Effects of Weather on Corticosterone Responses in Wild Free-Living Passerine Birds

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Harsh weather can have devastating effects on both the survival and the breeding success of wild animals. Corticosterone, released in response to the stress caused by harsh conditions, may trigger physiological and behavioral changes that help ameliorate these effects. We examined three species of Arctic-breeding passerine birds for correlations between circulating plasma corticosterone levels and weather conditions at the time of capture. Furthermore, because persistently poor weather conditions may be required to initiate a stress response, we also looked for a relationship between corticosterone levels and weather conditions over the 24 and 72 h preceding capture. None of the three species showed substantial effects of weather on unstressed corticosterone levels during the breeding season, although one species showed a significant relationship with stress-induced corticosterone levels. In two species, however, variations in weather during molt (an energetically costly period when birds replace their feathers) explained from 35 to 88% of the individual variation in corticosterone levels. In a third molting species, weather conditions in the preceding 24 and 72 h explained between 20 and 30% of the individual variation in corticosterone levels. It thus appears that adverse weather may be a potent stimulator of corticosterone release during molt, but not during the breeding season. Although extreme weather conditions (those experienced once every few years) can disrupt breeding, since none of the birds abandoned breeding we might conclude that the storms in this study were well within the ability of the birds to cope physiologically. © 2000 Academic Press

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When naturalists study fluctuations in populations of different species they find that inclement weather can have devastating effects on local populations (e.g., Andrewartha and Birch, 1954; Lack, 1954; Newton, 1998). Population declines can be caused by both short-term and long-term weather conditions and are driven by increased mortality, poor reproductive success, or both (Newton, 1998). Severe short-lived storms can cause tremendous local mortality in a variety of species (Newton, 1998). For example, severe storms at the beginning of the breeding season killed 60% of adult common sandpipers (*Actitis hypoleucos*). Low temperatures associated with these storms correlated significantly with the mortality rate—as conditions worsened more birds died (Holland and Yalden, 1991). Clearly, selection for physiological mechanisms that facilitate survival of individuals during harsh weather is high; but just as clearly, this mortality is not random. In another classic study, house sparrows (*Passer domesticus*) that survived a severe storm had higher body weights and were larger than those that died (Bumpus, 1899). Also, in the common sandpipers mentioned above, there was a suggestion that younger males preferentially survived (Holland and Yalden, 1995).

Furthermore, even if weather does not cause outright mortality, it can curtail reproductive success dramatically. Not only can reproductive failure affect an entire population (McNicholl, 1979), for example, by killing eggs, but subordinates may be more affected than dominant animals (Wingfield, 1984; Newton, 1998) and some individuals may be more sensitive to diminishing food supplies (Grant and Grant, 1980; Faaborg *et al.,* 1984). But what are the differences in physiology that allow one animal to survive and yet fail to save others or to let some individuals but not others successfully reproduce? Individual differences in the physiological responses to stress (i.e., those physiological responses designed to help an individual survive noxious environmental stimuli such as storms) may provide an explanation (Wingfield and Romero, 1999).

Several recent studies have attempted to link one of the hormones released during stress, corticosterone, with inclement weather in a variety of wild free-living species. Studies of reptiles suggest that increased temperatures during the summer result in enhanced corticosterone release in wild tuataras, *Sphenodon punctatus* (Tyrrell and Cree, 1998) and that corticosterone levels in western fence lizards (*Sceloporus occidentalis*) are both negatively correlated with body condition in the field (Dunlap and Wingfield, 1995) and positively correlated with temperature in the laboratory (Dunlap, 1995). Data from brief periods of inclement weather such as storms, however, have been collected primarily from avian species. Storms elevate corticosterone levels in dark-eyed juncos (*Junco hyemalis hyemalis*) in the winter (Rogers *et al.,* 1993), storm petrels (*Pelecanoides urinatrix*) outside of the breeding season (Smith *et al.*, 1994), Lapland longspurs (*Calcarius lapponicus*) when incubating eggs (Astheimer *et al.*, 1995), and white-crowned sparrows (*Zonotrichia leucophrys pugetensis*) when parents were feeding young (Wingfield *et al.*, 1983). Male song sparrows (*Melospiza melodia*) also increase corticosterone levels in response to storms throughout the breeding season (Wingfield, 1985b), but females fail to show this response (Wingfield, 1985a). In the white-crowned sparrows, elevated corticosterone levels also were correlated with marked changes in behavior, including abandonment of nests (Wingfield *et al.*, 1983). It thus appears that storms can stimulate corticosterone release throughout the annual cycle. Individual differences in the success of this

response, then, may underlie differential survival and breeding success during severe storms.

