The adrenocortical responses to stress in breeding male Chaffinches *Fringilla coelebs* and Bramblings *F. montifringilla* in Sweden

BENGT SILVERIN & JOHN WINGFIELD

Abstract

There is growing evidence that birds, and possibly other vertebrates, modulate the adrenocortical response to acute stress as measured by increases in plasma levels of corticosterone following capture and handling. Field-endocrine investigations of these adrenocortical responses to capture stress have begun to indicate ecological bases for such endocrine phenomena. One hypothesis states that populations of birds breeding under extreme conditions such as in Arctic and subarctic habitats, where the breeding season also is short, should suppress the adrenocortical response to acute stress so as to allow onset of breeding under potentially severe conditions. To test this we measured increases in circulating levels of corticosterone following capture and handling in a population of male Chaffinches *Fringilla coelebs* breeding in southern Sweden. The dynamics of changes in corticosterone levels during this capture stress protocol were compared with those collected from male Brambling *F. montifringilla* breeding in a subalpine habitat in northern Sweden where conditions are more severe and the breeding season short. Contrary to the predictions, male Bramblings showed a greater adrenocortical response to stress as indicated by the pattern of corticosterone levels in blood. Both male Bramblings and Chaffinches show marked individual variations in the pattern of corticosterone changes following capture. In Chaffinches the initial corticosterone were negatively correlated with body mass and body size expressed as ratio of body mass to wing length cubed. The percent increase in corticosterone and maximum levels were also correlated with fat score. Male Bramblings showed no relationship of corticosterone dynamics with body condition. Furthermore, there was no relationship to plumage variability (i.e. from black plumage on the head and upper thorax to grey, streaked, female-like males). Although several avian species have been shown to reduce their adrenocortical responsiveness to acute stress in severe environments, these data suggest that other factors may regulate the hypothalamo-pituitary-adrenal cortex axis as well.

Bengt Silverin, Department of Zoology, University of Göteborg, Box 463, S 405 30 Göteborg, Sweden.
John C. Wingfield, Department of Zoology, University of Washington, Box 351800, Seattle, Washington 98195, USA.

Received 3 April 2001, Accepted 20 November 2001, Editor: D. Hasselquist

It has been known for decades that stressful stimuli elicit a marked increase in corticosterone secretion in birds as in other vertebrates (e.g. Holmes & Phillips 1976, Greenberg & Wingfield 1987). Sustained high levels of glucocorticosteroids can inhibit reproduction and in the long term lead to severe debilitation and even death (e.g. Harvey et al. 1984, Greenberg & Wingfield 1987, Moore & Miller 1984, Sapolsky 1992). However, it is becoming clear that the initial rise in glucocorticosteroid secretion may actually trigger beneficial physiological and behavioral changes that redirect the individual away from non-essential activities (such as reproduction, territorial behavior) to emergency activities that directly potentiate survival and avoid the deleterious effects of chronic stress (Sapolsky 1992, Wingfield 1988, 1994). In birds, these short-term responses have been called "facultative physiological and behavioral patterns" that make up the emergency life history stage (ELHS), and appear to be driven by corticosterone secretion. Extensive evidence from the laboratory shows that corticosterone can suppress reproductive and territorial behaviors; potentiate foraging and irruptive "escape"-like behavior, mobilize glucose, and save energy by increasing night restfulness (see Astheimer et al. 1992, Wingfield 1994, Wingfield et al. 1995, 1998 for details). Additionally, there is also extensive evidence that avian populations in an ELHS in response to a potentially stressful stimulus such as severe weather show elevated
circulating levels of corticosterone (e.g. Wingfield 1988, 1994).

Recent field studies have indicated, however, that some avian populations may modulate their adrenocortical responsiveness to stress either seasonally (i.e. as a function of reproductive status), or within a population, i.e. individual variation (e.g. Wingfield 1994). Originally it was proposed that avian populations that breed in severe environments, especially when the breeding season is very short, should have a suppression of the adrenocortical response to stress. This would be adaptive as it would allow reproduction to proceed despite potentially stressful conditions. Any detrimental influences of a reduced capacity to respond to stress would be greatly outweighed by increased potential reproductive success and thus fitness (Wingfield 1988, 1994). Modulation of the adrenocortical response to acute stress appears to be widespread, at least in birds (Wingfield 1994, Wingfield et al. 1992, 1994a, b, 1995, Silverin 1996, Silverin et al. 1996).

