterson ED, Nolan V Jr (1976) Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-Eyed Juncos (*Junco hyemalis hyemalis*) *Ecology* 57: 679–693
- Ketterson ED, Nolan V Jr (1983) The evolution of differential migration. *Curr Ornithol* 1: 357–402
- Koivula K, Orell M, Rytkonen S (1996) Winter survival and breeding success of dominant and subordinate Willow Tits *Parus montanus*. *Ibis* 138: 624–629
- Lopez Ornat A, Greenberg R (1990) Sexual segregation by habitat in migratory warblers in Quintana Roo, Mexico. *Auk* 107: 539–543
- Lovette IJ, Holmes RT (1995) Foraging behavior of American redstarts in breeding and wintering habitats: implications for relative food availability. *Condor* 97: 782–791
- Lundberg P (1985) Dominance behaviour, body weight and fat variations, and partial migration in European Blackbirds *Turdus merula*. *Behav Ecol Sociobiol* 17: 185–189
- Lynch JF (1989) Distribution of overwintering nearctic migrants in the Yucatan Peninsula. I. General patterns of occurrence. *Condor* 91: 515–544
- Lynch JF, Morton ES, Voort ME van der (1985) Habitat segregation between the sexes of wintering Hooded Warblers (*Wilsonia citrina*). *Auk* 102: 714–721
- Marra PP, Sherry TW, Holmes RT (1993) Territorial exclusion by a long-distance migrant warbler in Jamaica: a removal experiment with American redstarts (*Setophaga ruticilla*). *Auk* 110: 565–572
- Nagra CL, Breitenbach RP, Meyer RK (1963) Influence of hormones on food intake and lipid deposition in castrated pheasants. *Poultry Sci* 42: 770–775
- Nisbet ICT and Medway L (1972) Dispersion, population ecology, and migration of Eastern Great Reed Warblers (*Acrocephalus orientalis*) wintering in Malaysia. *Ibis* 114: 451–454
- O'Reilly KM, Wingfield JC (1995) Spring and autumn migration in arctic shorebirds: same distance, different strategies. *Am Zool* 35: 222–233
- Parrish JD, Sherry TW (1994) Sexual habitat segregation by American redstarts wintering in Jamaica: importance or resource seasonality. *Auk* 111: 38–49
- Piper WH, Wiley RH (1990) The relationship between social dominance, subcutaneous fat, and annual survival in wintering White-Throated Sparrows (*Zonotrichia albicollis*). *Behav Ecol Sociobiol* 26: 201–208
- Pyle P, Howell SNG, Yunick RP, DeSante DF (1987) Identification guide to North American passerines. Slate Creek Press, Bolinas, Calif
- Rogers CM (1987) Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology* 68: 1051–1061
- Rogers CM, Ketterson ED, Nolan V Jr (1993) Geographic variation in winter fat of dark-eyed juncos: displacement to a common environment. *Ecology* 74: 1183–1190
- Rowher S, Wingfield JC (1981) A field study of social dominance, plasma levels of luteinizing hormone and steroid hormones in wintering Harris' Sparrows. *Z Tierpsychol* 57: 173–183
- SAS (1997) JMP. Version 3.2.1 (Macintosh OS). SAS Institute, Cary, NC
- Schwabl H, Bairlein F, Gwinner E (1991) Basal and stress-induced corticosterone levels of Garden Warbler, *Sylvia borin*, during migration. *J Comp Physiol B* 161: 576–580
- Sherry TW, Holmes RT (1996) Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77: 36–48

- Sherwood L (1993) Human physiology: from cells to systems. West, St Paul, Minn
- Siegel HS (1980) Physiological stress in birds. *Bioscience* 30: 529–534
- Silverin B (1997) The stress response and autumn dispersal behaviour in willow tits. *Anim Behav* 53: 451–459
- Sliwa A (1991) Winter geographic and habitat distributions of two migratory warblers (Parulinae) in Jamaica, WI. MSc thesis, Berlin Free University
- Smith GT, Wingfield JC, Veit RR (1994) Adrenocortical response to stress in the Common Diving Petrel, *Pelecanoides urinatrix*. *Physiol Zool* 67: 526–537
- Wingfield JC (1985) Short term changes in plasma levels of hormones during establishment and defense of a breeding territory in male song sparrows, *Melospiza melodia*. *Horm Behav* 19: 174–187
- Wingfield JC (1988) Changes in reproductive function of free-living-birds in direct response to environmental perturbations. In: Stetson MH (ed) *Processing of environmental information in vertebrates*. Springer, Berlin Heidelberg New York, pp 121–148
- Wingfield JC (1994) Modulation of the adrenocortical response to stress in birds. In: Davey K, Peter R, Tobe S (eds) *Perspectives in comparative endocrinology*. National Research Council of Canada, Ottawa, pp 520–528
- Wingfield JC, Silverin B (1986) Effects of corticosterone on territorial behaviour of free-living male song sparrows, *Melospiza melodia*. *Horm Behav* 20: 405–417
- Wingfield JC, Moore MC, Farner DS (1983) Endocrine responses to inclement weather in naturally breeding populations of White-Crowned Sparrows (*Zonotrichia leucophrys pugetensis*). *Auk* 100: 56–62
- Wingfield JC, Vleck CM, Moore MC (1992) Seasonal changes of the adrenocortical response to stress in birds of the Sonoran desert. *J Exp Zool* 164: 419–428
- Wingfield JC, Deviche P, Sharbough S, Astheimer LB, Holberton RL, Suydam R, Hunt K (1994a) Seasonal changes in the adrenocortical responses to stress in redpolls, *Acanthis flammea*, in Alaska. *J Exp Zool* 270: 372–380
- Wingfield JC, Suydam R, Hunt K (1994b) The adrenocortical response to stress in Snow Buntings, *Plectrophenax nivalis*, and Lapland Longspurs, *Calcarius lapponicus*, at Barrow, Alaska. *Comp Biochem Physiol* 108: 299–306
- Wingfield JC, O'Reilly KM, Astheimer LB (1995) Modulation of the adrenocortical responses to acute stress in arctic birds: a possible ecological basis. *Am Zool* 35: 285–294
- Wunderle JM Jr (1992) Sexual habitat segregation in wintering Black-Throated Blue Warblers in Puerto Rico. In: Hagan JM, Johnston DW (eds) *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC, pp 299–307
- Wunderle JM Jr, Waide RB (1993) Distribution of overwintering Nearctic migrants in the Bahamas and Greater Antilles. *Condor* 95: 904–933