There are few studies of the impacts of weather on the stress response in wild animals (examples cited above), and sample sizes in each study are small. Consequently, we are unable to determine either general patterns among seasons or species (if they exist) or whether relatively moderate weather fluctuations also elicit elevated corticosterone levels. In the present study we examine relationships between weather conditions at the time of capture and circulating plasma corticosterone levels in three species of Arctic-breeding passerines: Lapland longspurs; redpolls (*Carduelis flammea*); and snow buntings (*Plectrophenax nivalis*). The arctic environment is useful for this study since it is notorious for inclement spring weather and summer storms. In addition, we observed changes in the behavior of these species during storms that are often associated with high corticosterone levels. After 24 h of snow and freezing temperatures many birds abandon territories and flock to relatively snow-free roads to feed (L. M. Romero, personal observations). Astheimer *et al.* (1995) also observed similar changes in behavior 72 h after the beginning of a storm. Consequently, we repeated our analyses using weather conditions over the 24 and 72 h preceding capture.

MATERIALS AND METHODS

Birds

All corticosterone data presented in this paper have been reported previously (Romero *et al.*, 1998a–d). They were collected as part of four different but related studies. Detailed descriptions of capture protocols, capture sites, blood collection, and corticosterone assay techniques are contained in those papers. Briefly, data included here were collected from 1994 to 1997 from three species studied at Barrow, AK (71.1° N, 156.4° W) and at the Toolik Lake Research Station (68° N, 149° W), located approximately 250 km south of Prudhoe Bay, Alaska. All snow buntings and redpolls were captured at Barrow and Lapland longspurs were captured at both Barrow and Toolik Lake. The time of capture was noted for each bird.

Within 3 min of capture a blood sample was col-

lected. Since corticosterone usually takes 3–5 min to begin increasing (Wingfield *et al.*, 1982), these samples are assumed to reflect nonstressed (baseline) levels. Stress-induced levels were obtained from control birds in the previous studies, which was a modified version of the capture stress protocol (Wingfield and Romero, 1999). These birds were injected intravenously (iv) with lactated Ringer's solution and placed in an opaque bag for 30 min (constituting a 30-min restraint period). Before release, birds were scored for fat stores using a semiquantitative scale from 0 (thinnest) to 5 (fattest) and reported as a mean of furcular and abdominal fat stores (Wingfield and Farner, 1978). Earlier studies indicated that corticosterone levels in males and females do not differ in these species at these times of the year (Astheimer *et al.*, 1994; Wingfield *et al.*, 1994a,b), so sex was ignored during analyses.

Birds were captured during two times of the year—early during the breeding season (May and early June) and while undergoing a prebasic molt (late July and August). Since both the baseline and stress-induced corticosterone levels differ dramatically during these seasons (Romero *et al.*, 1998b–d), we ran separate analyses during each season. In addition, corticosterone release in molting redpolls differs by age (Romero *et al.*, 1998d), so adult and juvenile redpolls were analyzed separately. No such difference has been found in Lapland longspurs or snow buntings (Romero *et al.*, 1998b,c) so adults and juveniles were combined. The breeding birds were all adults for each species.