Before designing experiments to determine the mechanisms underlying such modulation of the hypothalamo-pituitary-adrenal cortex axis, it is first necessary to gain some insight into the ecological bases of these phenomena. Why do vertebrates modulate their responsiveness to stress, and is there a single base for this, or has the ability evolved several times for different environmental contingencies. Such knowledge would help greatly in designing appropriate experiments in the laboratory. Field endocrinology techniques allow us to sample free-living individuals in different localities and seasons. In this way we are able to compare adrenocortical responsiveness to stress in many species and populations in relation to their ecological bases. Additionally we can compare different groups for phylogenetic differences.

In this communication we test the hypothesis that avian species nesting in a sub-Arctic region where spring weather is severe and the breeding season very short, have a reduced adrenocortical response to stress that allows nesting to continue despite potentially stressful conditions (e.g. Wingfield 1988, 1994). To obtain an insight into selection pressures during the nesting period we compared the elevation of corticosterone levels in blood of breeding male Chaffinches Fringilla coelebs at a temperate zone breeding site in southern Sweden with those of a closely related species, the Brambling F. montifringilla, nesting at a subarctic site in Swedish Lapland.

**Methods**

**Study sites**

Breeding male Chaffinches were trapped in Japanese mist nets in forest areas near Göteborg (57°42’N), southwest Sweden. These site areas were at Gunnebo, an area with mixed forest and a lake, the Botanical Garden, with rock outcrops and extensive mixed forest including European species as well as trees and plants from the Holarctic region, and Hyssna, a field station of the University of Göteborg, consisting of coniferous boreal forest with scattered broad leaf trees and extensive bogs. Breeding male Bramblings were also trapped in Japanese mist nets but in the vicinity of Ammarnäs in northern Sweden (63°58’N). These sites were in an elfin birch forest near Ammarnäs, and hilly boreal forests with scattered bogs and broad leaf trees at Kraddsele, Bissan and Högöcken. Both studies were performed in 1994.

**Sampling procedures**

All birds were removed from the mist net as soon as possible after capture and an initial blood sample collected from a wing vein into a heparinized capillary tube. Each sample (see below) was 30–40 µl in volume. Capillary tubes were sealed at one end with molding clay and stored on ice until return to a field station (within 1–5 hours). Here blood was centrifuged, plasma harvested and stored frozen at -20°C. After blood samples were collected, all birds were banded with a numbered aluminum ring, body mass measured to the nearest 0.1g, and wing length measured to the nearest 0.5 mm. A further estimate of body size was determined by calculating the ratio of body mass to wing length cubed (see Smith et al. 1994). This ratio adjusts body mass for differences in size. Fat depots in the furculum and abdomen were assessed using an arbitrary scale (see Wingfield & Farner 1978) of 0–5 where 0 = no fat, and 5 = gross bulging fat bodies. For each bird the average of furcular and abdominal fat scores were recorded. Length of the cloacal protuberance measures 8–12 mm in length (e.g Wingfield & Farner 1993). All birds captured in this study had fully developed cloacal protuberances and were clearly territorial suggesting that they were all in a fully reproductive state.
**Plumage rank in male Bramblings**

Male Bramblings sampled in the vicinity of Ammarnäs showed variation in nuptial plumage from males with solid black feathering on the head, nape and upper back, through males with white, gray and brown specks on black in these regions, to males with heavily streaked gray and brown plumage (i.e. female-like, see Cramp 1992). The most-black males also had brighter brick red plumage on the throat, upper breast and wings. Female-like males had paler and browner red pigment in these regions, often suffused with grey and dark brown streaks. Males were ranked according to plumage type with rank 1 being the most uniformly black and brick red to rank 15, the most female-like and thus with least black and brick red plumage.

