

Endocrine Responses to Unpredictable Environmental Events: Stress or Anti-Stress Hormones?¹

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SYNOPSIS. In addition to seasonal changes in morphology, physiology and behavior that occur in predictable annual cycles, there are facultative responses to unpredictable events known as labile (*i.e.*, short-lived) perturbation factors (LPFs). These rapid behavioral and physiological changes have been termed the “emergency” life history stage (ELHS) and serve to enhance life-time fitness. Glucocorticosteroids interacting with other hormones in the hypothalamo-pituitary-adrenal (HPA) cascade, initiate and orchestrate the ELHS within minutes to hours. Components of the ELHS include: redirection of behavior from a normal life history stage to increased foraging, irruptive-type migration during the day, enhanced restfulness at night, elevated gluconeogenesis and recovery once the perturbation passes. These physiological and behavioral changes allow an individual to avoid potential deleterious effects of stress that may result from chronically elevated levels of circulating glucocorticosteroids over days and weeks. In other words, acute rises in glucocorticosteroids following perturbations of the environment may actually avoid chronic stress and serve primarily as “anti-stress” hormones. Several field studies in diverse habitats indicate that free-living populations have elevated circulating levels of corticosteroids when in an ELHS. However, expression of an ELHS may not always be advantageous and there is accumulating evidence from birds that the adrenocortical responses to LPFs are modulated both on seasonal and individual levels. These data suggest that glucocorticosteroid secretions in response to LPFs not only trigger physiological and behavioral responses but also allow flexibility so that the response is integrated in relation to time of year (normal LHS) as well as individual differences owing to body condition, disease and social status.

INTRODUCTION

I've lived in a good climate, and it bores the hell out of me. I like weather rather than climate.

John Steinbeck, “Travels With Charlie” (1962)

There is no habitat on Earth that is entirely constant, or changes in a perfectly predictable manner. On the other hand it is also probably true to say that no habitat is completely unpredictable or chaotic. Therefore, organisms must be able to adjust their morphology, physiology and behavior to predictable changes in the environment, but also be ready to deal with unpredictable perturbations with little or no prior warning. The concept of predictability and unpredictability in both physical and social environments is illustrated well by the phrase from Steinbeck cited above. We all are familiar with the vagaries of weather. However, climate refers to the average regional environmental conditions that can be expected over the year. Even the most severe climate has a strong predictable component (*e.g.*, the changing seasons) and organisms can thus prepare for future changes. In contrast, weather represents the local conditions at any time that may, or may not, be consistent with the predicted climate (Wingfield and Ramenofsky, 1999). Weather is not the only source of unpredictable events (labile perturbation factors—LPFs). Other examples include sudden changes in social status, increased predator numbers, decreased food resources, and disease (Wingfield *et*

al., 1998; Wingfield and Ramenofsky, 1999; Wingfield, 2001).

Animals use environmental cues such as changing day length, temperature and rainfall to predict future events and adjust life history stages (LHSs) accordingly (Fig. 1). However, responses to LPFs require more rapid responses without possibility of anticipatory changes. This response has been collectively termed the emergency life history stage (ELHS) and serves to direct the individual away from normal LHSs into a physiological and behavioral state that will allow survival in the best condition possible (Fig. 1, Wingfield *et al.*, 1998). If the individual is unable to acclimate to the LPF, or move away from it, then symptoms of stress and eventually death will occur (Wingfield and Ramenofsky, 1999; Wingfield and Romero, 2000). In this chapter we suggest that the ELHS is a mechanism by which animals not only deal with LPFs, but also integrate adjustments in life history cycles to accommodate the stochastic nature of the interrelationships of predictability and unpredictability.

Changes in responsiveness to LPFs may have an ecological basis

The frequency and magnitude of unpredictable perturbations vary along environmental gradients. Behavioral responsiveness (or latency of response) of animals to LPFs might reflect this variability. For instance, behavioral responses of seabirds to variability in food resources reflects their phylogenetic and ecological characteristics as well as that of their prey (Kitaysky, 1999; Kitaysky and Golubova, 2000; Kitaysky *et al.*, 2000). In animals relying on continuously available food re-