Weather Data

Weather data from the Toolik Lake Research Station were collected by Dr. G. Shaver and the Ecosystems Center at the Marine Biological Laboratory at Woods Hole, Massachusetts, as part of the Long Term Ecological Research program in the Arctic. All birds were trapped within approximately 5 km of the Toolik Lake weather station. Data were collected every minute and averaged or totaled every hour. For these analyses we included weather data for: air temperature (°C) at 1 m above the ground; wind speed (m/s) at 1 m; relative humidity at 1 m; and total unfrozen precipitation (mm). Weather data are reported on the hour, so the nearest hourly means are assumed to indicate the

conditions at the time of capture. We also computed means for temperature, wind speed, relative humidity, and total accumulations for precipitation, for the 24- and 72-h periods prior to capture. Furthermore, we determined the minimum temperature reached during the previous 24 and 72 h. Unfortunately, rainfall data are unavailable for 1995, so rainfall was excluded from the analyses of breeding Lapland longspurs.

Means for 24 and 72 h were analyzed because of field observations indicating weather effects on behavior across these periods. During a moderate storm at Toolik Lake in 1996 when birds were beginning to establish territories, we observed birds temporarily abandoning their territories and flocking to the road in search of forage (L. M. Romero, personal observations). This behavior began approximately 24 h after the temperature dropped and snow began to fall. In addition, Astheimer *et al.* (1995) described a more severe 3-day storm at Toolik Lake in 1989. They reported both increased flocking behavior and an augmentation of stress-induced corticosterone levels near the end of this storm. Thus, given the dramatic changes in behavior seen after 24 and 72 h of poor conditions, we also tested whether recent weather history was more important to the stress response than were conditions at the time of capture.

Weather data from Barrow were collected by the U.S. National Oceanographic and Atmospheric Administration (NOAA) and all birds were captured within 3 km of their station. We used air temperature, wind speed, relative humidity, and accumulated precipitation. NOAA reports a 3-h mean or accumulation, starting at midnight, so the nearest 3-h means are assumed to indicate conditions at the time of capture. As with the Toolik Lake data, we then computed means and minimum temperatures for the 24- and 72-h periods prior to capture.

Statistics

Weather data were divided into three groups: the hour of capture (including temperature, wind speed, relative humidity, and rainfall); data from the previous 24 h (24 h mean temperature, 24 h mean wind speed, 24 h minimum temperature, and 24 h accumulated rainfall); and data from the previous 72 h (72 h mean temperature, 72 h mean wind speed, 72 h minimum temperature, and 72 h accumulated rainfall). We in-

cluded fat stores as a covariate in the analyses. For each group of data we performed stepwise regressions comparing all factors to both baseline and stress-induced corticosterone levels. We repeated the analyses for each species for both the breeding season and the molt and for adult and juvenile molting redpolls. A $P < 0.05$ was required to retain each factor in the model.

We ran separate analyses for each species (i.e., did not include them in the same statistical model) because we have neither the background nor knowledge to compare absolute corticosterone levels among species, nor do we know whether weather influences those levels differently in each species. Similarly, we included different analyses for the hour of capture and 24- and 72-h means since they are *a priori* comparisons, even though many of the variables (e.g., temperature) were correlated.

Because regression is the most general form of the general linear model, it is not under all of the constraints imposed on an analysis of variance (ANOVA), which is a more specific general linear model. Thus P values for performing more than one regression do not need to be adjusted for multiple comparisons (Sokal and Rohlf, 1981). The reason is that ANOVA is looking for a treatment effect, so with an α level of 0.01, one expects 99/100 repetitions of an experiment to find that the same treatment differences exist. Regressions are different. If one runs 100 regressions, with an α level of 0.01, one expects 99 to have the same equation for explaining the relationship between variables. ANOVA determines if one has a treatment effect and regression describes the relationship. Running multiple ANOVAs increases the risk of making a Type I error. This is why a Bonferonni or similar adjustment is required. Repeated regressions, on the other hand, do not have the same risk. The risk of running repeated regressions is not the risk of making a Type I error; rather, it is calculating an incorrect β in the regression equation (i.e., the incorrect slope and/or intercept from the regression equation). Consequently, running repeated regressions does not have an associated inflated experiment-wide error rate so that P values did not need to be corrected in this study.

We also performed a principal components analysis on the weather variables and repeated the regressions using the first two principal components. This procedure did not provide any further explanatory power and so results are not presented.