**Capture stress protocol**

When comparing the intensity of adrenocortical responses to stress between breeding male Chaffinches and Bramblings, it was critical that all individuals be stressed in as close to identical manner as possible. In wild birds capture, handling and restraint is known to elicit a marked increase in circulating corticosterone (e.g. Holmes & Phillips 1976, Harvey et al. 1984, Wingfield et al. 1982). We assumed that elevation of circulating corticosterone following capture was comparable across species. This protocol has been applied to a wide spectrum of species (see Schwabl et al. 1991, Wingfield et al. 1992, Wingfield 1994 for details). Approximately 30–40 μl of whole blood was collected from a wing vein as soon as possible after capture (see above). Time was noted as soon as the bird hit the net and again when the first sample was collected. Most samples were collected within 1–2 minutes and this time group was designated Min 1 for convenience in the figures. Additional samples were then collected at 5, 10, 30 and 60 minutes following capture (i.e. Min 5, Min 10, Min 30 and Min 60 in the figures). Plasma levels of corticosterone in these samples indicated the degree and time course of the response to capture, handling and restraint.

**Corticosterone assay**

After extraction in dichloromethane, plasma levels of corticosterone were measured by a direct radioimmunoassay method identical to that described by Wingfield et al. (1992). All samples were measured in duplicates, and all were run in one assay to avoid interassay variations. Included in the assay were 3 solvent blanks, and 3 samples from a plasma pool as a check on reliability criteria. Based on these plasma pool samples the accuracy of measurements were 96.3%.

**Statistical analysis**

Changes in corticosterone levels with time after capture were compared by two-way analysis of variance (ANOVA) between species, and for repeated measures (i.e. time after capture). Within a species, changes in corticosterone were compared by Fisher’s Least Significant Difference test (PLSD). Comparisons between species, where appropriate, were made by Student’s t-test, unpaired and two tailed.

Comparisons between species of body mass, body size, fat score, initial and maximum corticosterone levels generated during the capture stress protocol, were made. Dynamics of the response included percent increase (i.e. percent increase of plasma corticosterone level from the initial value to its highest level during the capture stress protocol) and rate of increase (i.e. the rate of increase from the initial value to the highest concentration during the capture stress protocol – ng/ml/min) of corticosterone following capture were all compared by Student’s t-test or non-parametric Mann-Whitney U-test where appropriate.

To further analyze the dynamics of changes in plasma corticosterone levels during the capture stress protocol, we correlated mensural characters with the dynamics of corticosterone changes. Past investigations have revealed major differences in adrenocortical responsiveness to stress with body condition (see Wingfield 1994, and Wingfield et al. 1995 for full discussion). Spearman Rank Correlation Coefficients were calculated to indicate significant relationships after Bonferroni corrections of Rho.

Since male Bramblings show marked plumage variability, possibly related to age (Cramp et al. 1994), we also correlated plumage rank with mensural characters and measures of corticosterone dynamics described above. Again, Spearman Rank Correlation Coefficients were used to identify significant relationships. Additionally, we grouped male Bramblings into three categories in relation to plumage. One group, “black males” had the most extensive black plumage and bright brick red color. The second group, “intermediate males” had extensive gray and brown specks and streaks on a black and brick red background. The third group, “female-like males” had mostly gray and brown streaks with little
black background, and dull brick red or even brown on the throat and upper breast. Body mass and size, fat score and corticosterone dynamics described above were compared by one-way ANOVA. Significant differences were assessed by Fisher’s PLSD tests for equal sample size and Scheffe’s F-test for unequal sample sizes.

Results

Adrenocortical responses to capture stress
Both male Chaffinches and Bramblings showed a marked elevation of corticosterone following capture and handling (Figure 1, upper panel; $F = 80.682$, $\text{df} = 4$, $P < 0.001$).
Figure 3. Comparisons between breeding male Bramblings and Chaffinches of corticosterone dynamics following capture and handling. Bars are means and vertical lines SE. N = 9 for Chaffinches and 15 for Bramblings.

