

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

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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.

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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 Hübäcken. 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 0.1 g, 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 Ammanäs 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 μ l 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 dichlorometane, 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

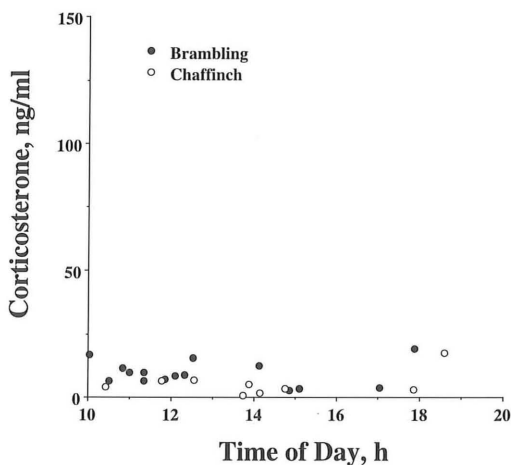
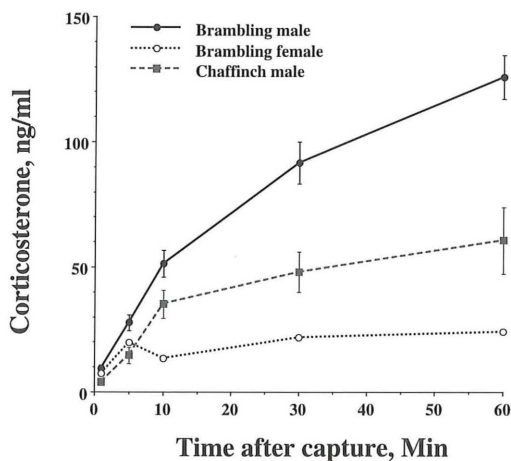


Figure 1. Changes in corticosterone following capture and handling (upper panel) in breeding male Chaffinches and Bramblings, and a single female Brambling. Points are means and vertical lines the standard errors. $N=9$ for Chaffinches and 15 for male Bramblings. The lower panel shows individual corticosterone levels at time Min 1 for both species as a function of time of day.

Förändringar i plasma corticosteron efter fångst och handhavande (time after capture) av häckande hanar av bofink (Chaffinch) och bergfink (Brambling) samt en bergfink-hona (övre figuren). Punkter är medelvärden och vertikala linjer SE. $N=9$ för bofink och $N=15$ för bergfink (hanar). Den undre figuren visar individernas plasma corticosteron nivåer vid tiden Min 1 i relation till tid på dagen för respektive art.

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

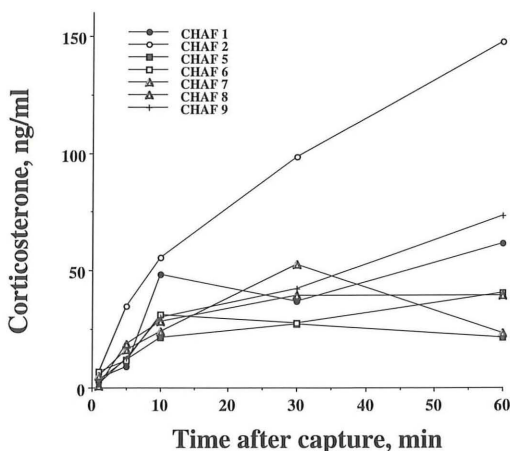
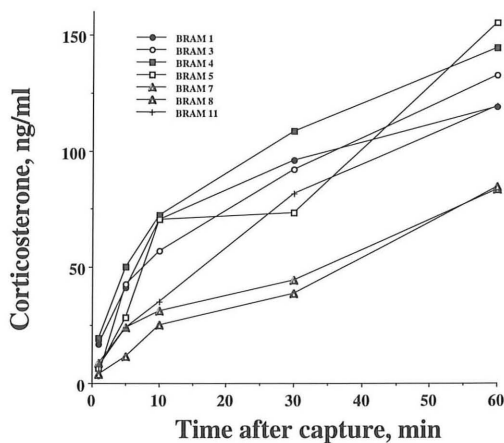


Figure 2. Individual variation in changes of plasma corticosterone levels after capture and handling. Each point is identified as an individual bird. Upper panel refers to Brambling (BRAM) and lower panel to chaffinch (CHAF). Figures after the abbreviations refer to bird number from the data books. Individuell variation i hur plasma corticosteron förändras efter fångst och handhavandet. Varje punkt avser en individ. Övre figuren visar bergfink (BRAM). Nedre figuren visar bofink (CHAF). Siffror efter förkortningarna avser varje fågels identifikationskod (från ringmärkningsprotokollen).