RESULTS

Breeding Season

Weather had few consistent relationships with baseline corticosterone levels during the breeding season (Table 1). Weather appeared to have no affect on redpolls, and although several weather variables had a significant affect in Lapland longspurs, they explained little of the overall variation (between 3 and 6%). Weather variables during the hour of capture explained 16% of the variation in baseline corticosterone levels in snow buntings ($P < 0.03$–0.04), but there were no correlations with weather over the preceding 24 or 72 h.

Stress-induced corticosterone levels during the breed-

TABLE 1

Baseline Corticosterone Correlations with Weather during the Breeding Season

Species	Hour of capture	24-h mean	72-h mean
Lapland longspur, $n = 172$	Relative humidity, $R^2 = 0.032$, $P < 0.02$	Wind speed, $R^2 = 0.057$, $P < 0.001$	Temperature, $R^2 = 0.050$, $P < 0.002$
Snow bunting, $n = 58$	Wind speed, $R^2 = 0.091$, $P < 0.03$ Temperature, $R^2 = 0.073$, $P < 0.04$ Total $R^2 = 0.164$	None	None
Redpoll, $n = 33$	None	None	None

Note. Results during breeding of stepwise regressions on weather factors (discussed in detail in the text) and baseline corticosterone levels. R^2 values for temperature variables are all negative (corticosterone values increase as temperatures decrease). ''None'' indicates that no weather variable correlated with corticosterone levels at or below the $P < 0.05$ threshold required in the model.

TABLE 2
Stress-Induced Corticosterone Correlations with Weather during the Breeding Season

Species	Hour of capture	24-h mean	72-h mean
Lapland longspur, $n = 55$	Temperature, $R^2 = 0.207$, $P < 0.002$ Wind speed, $R^2 = 0.099$, $P < 0.03$ Fat stores, $R^2 = 0.064$, $P < 0.051$ Total $R^2 = 0.370$	None	Temperature, $R^2 = 0.236$, $P < 0.0001$ Wind speed, $R^2 = 0.154$, $P < 0.003$ Total $R^2 = 0.390$
Snow bunting, $n = 24$	Relative humidity, $R^2 = 0.171$, $P < 0.04$	None	None
Redpoll, $n = 14$	Fat stores, $R^2 = 0.464$, $P < 0.006$	Fat stores, $R^2 = 0.464$, $P < 0.006$	Fat stores, $R^2 = 0.464$, $P < 0.006$

Note. Results during breeding of stepwise regressions on weather factors (discussed in detail in the text) and stress-induced corticosterone levels. R^2 values for temperature variables are all negative (corticosterone values increase as temperatures decrease). ''None'' indicates that no weather variable correlated with corticosterone levels at or below the $P < 0.05$ threshold required in the model.

ing season also were not strongly correlated with the measured weather variables (Table 2). In snow buntings, only relative humidity during the hour of capture reached significance ($P < 0.04$). Redpolls showed no effects of weather, although fat stores were highly negatively correlated with stress-induced corticosterone levels. Weather was significantly correlated with stress-induced corticosterone levels in Lapland longspurs. Results from the hour of capture and the 72-h mean explained nearly 40% of the data ($P < 0.002$–0.051 and $P < 0.0001$–0.003, respectively). The 24-h means of these weather variables, however, showed no significant relationships.

A representative graphical presentation of both baseline and stress-induced data compared to temperature at the time of capture is presented in Fig. 1A for breeding Lapland longspurs and is included to show the lack of any strong correlations. The data are similar for both the 24- and the 72-h means, as well as for other weather variables, and furthermore are similar in the other two species (data not shown).

Molt

In contrast to results from the breeding season, baseline corticosterone levels were highly correlated with weather conditions when birds were molting (Table 3). In extremely significant relationships ($P < 0.0001$), various weather measurements along with body condition explained between 47 and 53% of the variation in baseline corticosterone levels in Lapland longspurs. This pattern held true for weather at the hour of capture and for the 24- or 72-h means. There was a similar significant relationship in redpolls, with

weather explaining from 35 to 59% of the variability in corticosterone levels in adults and from 44 to 88% of the variability in juveniles. Baseline corticosterone levels in snow buntings, on the other hand, had a weak correlation with weather. Both wind speed at the hour of capture ($P < 0.04$) and 24-h mean rainfall levels ($P < 0.05$) correlated with corticosterone levels, but they explained only approximately 6% of the variation. The relationship strengthened, however, when using 72-h means, where weather explained about 19% of the variation ($P < 0.002$–0.03).