Jämförelse av förändringar i plasma corticosteron (% ökning) efter fångst och handhavande av hanar av bergfink och bofink. Staplarna avser medelvärde och vertikala linjer SE. N = 9 för bofink och N = 15 för bergfink.

DF = 4, p < 0.0004), although in Bramblings this response was greater (F = 18.198, DF = 1, p < 0.0001). There was also a significant interaction of species and time after capture (F = 9.332, DF = 4, p < 0.0001). Initial corticosterone levels (i.e. at Min 1 after capture) showed no obvious variation with time of day (Figure 1, lower panel) in either species suggesting that diel rhythms of corticosterone did not explain the difference in response to capture stress. A single female Brambling was also captured and sampled. Her profile of corticosterone following capture is presented in Figure 1 also (upper panel). The female’s profile did not show any considerable increase with handling time, which is in sharp contrast to the pattern in male Bramblings, and also different from the pattern in male Chaffinches.

Individual variations in the adrenocortical responses to the capture stress protocol are revealed in Figure 2. In Bramblings all males showed a marked elevation of corticosterone during 60 min of handling but some more than others (see birds BRAM 7 and 8 versus BRAM 4 and 5, Figure 2). In Chaffinches, many males showed a rather muted response (e.g.
Table 1. Spearman Rank correlations of body mass, fat score, and corticosterone dynamics during the capture stress protocol in breeding male Chaffinches Fringilla coelebs.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Initial B level</th>
<th>Maximum B level</th>
<th>% increase in B</th>
<th>Rate of B increase*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Initial B nivå</td>
<td>Maximal B nivå</td>
<td>% ökning av B</td>
<td>B ökningstakt</td>
</tr>
<tr>
<td>Body mass (n=8)</td>
<td>Rho = -0.88</td>
<td>Rho = -0.62</td>
<td>Rho = 0.19</td>
<td>Rho = -0.14</td>
</tr>
<tr>
<td></td>
<td>z = -2.331</td>
<td>z = -1.6378</td>
<td>z = 0.507</td>
<td>z = -0.378</td>
</tr>
<tr>
<td></td>
<td>p = 0.02</td>
<td>p = 0.102</td>
<td>p = 0.612</td>
<td>p = 0.612</td>
</tr>
<tr>
<td>Fat score (n=9)</td>
<td>Rho = 0.211</td>
<td>Rho = -0.61</td>
<td>Rho = -0.77</td>
<td>Rho = -0.580</td>
</tr>
<tr>
<td></td>
<td>z = 0.600</td>
<td>z = -1.714</td>
<td>z = -2.171</td>
<td>z = -1.640</td>
</tr>
<tr>
<td></td>
<td>p = 0.551</td>
<td>p = 0.0865</td>
<td>p = 0.03</td>
<td>p = 0.101</td>
</tr>
<tr>
<td>Body size**</td>
<td>Rho = -0.88</td>
<td>Rho = -0.57</td>
<td>Rho = 0.37</td>
<td>Rho = -0.24</td>
</tr>
<tr>
<td></td>
<td>z = -2.331</td>
<td>z = -1.151</td>
<td>z = 0.982</td>
<td>z = -0.63</td>
</tr>
<tr>
<td></td>
<td>p = 0.02</td>
<td>p = 0.131</td>
<td>p = 0.326</td>
<td>p = 0.529</td>
</tr>
</tbody>
</table>

* Measured in ng/ml/min. Mått i ng/ml/min.

** Ratio of mass/wing length cubed x 10^-5. Kroppsvikt/vinglängden^3 x 10^-5.

After Bonferroni correction applied, a = 0.02. Efter Bonferroni korrektion, a = 0.02.

CHAF 5 and 6) whereas others underwent a marked increase in corticosterone (e.g. CHAF 2, Figure 2).