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; $F=80.682$,

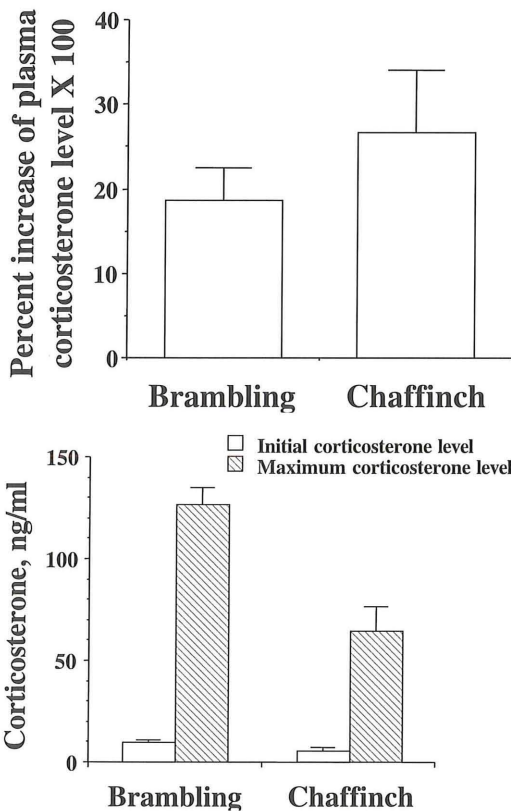


Figure 3. Comparisons between breeding male Bramblings and Chaffinches of corticosterone dynamics following capture and handling. Bars are means and vertical lines SE. N = 9 for Chaffinches and 15 for Bramblings.

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 con-

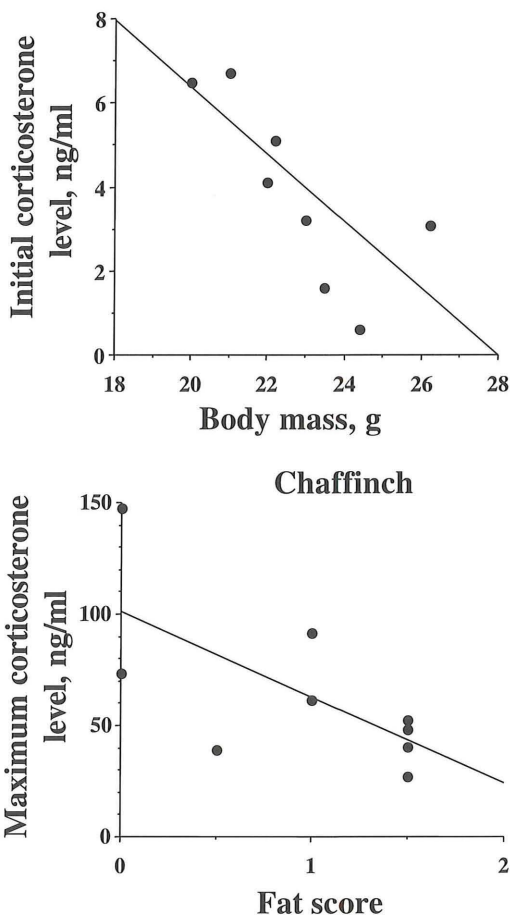


Figure 4. Correlation of initial corticosterone level (i.e. Min 1) and body mass (upper panel), and percent increase in corticosterone during the capture stress protocol and fat score (lower panel) in breeding male Chaffinches. Line represents best fit regression.

Korrelation mellan initial corticosteron nivå (d.v.s. vid tiden Min 1) och kroppsvikt (body mass; övre figuren), och procent ökning i corticosteron under fångst och handhavande i relation till fettreserver (maximum corticosteron level; undre figuren) hos häckande bofinkshänar. Linjen är den som passar bäst till regressionen.

trast 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*.

Spearman rank korrelationer mellan kroppsvikt, fettreserver och corticosteron förändringar under fångststress hos häckande hanar av bofink Fringilla coelebs.

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

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

** Ratio of mass/wing length cubed $\times 10^{-5}$. *Kroppsvikt/vinglängden³ $\times 10^{-5}$.*

After Bonferroni correction applied, $\alpha = 0.02$. *Efter Bonferroni korrektion, $\alpha = 0.02$.*

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 = $3.20 \pm 0.04 \times 10^{-5}$; Chaffinch = $3.26 \pm 0.11 \times 10^{-5}$). 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 corti-

costerone 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*.