Stress-induced corticosterone levels were also highly correlated with weather conditions in these species during molt (Table 4). Highly significant correlations (P values from 0.003 to 0.0006) in Lapland longspurs explained from 40 to over 73% of the variability in stress-induced corticosterone levels. This effect was consistent from the hour of capture to both 24- and 72-h means. Similar significant correlations occurred in adult redpolls, with 36% of the variation explained by wind speed at the hour of capture to over 60% of the variation explained by weather conditions over the preceding 72 h (P values from 0.02 to 0.0001). Although no weather variable correlated with stress-induced corticosterone levels at the hour of capture in juvenile redpolls, temperature explained between 48 and 58% ($P = 0.009$ and 0.003) of the variability over the preceding 24 and 72 h. In snow buntings, temperature over 24 and 72 h explained between 25 and 30% of the variation ($P < 0.003$ and 0.0007, respectively), but only rainfall correlated with stress-induced corticosterone levels during the hour of capture.

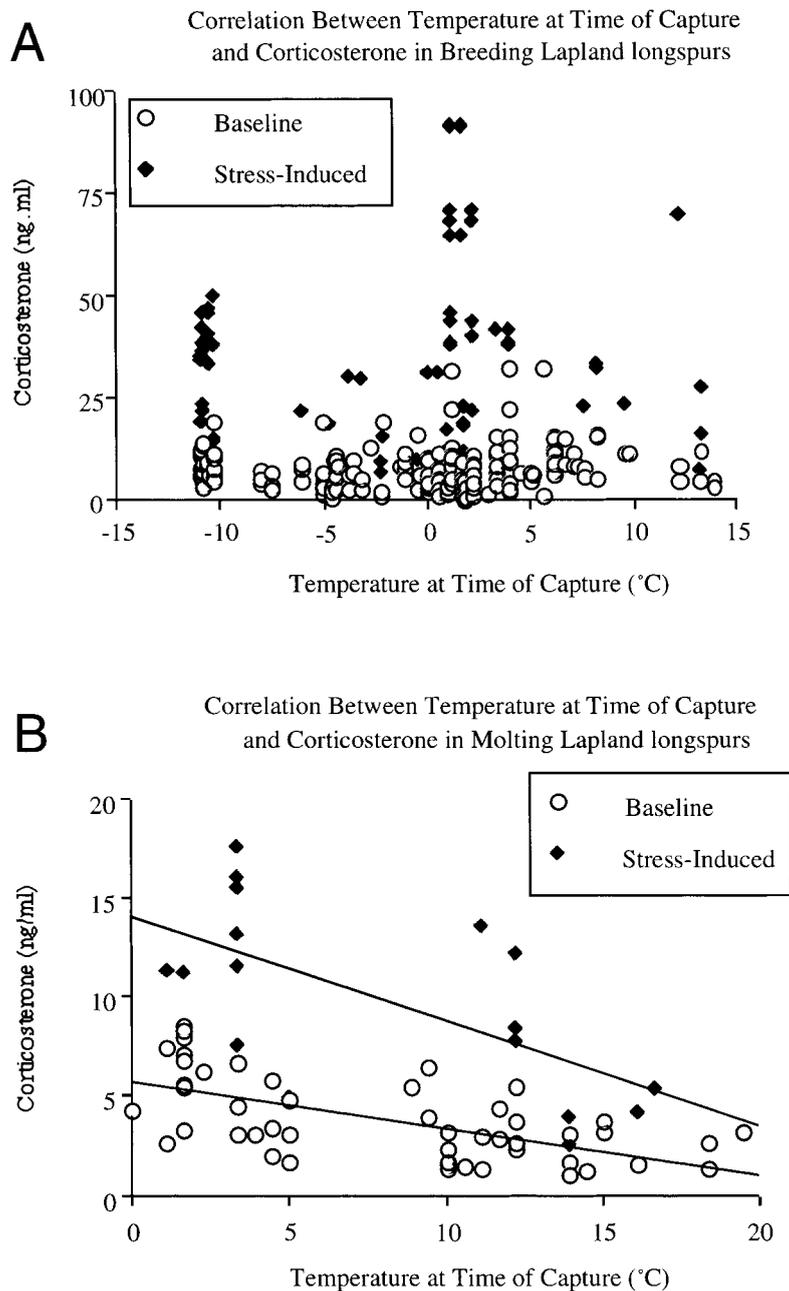A representative graphical presentation of both base-