Comparisons between Bramblings and Chaffinches

Body masses were not different between the two species (Brambling = 22.29±0.33 g, n = 15; Chaffinch = 22.79±0.69 g, n = 8; t = -0.747, p = 0.464) and neither was fat score (Brambling = 0.60±0.15, n = 15; Chaffinch = 0.94±0.21, n = 9; t = -1.37, p = 0.18). Indeed on a scale of 0–5, both species were lean. If body mass was adjusted for body size (i.e. the ratio of body mass to wing length cubed), there was still no difference between species (Brambling = 3.20±0.04x10^-5; Chaffinch = 3.26±0.11x10^-5). Initial levels of corticosterone (i.e. Min 1) were also not different (Figure 3 upper panel, t = 1.937, p = 0.066, DF = 22), but maximum corticosterone levels generated during the capture stress protocol were highly significantly greater in breeding male Bramblings (Figure 3 upper panel, t = 4.272, p = 0.0003, DF = 22). This difference appeared to be due to the rate of corticosterone increase in ng/ml/min (Figure 3 lower right panel, t = 3.833, p = 0.0009, DF = 22) and not the percent increase in corticosterone levels (Figure 3 lower left panel, t = -1.088, p = 0.289, DF = 22).

There was no relationship between initial corticosterone level, percent increase, rate of increase or maximum level generated during the stress protocol with body mass, body size or fat score in male Bramblings (data not shown). However, in the Chaffinch, there was a significant negative relationship between initial (i.e. Min 1) corticosterone level with body mass and body size (Figure 4, Table 1), but a similar relationship with maximum corticosterone levels was not significant (Table 1). Percent increase in corticosterone level during the capture stress protocol also showed an almost significant negative relationship with fat score. Maximum corticosterone levels and fat score were not quite significantly correlated (Table 1). All other relationships were not significant (Table 1).

Plumage variability in male Bramblings

There were no significant relationships between rank with body mass, body size, fat score or any of the dynamics of changes in corticosterone levels following the capture stress protocol (Table 2). If the ranks were divided up into three groups (black males, intermediate and female-like males), ANOVA revealed no significant differences in any of the above parameters (Table 3). These tests, however, are based on rather small sample sizes for each
Table 2. Spearman rank coefficients of plumage rank with body mass, fat score and corticosterone (B) dynamics in breeding male Bramblings Fringilla montifringilla.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Rho</th>
<th>z</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass</td>
<td>0.18</td>
<td>0.676</td>
<td>0.50</td>
</tr>
<tr>
<td>Body size</td>
<td>0.20</td>
<td>0.735</td>
<td>0.46</td>
</tr>
<tr>
<td>Fat score</td>
<td>-0.13</td>
<td>-0.501</td>
<td>0.62</td>
</tr>
<tr>
<td>Initial B level</td>
<td>-0.23</td>
<td>-0.869</td>
<td>0.38</td>
</tr>
<tr>
<td>Maximum B</td>
<td>-0.28</td>
<td>-1.069</td>
<td>0.28</td>
</tr>
<tr>
<td>% increase in B</td>
<td>0.05</td>
<td>0.200</td>
<td>0.84</td>
</tr>
<tr>
<td>Rate of B increase*</td>
<td>-0.30</td>
<td>-1.109</td>
<td>0.27</td>
</tr>
</tbody>
</table>

*Ratio of mass/wing length cubed x 10^5. Kroppsvidk/vinglängden^3 x 10^-5.
*Measured in ng/ml/min. Mätt i ng/ml/min.

...and it is worth to note that black males had 20–30% higher levels of initial and maximum corticosterone levels as compared with intermediate and female-like males.

**Discussion**

The initial hypothesis was that bird species breeding in an unpredictable sub-arctic habitat should have a reduced adrenocortical response to stress as compared to those breeding in a more stable temperate habitat. Although the hypothesis has gained support from a study on the Willow Warbler Phylloscopus trochilus (Silverin et al. 1996) breeding in exactly the same areas as Chaffinches and Bramblings included in the present study, the results from the latter two species did not support the hypothesis. Although there were marked individual variations in the adrenocortical response to stress, male Bramblings, breeding at Ammarnäs in northern Sweden, showed a greater response than did male Chaffinches breeding at Göteborg in southwest Sweden. These contradictory results indicate that other factors than an unpredictable environment and a short breeding season also must be involved in the evolution of the avian stress response. Similar results have been found for the Arctic breeding Gambel’s White-crowned Sparrow Zonotrichia leucophrys gambelii in northern Alaska (Romero et al. 1997).