Resultat av Spearman rank korrelationer mellan dräkt-ranking (en 15-gradig skala från honligt gråvatrad till helsvart dräkt) och kroppsvikt, fettreserver och corticosteron (B) förändringar under fångststress hos häckande hanar av bergfink *Fringilla montifringilla*.

Parameter	Rho	z	p
Body mass <i>Kroppsvikt</i>	0.18	0.676	0.50
Body size [†] <i>Kroppstorlek</i>	0.20	0.735	0.46
Fat score <i>Fettreserver</i>	-0.13	-0.501	0.62
Initial B level <i>Basnivå för B</i>	-0.23	-0.869	0.38
Maximum B <i>Maximal B nivå</i>	-0.28	-1.069	0.28
% increase in B <i>% ökning i B</i>	0.05	0.200	0.84
Rate of B increase* <i>B ökningstakt</i>	-0.30	-1.109	0.27

[†]Ratio of mass/wing length cubed $\times 10^{-5}$. *Kroppsvikt/vinglängden³ $\times 10^{-5}$* .

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

group, 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 in-

cluded 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

Table 3. Comparison of body mass, fat score and corticosterone dynamics in male Bramblings *Fringilla montifringilla* grouped as to plumage type.

Kroppsvikt, fettreserver och corticosteron (B) förändring under fångststress för bergfinkhanar *Fringilla montifringilla med olika dräktfärg (svarta, intermediära resp. honlika hanar).*

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

[§]Ratio of mass/wing length cubed x 10⁻⁵. *Kroppsvikt/vinglängden³ x 10⁻⁵.*

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

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 Ammannäs) 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 Ammannäs (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). Hogstad 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

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 south-west 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.

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Sammanfattning

Stresskänslighet hos häckande hanar av bofink och bergfink i Sverige

Väl känt är att ett brett spektrum av miljöstimuli ökar binjurens corticosteronsekretion hos frilevande fåglar, d.v.s. fåglarna blir stressade. Om stressen blir långvarig (dagar eller längre) kan effekterna bli dramatiska och ofta leda till individens död. Det finns få exempel på att frilevande djur utsätts för en kronisk stress (något som däremot är vanligt hos burhållna djur). Dock utsätts frilevande djur regelbundet – dock med oförutsägbara tidsintervaller – för kortvarig (akut) stress av olika slag. Senare års forskning har klart visat att den stressinducerade ökningen av corticosteronsekretionen inducerar fakultativa fysiologiska och beteendemässiga förändringar som anpassar individen till de rådande miljöbetingelserna. Det snabbaste svaret på en akut stressituation är oftast att individen försätts i ett "slåss eller fly" tillstånd. Detta svar regleras av det s.k. SAMS-systemet. Förenklat uttryckt innebär detta att binjuremärgen sekundsnabbt svarar på miljöstimuli i form av ett omedelbart avgivandet av adrenalin och noradrenalin. Mer långsiktiga förändringar regleras av ett annat system – det s.k. HPA-systemet (hypothalamus-hypofys-binjure axeln). Även detta system aktiveras av en akut stressituation, men svaret kommer först 2–3 minuter efter det att individen börjat utsättas för stressen. När HPA-systemet aktiveras ökar binjurebarkens produktion och sekretion av hormonet corticosteron. Djuret är normalt maximalt stressat efter 30–60 minuter exponering. Den ökade corticosteronsekretionen inducerar förändringar (andra än vad SAMS-systemet gör) i beteende och fysiologi så att fortplantnings- och revirbetenande reduceras (eller t.o.m. försvinner helt). Hormonet ökar individens födosöksaktivitet, ökar dess flyttningssoro, mobiliserar glukosreserver i kroppen mm.

Allt för att undvika att hamna i en kronisk stressituation.

Fåglarnas stresskänslighet modifieras emellertid av en mängd faktorer, t.ex. tid på säsongen och häckningsfas, engagemang i föräldraskap, populationstäthet, ålder, social status och näringsstatus. En ökad stresskänslighet innebär en snabbare och kraftigare ökning av corticosteronsekretionen och därmed en förändring av fågelns beteende från fortplantning till överlevnad. Man har därför antagit att fåglar (arter eller populationer) som häckar i karga, hårda miljöer (t.ex. i arktiska eller alpina miljöer) med snabba, oförutsägbara miljöförändringar (t.ex. dåligt väder) och kort häckningsäsong, 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 Lappland som under några dagar utsätts på dagstemperaturer under +5C[∞] 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 +10C[∞] normalt överger sina bon därför att det "kalla" vädret stressar fåglarna (ökar corticosteronsekretionen). Den därmed ökade corticosteronsekretionen omdirigerar beteendet från t.ex. ruvning till födosök och övergivande av boet. Att det verkligen är hormonet som åstadkommer 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 systerarten bofink som häckar i södra Sverige.