FIG. 1. Baseline and stress-induced corticosterone levels in Lapland longspurs compared to temperature at the time of capture during breeding (A) and molt (B). Lines represent significant correlations as described in the text. Note differences in scale of corticosterone levels.

line and stress-induced data compared to temperature at the time of capture is presented in Fig. 1B for molting Lapland longspurs. The data are similar for both the 24- and the 72-h means, as well as for other weather variables, and furthermore are similar in the other two species (data not shown).

DISCUSSION

Although many of the analyses presented here were statistically significant, some of the correlations explained little of the individual variation in either baseline or stress-induced corticosterone levels. Further-

TABLE 3

Baseline Corticosterone Correlations with Weather during Molt

Species	Hour of capture	24-h mean	72-h mean
Lapland longspur, $n = 50$	Temperature, $R^2 = 0.375$, $P < 0.0001$	Temperature, $R^2 = 0.382$, $P < 0.0001$	Temperature, $R^2 = 0.420$, $P < 0.0001$
	Fat stores, $R^2 = 0.083$, $P < 0.01$	Wind speed, $R^2 = 0.099$, $P < 0.005$	Wind speed, $R^2 = 0.050$, $P < 0.04$
	Relative humidity, $R^2 = 0.069$, $P < 0.02$	Fat stores, $R^2 = 0.051$, $P < 0.03$	
	Total $R^2 = 0.526$	Total $R^2 = 0.532$	Total $R^2 = 0.470$
Snow bunting, $n = 73$	Wind speed, $R^2 = 0.063$, $P < 0.04$	Rainfall, $R^2 = 0.055$, $P < 0.05$	Minimum temperature, $R^2 = 0.133$, $P < 0.002$
			Rainfall, $R^2 = 0.058$, $P < 0.03$
			Total $R^2 = 0.191$
Redpoll			
Adults, $n = 44$	Wind speed, $R^2 = 0.178$, $P < 0.005$	Temperature, $R^2 = 0.382$, $P < 0.0001$	Minimum temperature, $R^2 = 0.505$, $P < 0.0001$
	Rainfall, $R^2 = 0.082$, $P < 0.04$	Minimum temperature, $R^2 = 0.109$, $P < 0.005$	Temperature, $R^2 = 0.086$, $P < 0.006$
	Temperature, $R^2 = 0.092$, $P < 0.03$		
	Total $R^2 = 0.352$	Total $R^2 = 0.491$	Total $R^2 = 0.591$
Juveniles, $n = 20$	Temperature, $R^2 = 0.444$, $P < 0.002$	Temperature, $R^2 = 0.744$, $P < 0.0001$	Temperature, $R^2 = 0.805$, $P < 0.0001$
		Fat stores, $R^2 = 0.084$, $P < 0.01$	Fat stores, $R^2 = 0.079$, $P < 0.005$
		Total $R^2 = 0.828$	Total $R^2 = 0.883$

Note. Results during molt of stepwise regressions on weather factors (discussed in detail in the text) and baseline corticosterone levels. R^2 values for temperature variables are all negative (corticosterone values increase as temperatures decrease).

more, many statistically significant results were supported by marginal P values ($0.02 < P < 0.05$). These results were likely a result of the large sample sizes in these data sets and smaller sample sizes would be unlikely to reach significance. These marginal P values also were supporting results where not much of the variation was explained (R^2 less than about 6%). Consequently, many of these results may have

little biological relevance (Underhill, 1999). If these analyses are disregarded, a clearer picture of weather's effects on corticosterone levels emerges. Table 5 summarizes the results of Tables 1–4 after removing analyses with low explanatory power and presents the amount of individual variation explained by weather in those cases where there was a strong correlation.