The stress response pattern observed among male Chaffinches agrees with the expected pattern, and also with that observed in male Willow Warblers breeding in the same areas in southwest Sweden (Silverin et al. 1996). That is, exposing Chaffinches and Willow Warblers from southern Sweden to stress causes plasma levels of corticosterone to increase rapidly. Such an increase may redirect the behaviour of the breeding bird away from reproduction toward "survival" by affecting behaviours such as dispersal, territoriality and food searching (Dolink & Blyumental 1967, Wingfield & Silverin 1986, Silverin 1986, Astheimer et al. 1992, Silverin 1996). Chaffinches may start egg clutches from late April to mid-June, but up to 90% of the nests within a population may be taken by different predators (Svensson 1978, Hanski & Laurila 1993). Although two successful broods are unusual for Chaffinches, they may lay up to three replacement clutches following clutch loss, and the building of a new nest may begin already within a couple of days after nest desertion (Newton 1964). Obviously, nest-losses must be an important factor in the selection of the reproduction strategy of the Chaffinch. However, temporarily elevated levels of corticosterone are not likely to result in dramatic effects on the reproductive success of Chaffinches as they obviously return to egg-laying rapidly after nest desertion and as they can produce eggs during a rather long period of time. A rapid increase in plasma levels of corticosterone might be adaptive since it may initiate short-lasting dispersal behaviour, and give the Chaffinch a possibility to lay the new clutch in an area with a lower predation pressure.

Despite the fact that the Brambling is one of the most common bird species in the Fennoscandian subalpine forests, its winter behaviour is better known than its behaviour during the breeding season. Although Chaffinches and Bramblings are two closely...
related species their breeding strategies differ markedly. For example, in their choice of breeding grounds Chaffinches are highly site-tenacious, while Bramblings change their breeding areas each year. Bramblings arrive later on the breeding grounds in the north than do Chaffinches. In a study in northern Finland (same latitude, but lower altitude, as Ammarnäs) Chaffinches started to establish territories around 20 April, and the last territory established, with a successful nesting, occurred 12 June. The corresponding dates for Bramblings were 9 May and 28 June (Mikkonen 1985). Female Bramblings appear on the breeding grounds before males have established territories. This situation is in contrast to that in Chaffinches where the first females arrive about one week after males have started to establish their territories. Bramblings nest in loose aggregations of 2–8 pairs, and the male defends a small unstable song-territory centered around the female and the vicinity of the nest, whereas male Chaffinches spread out singly and defend their own large territories (Mikkonen 1985). As a result of their nomadic tendency during the breeding season, the density of the breeding population of Bramblings varies enormously between years at Ammarnäs (Cederholm et al. 1974, Enemar et al. 1984, Lindström 1987). In certain years more than half of the Brambling population may abandon their nests and the breeding area as a result of reduced insect abundance. In such years production of fledglings in the population can be almost nil, whereas the fledgling production of other insectivorous species such as the Willow Warbler is unaffected (Hogstad 1982). Rogstad concluded that Bramblings are poorly adapted to a variable food situation, and that they are more vulnerable to decreasing food availability during the breeding season than other insect feeders in the Subalpine birch forest. He assumes that the availability of insects in some way affects the physiological mechanisms regulating the breeding behaviour of the Bramblings.

Bramblings are also known to frequently abandon their territories in bad weather, and aggregate in flocks to feed for several days. Eventually they leave the breeding area permanently (Mikkonen 1981, 1984). It is to be noted that new nests are not found