Fåglarnas stresskänslighet testades med en standardiserad, internationellt använd, metod. Omedelbart efter att fågeln fastnat i ett slöjnat (d.v.s. inom 2 minuter) tas ett första blodprov (20–30 µl) från vingvenen. Därefter stoppas fågeln i en tygpåse och förvaras där under en timme. Med vissa bestämda intervall (5, 10, 30, 60 minuter) tas fågeln fram och ett nytt blodprov tas. Härmed kan vi få fram *hur snabbt* fågeln reagerar på stressen och *hur mycket* den stressas. Efter sista blodprovet släpps fågeln åter fri. Om fågeln ej utsätts för ytterligare stressorer kommer stresshormonhalterna normalt att vara tillbaka vid utgångsläget (d.v.s. nivån för en ostressad individ) efter 3–4 timmar. Påsen fungerar således som stressfaktor. Blodproverna centrifugeras, plas-

man fryses 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.

Resultaten var entydiga och *stödde ej* den uppsatta hypotesen. Både bofink och bergfinkshanarna visade sig vara extremt stresskänsliga. Detta innebär att bofinken följde det förväntade mönstret, men ej bergfinken. En enda bergfinkshona fångades. Denna enda individ visade, tvärt emot hanarna, en låg stresskänslighet. Där fanns inga skillnader i kropps massa eller fettindex mellan bofink och bergfinkshanarna. Detta även om kroppsmassan justerades för kroppsstorlek. De basala corticosteronnivåerna skiljde sig inte åt mellan arterna. Däremot ökade hormonnivåerna till signifikant högre koncentrationer i bergfinkshanarna än i bofinkshanarna – alltså tvärt mot vad hypotesen förutsade. Några samband mellan corticosteronhalterna eller hur snabbt hormonnivåerna ökade och kroppsstorlek eller fettupplagring kunde inte hittas. Resultaten antyder att även andra faktorer än miljöns oförutsägbarhet och tiden tillgänglig för fortplantning är av betydelse för selektion av fåglars stresskänslighet. Bergfinkar är väl kända för sitt nomadiska beteende, något som gör att populationstätheten i en fjälldal kan variera kraftigt mellan åren. Välkänt är också att bergfinkarna vissa år med låg insektstillgång helt kan överge sina bon, med ett mycket lågt antal utflugna ungar som resultat. Detta samtidigt som

ungfågelproduktionen hos andra insektsätande arter i samma fjällbjörkskog, t.ex. lövsångare, påverkas mycket lite. Bergfinken tycks dåligt anpassad till en varierad näringstillgång och därmed mer sårbar än andra arter om av någon anledning insektstillgången sjunker under häckningssäsongen. Likaså är det känt att bergfinkar lätt överger sina bon vid dåligt väder och kan samla ihop sig, även under häckningstiden, i stora flockar. Huruvida de återupptar häckningen någon annan stans är inte känt. Dessa beteenden måste initieras av någon inre fysiologisk mekanism och den troliga faktorn är ökad corticosteronsekretion. Den höga stresskänslighet som bergfinken uppvisar mot fångst och hanterande gör det högst sannolikt att de är lika känsliga för perioder med liten matförekomst och perioder med dåligt väder. Båda tillstånden är välkända stressfaktorer som kan öka corticosteronsekretionen hos djur. De här framtagna resultaten kan således förklara de beteendekologiska skillnader som t.ex. lövsångare och bergfink uppvisar vid extrema närings- och vädersituationer i fjällen. Varför har dessa skillnader utselekerats? Kanske beror det på att bergfinken har en längre förväntad livslängd än lövsångaren och att den därigenom har råd att vänta ett år med fortplantningen om miljöbetingelserna är dåliga. Något som lövsångaren, med en kortare förväntad livslängd, ej har. Troligen ökar bergfinken sin livslånga fortplantningsframgång om den struntar i att häcka under år då möjligheterna att föda upp optimalt antal ungar är små, och då istället koncentrerar sig på att själv äta den mat den hittar.