TABLE 4

Stress-Induced Corticosterone Correlations with Weather during Molt

Species	Hour of capture	24-h mean	72-h mean
Lapland longspur, $n = 16$	Temperature, $R^2 = 0.407$, $P < 0.006$	Wind speed, $R^2 = 0.557$, $P < 0.0006$	Minimum temperature, $R^2 = 0.475$, $P < 0.003$
		Temperature, $R^2 = 0.175$, $P < 0.01$	
		Total $R^2 = 0.732$	
Snow bunting, $n = 35$	Rainfall, $R^2 = 0.155$, $P < 0.04$	Temperature, $R^2 = 0.249$, $P < 0.003$	Minimum temperature, $R^2 = 0.296$, $P < 0.0007$
Redpoll			
Adults, $n = 26$	Wind speed, $R^2 = 0.361$, $P < 0.002$	Temperature, $R^2 = 0.463$, $P < 0.0001$	Minimum temperature, $R^2 = 0.602$, $P < 0.0001$
		Minimum temperature, $R^2 = 0.126$, $P < 0.02$	
		Total $R^2 = 0.589$	
Juveniles, $n = 13$	None	Temperature, $R^2 = 0.484$, $P < 0.009$	Temperature, $R^2 = 0.575$, $P < 0.003$

Note. Results during molt of stepwise regressions on weather factors (discussed in detail in the text) and stressed-induced corticosterone levels. R^2 values for temperature variables are all negative (corticosterone values increase as temperatures decrease).

TABLE 5

Summary of Results

Species	Breeding		Molt	
	Baseline	Stress	Baseline	Stress
Lapland longspur	No	Yes	Yes	Yes
		37–39%	47–53%	41–73%
Snow bunting	No	No	Yes	Yes
			19%	25–30%
Redpoll				
Adult	No	No	Yes	Yes
			35–59%	36–60%
Juvenile			Yes	Yes
			44–88%	48–58%

Note. Weather was considered to have a significant effect on corticosterone levels for each species and during each season if at least one analysis (hour of capture or 24- or 72-h mean) resulted in a strong correlation ($P < 0.01$) that explained approximately 5% or more of the variation. Percentages refer to the percentage of the variation explained by weather.

It is clear from Table 5 that weather conditions during the breeding season have little explanatory power of individual variation in corticosterone levels. In contrast, weather appears to have a dramatic influence on corticosterone levels when birds are molting. In two species (Lapland longspurs and redpolls), often over 50% of the individual variation in corticosterone levels can be attributed to the weather conditions during or near the time of capture. It thus appears that weather dramatically elevates corticosterone levels during molt, but not during breeding. This result does not reflect more severe storms during molt. Temperature, for instance, spanned roughly an equivalent range during each season (approximately 25°C during breeding and 20°C during molt, Fig. 1).

The evidence that corticosterone levels during molt were linked to weather conditions, whereas little evidence for such a link exists during breeding (Table 5), was unexpected. It is presently unclear whether this is due to physiological differences during breeding or during molt; and arguments can be made for both. Given the deleterious effects corticosterone can have on breeding (Moberg, 1985; Wingfield, 1988; Sapolsky, 1992), perhaps birds become less responsive to weather conditions during breeding in order to prevent deleterious corticosterone increases. Alternatively, molt is an energetically costly undertaking (Murphy and King, 1992), and perhaps birds require the beneficial meta-

bolic effects of corticosterone during molt in order to ameliorate the affects of weather (although this might not explain correlations with stress-induced corticosterone levels). Additionally, corticosterone levels are so low during molt compared to the breeding season (Romero *et al.*, 1998b–d) that perhaps the response to adverse weather conditions is magnified at this time of the year.