---

Table 3. Comparison of body mass, fat score and corticosterone dynamics in male Bramblings _Fringilla montifringilla_ grouped as to plumage type. _Kroppsvikt, fettreserver och corticosterone (B) förändring under fängststress för bergfinkhanar_ _Fringilla montifringilla_ _med olika dräktfärg_ (svarta, intermediära resp. honlika hanar).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Black <em>Svart</em></th>
<th>Intermediate <em>Intermediär</em></th>
<th>Female-like <em>Honlik</em></th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass <em>Kroppsvikt</em></td>
<td>21.9 ± 0.35</td>
<td>22.7 ± 0.82</td>
<td>22.3 ± 0.51</td>
<td>0.41  (0.67)</td>
</tr>
<tr>
<td>Body size <em>Kroppstorlek</em></td>
<td>3.1 ± 0.08</td>
<td>3.2 ± 0.07</td>
<td>3.2 ± 0.07</td>
<td>1.11  (0.36)</td>
</tr>
<tr>
<td>Fat score <em>Fettreserver</em></td>
<td>0.9 ± 0.29</td>
<td>0.3 ± 0.20</td>
<td>0.6 ± 0.24</td>
<td>1.46  (0.27)</td>
</tr>
<tr>
<td>Initial B level <em>Basnivå för B</em></td>
<td>11.3 ± 2.22</td>
<td>8.6 ± 2.40</td>
<td>8.4 ± 2.28</td>
<td>0.47  (0.64)</td>
</tr>
<tr>
<td>Maximum B <em>Maximal B nivå</em></td>
<td>144.7 ± 17.7</td>
<td>116.3 ± 17.1</td>
<td>117.6 ± 4.66</td>
<td>1.23  (0.32)</td>
</tr>
<tr>
<td>% increase in B <em>% ökning i B</em></td>
<td>14.4 ± 2.89</td>
<td>22.43 ± 10.48</td>
<td>18.84 ± 5.80</td>
<td>0.32  (0.73)</td>
</tr>
<tr>
<td>Rate of B increase *</td>
<td>2.2 ± 0.29</td>
<td>2.0 ± 0.26</td>
<td>1.8 ± 0.09</td>
<td>0.79  (0.48)</td>
</tr>
</tbody>
</table>

*Ratio of mass/wing length cubed x 10^−5. _Kroppsvikt/vinglängden^3 x 10^−5._

*Measured in ng/ml/min. Mått i ng/ml/min.
in an area where large numbers of Brambling nests have been abandoned (Enemar, pers. comm.). Despite a catastrophic reproductive outcome in one year, breeding density the next year can be higher. Some internal factor must initiate this dispersal behaviour of the Bramblings, and corticosterone is a prime suspect. Bad weather situations are known to increase adrenal secretion of corticosterone in more southerly breeding species (e.g. Wingfield 1984, 1988). That reduced food availability also may elevate corticosterone levels in free-living birds have been shown in several studies (Rohwer & Wingfield 1981, Schwabl et al. 1985, Wingfield 1988). The intensity with which Bramblings responded to handling stress makes it most likely that they also respond to a bad weather situation and to food restrictions with a rapid increase in plasma levels of corticosterone. Especially since it is known that a lean male Brambling may lose up to 6% of its body weight during one day of bad weather (Hogstad 1982). However, not only will elevated corticosterone levels make territorial birds abandon their territories, but also increase their foraging activity (Silverin 1986, Astheimer et al. 1992). As elevated plasma levels of corticosterone can induce dispersal behaviour in birds (Wingfield & Silverin 1986, Silverin 1996), the observed stress response can explain why Bramblings abandon their nests more easily than other species. This conclusion is supported by the observation that there does not seem to exist a population of floating Willow Warblers at Ammarnäs (a species with a reduced stress response), whereas there is a large population of floating Bramblings, dominated by males, in the same area (Cederholm et al. 1974).

How come that the adrenocortical response to stress in male Bramblings does not show the same pattern as that seen in male Willow Warblers breeding in the same northern sub-arctic habitat, i.e. a reduced stress response (Silverin et al. 1996), but that the stress response is even more pronounced than that observed in Chaffinches breeding in southwest Sweden? Perhaps this difference has evolved as a result of differences in lifetime expectancies. A breeding Willow Warbler has a very small chance to survive till the following breeding season. Consequently, a willow warbler breeding in a northern unpredictable climate should make every effort possible to produce offspring from its first clutch during its first year of breeding, even at the cost of eventually reducing its survival rate till the coming year. Bramblings, on the other hand, have significantly longer lifetime expectancy than willow warblers, 2–3 years. In response to detrimental changes in the environment a long-lived species like the Brambling can make a decision between increasing its investments in current reproduction or instead invest in future reproduction. Several field studies on birds have shown that increasing the parental investments in raising the current brood reduces the winter survival rate or future fecundity of the parents (Krebs & Davies 1991). Furthermore, stress can have adverse effects on parasite load and immunocompetence and this may be mediating the reduction in survival and future reproduction (Wingfield & Silverin 2001). Thus Bramblings may, contrary to the Willow Warbler, eventually increase their lifetime reproductive success by abandoning their nests with eggs or nestlings in years with low insect availability. Instead they increase their own foraging activity and invest in a new clutch somewhere else the following year. Increasing corticosterone levels, as a result of some environmental stressor, would most likely induce the necessary dispersal behaviour. Wingfield et al. (1995) found no effect of longevity on the adrenocortical stress response across many avian taxa. However, this result may have been confounded by broad phylogenetic differences. Further comparisons of adrenocortical responses to stress in closely related taxa with different longevity are essential to clarify this issue.

Acknowledgement

This study was supported by grants from the Swedish National Science Research Council, the "Schwartz foundation" and "Kungl. Vetenskaps- och Vitterhetssamhället" to BS, and a grant from the Office of Polar Programs, National Science Foundation U.S.A. to JCW. We acknowledge Barbro Löfåtertz for the technical assistance with the corticosterone assay, and Björn Arvidsson for the time consuming assistance with the field work.

References

and migratory periods in chaffinches (Fringilla coelebs) and some other temperate zone passerine birds. Condor 69: 435–468.


Wingfield, J.C., Suydam, R. & Hunt, K. 1994b. The adrenocortical responses to stress in snow buntings (Plectrophenax nivalis) and lapland longspurs (Calcarius lapponi-
Allt för att undvika att hamna i en kronisk stresssituation.

Fåglarnas stresskänslighet modifieras emellertid av en mängd faktorer, t.ex. tid på säsongen och häckningsfas, engagemang i föräldrarskap, populatioanstället, ålder, social status och näringsstatus. En ökad stresskänslighet innebär en snabbare och kraftigare ökning av corticosteronsekretionen och därmed en förändring av fågels beteende från fortproatning till överlevnad. Man har därför antagit att fåglar (arter eller populationer) som häckar i karga, hård miljöer (t.ex. i artkiska eller alpina miljöer) med snabba, oförsägbara miljöförändringar (t.ex. dåligt väder) och kort häckningssäsong, bör vara ganska okänsliga för stresspåverkan. Att så är fallet har också visats i ett antal undersökningar. Detta gäller även fåglar i subalpina miljöer i Sverige.

Exempelvis är lövsångare som häckar i den svenska fjällvärlden relativt okänsliga för stress, medan lövsångare i södra Sverige är mycket stresskänsliga. Detta medför bland annat att en lövsångare i Lolland som under några dagar utsätts på dagstemperaturer under +5°C inte överger sitt bo (stressfaktorn, d.v.s. den låga temperaturen, är inte tillräckligt stark för att inducera en ökad stresshormonsekretion), medan häckande lövsångare i södra Sverige som utsätts för dagstemperaturer under +10°C normalt överger sina bon därför att det "kalla" vädret stressar fåglarna (ökar corticosteronsekretionen). Den därmed ökade corticosteronsekretionen omdrigar beteendet från t.ex. runven till födosök och övrigvande av boet. Att det verkliga är hormonet som ästadkommer dessa beteendeförändringar kan experimentellt relativt lätt visas genom så kallade "replacement studies". Den här förelagda studien testar hypotesen om att bergfinkar som häckar i subalpina regioner i norra Sverige har en lägre stresskänslighet än ysterarten bofink som häckar i södra Sverige.

man frysas och analyseras vid ett senare tillfälle på sitt hormoninnehåll.

Studierna genomfördes 1994 på häckande bergfinkhanar i fjällbjörkskog i Ammarnäs (Lycksele lappmark), samt på häckande bofinkhanar lövskogsområden i Göteborg.