There is little support from these data that either 24 or 72 h of poor weather are more important in affecting corticosterone levels for redpolls and Lapland longspurs than are the conditions at the time of capture. This is surprising given the fact that some breeding birds experienced a moderately severe storm during the period of this study (at the Toolik Lake field station from May 19 to May 22, 1995). Temperatures during this storm stayed between −8 and −12°C for several days. In all species but snow buntings and juvenile redpolls, however, weather conditions over the preceding 24 or 72 h had as much explanatory power as did conditions at the time of capture, even though both we and Astheimer *et al.* (1995) saw marked behavioral changes after moderate and severe storms (see Materials and Methods). There are at least three possible explanations for this disparity. First, poor weather may immediately stimulate corticosterone release, but that the magnitude of the response increases as the poor weather persists. This is unlikely, however, since the persistence of poor weather conditions is reflected in the 24 and 72 h temperature means. Second, the elevated corticosterone levels in response to poor weather were not the primary cause of the altered behavior seen in the field. Third, the effects of weather may become more acute as the breeding season progresses; the data analyzed here were collected early in the breeding season (during pair formation and nest building) whereas the storm Astheimer *et al.* reported occurred while birds were incubating eggs. Other studies also report corticosterone responses to storms later in the breeding season (Wingfield *et al.*, 1983; Wingfield, 1985a,b). Further experiments will be required to distinguish among these hypotheses.

Molting snow buntings, however, appear to have had a different reaction to weather conditions than do either redpolls or Lapland longspurs. Not only are the correlations not particularly strong until poor weather has persisted for some time, but weather conditions

explain less of the variation in corticosterone levels. Whereas from 35 to 88% of the individual variation in corticosterone levels in Lapland longspurs and redpolls are explained by weather conditions, only between 20 and 30% of the individual variation in snow buntings can be explained. Intriguingly, this difference correlates with how these species modify their hypothalamic–pituitary–adrenal (HPA) axes during molt. Both redpolls and Lapland longspurs modulate corticosterone release during molt by altering the amounts of CRF and/or arginine vasotocin (the two primary peptides stimulating ACTH release) released from the hypothalamus (Romero *et al.*, 1998c,d). Snow buntings, on the other hand, modulate corticosterone release by altering the levels of ACTH released from the anterior pituitary (Romero *et al.*, 1998b).

Although several recent studies have emphasized the role of body condition, as measured by the degree of fat stores, in modulating corticosterone levels (Wingfield *et al.*, 1994b, 1997; Schwabl, 1995), body condition was not strongly correlated with corticosterone levels in two of these species. This result was despite fat scores ranging from 0 to 3 in these species. Although fat stores were included as a factor in each of the statistical models, in only one instance was there a significant and strong correlation between fat stores and corticosterone levels. Instead, weather appears to be the more important factor measured in this study in modulating corticosterone levels. These results are in marked contrast to the studies cited above, but similar to findings in other studies (Smith *et al.*, 1994; Silverin *et al.*, 1997). The dramatic relationship between fat and corticosterone levels in breeding redpolls was the exception in this study. Although the sample size was low in this particular analysis, the relationship has been reported in another study as well with the same population (Wingfield *et al.*, 1994a). It thus appears that poorer condition is correlated with corticosterone levels only in certain species, and at least when severe starvation is absent, is not a general predictor of corticosterone levels in all species.

In conclusion, in the species studied, we found that weather can have a dramatic affect on both baseline and stress-induced corticosterone levels during molt, but not during breeding. Although severe storms will likely stimulate corticosterone release regardless of the season (since this has been shown in other species, Smith *et al.*, 1994; Astheimer *et al.*, 1995), daily fluctuations in weather conditions only appear to explain individual variation in corticosterone levels at some times of the year. It remains to be determined if the corticosterone response to weather in molting or breeding birds is more typical of the rest of the yearly cycle. Regardless, at least during molt it appears as though the sensitivity of the corticosterone response to weather conditions may provide the underlying physiological mechanism helping individual survival during periods of harsh weather.

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