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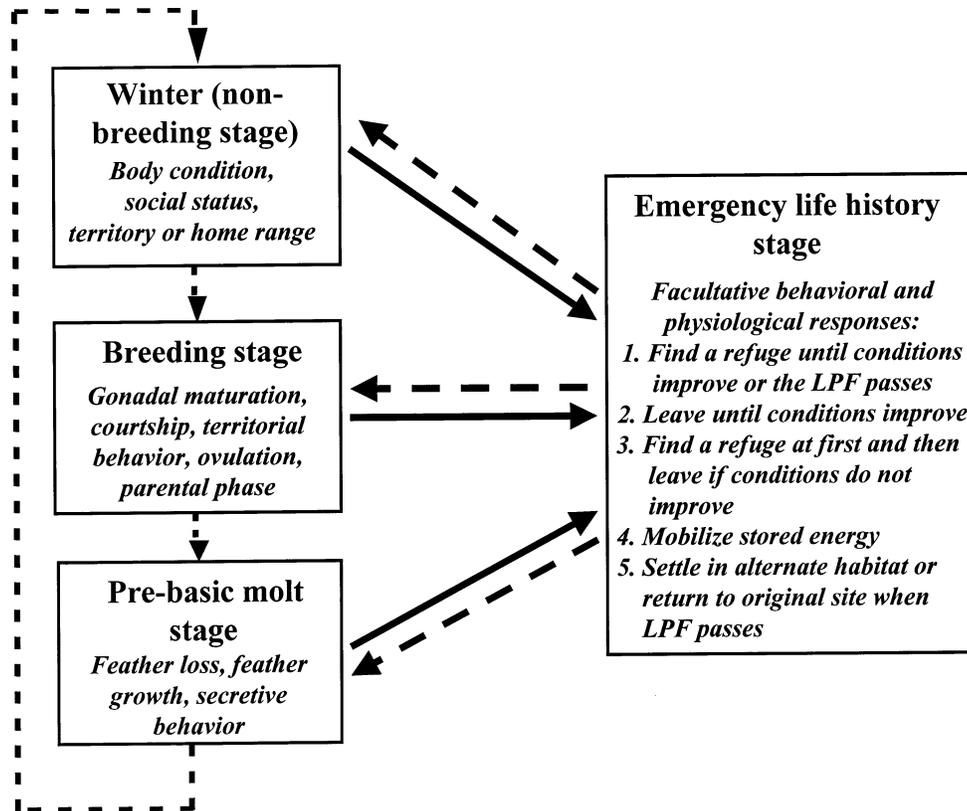


FIG. 1. Temporal sequence of life history stages (LHSs, left hand side) in a typical non-migratory bird. Each box contains examples of behavioral and physiological sub-stages that are unique to each LHS. The temporal sequence of LHSs is unidirectional and each LHS is timed by environmental cues transduced through neuroendocrine and endocrine secretions. Note that this cycle progresses as a function of the predictable life cycle, *e.g.*, the seasons. Superimposed on this predictable life cycle are unpredictable events (labile perturbation factors, LPFs) in the environment such as presence of predators, inclement weather, sudden changes in social status. These LPFs are disruptive to the normal temporal progression of LHSs and many have the potential to be stressful. If the LPF is severe, or prolonged (several days or more) then the individual may have to abandon its normal LHS and adopt temporary emergency physiology and behavior to endure the LPF in the best condition possible. The emergency life history stage (ELHS, right hand box) is a facultative LHS that can be triggered by LPFs at any time in the life cycle (arrows with solid lines). It also comprises unique sub-stages that allow the individual to combat the LPF and maximize fitness. Once the LPF passes, the animal can return to the appropriate LHS (arrows with broken lines). From Wingfield *et al.* (1997); Jacobs and Wingfield (2000).

sources, even a short-term decrease in food availability might trigger an ELHS. In animals relying on highly variable food resources, only a severe long-term food shortage should trigger ELHS. So, the more predictable the environment (less stochastic), the quicker physiological and behavioral response to LPFs would be, whereas in less predictable environments (more stochastic) those responses are expected to be delayed.

In contrast to variability of LPFs and diversity of life history traits that allow animals to cope with them, the ELHS is a remarkably consistent trait among all vertebrates, and is aimed to maximize lifetime fitness. However, animals are faced with contrasting trade-offs in different LHSs. For example, outside of the reproductive season, survival seems paramount, whereas when breeding, the number of viable offspring produced during current *versus* future reproductive attempts must be maximized. Thus, the strategy that animals are pursuing when responding to LPFs should reflect which specific component of lifetime fitness is currently being maximized.

Components of the emergency life history stage

The life cycle of vertebrates consists of a series of life history stages (LHSs) each with unique set of sub-stages (Fig. 1). The temporal sequence of LHSs is fixed, although the number of LHSs varies from species to species and each stage is expressed at a time of year for which the stage has evolved to maximize fitness (Jacobs and Wingfield, 2000). State of an individual at any time is a function of the set of sub-stages expressed within a LHS. The emergency life history stage (ELHS) can be expressed at any time in the life cycle. The LPFs that trigger an ELHS are diverse, but the sub-stages within the ELHS are remarkably constant in all vertebrates studied to date (Fig. 1). They serve to direct the individual into a survival mode and then allow it to return to the normal LHS once the LPF passes. Behavioral and physiological components that make up the sub-stages of an ELHS are:

1. "Leave-it" strategy—movements away from LPFs

2. "Take-it" strategy—switch to an alternate set of energy conserving behavioral and physiological traits
3. "Take at first and then leave-it" strategy—switch to energy conserving mode first and then move away if conditions do not improve

Once a "strategy" has been adopted, then mobilization of stored energy sources such as fat and protein to fuel movement away from the source of the LPF, or to provide energy while sheltering in a refuge becomes critical. Finally, once the LPF passes, or the individual has moved away, then it must settle in alternate habitat once an appropriate site is identified, or, return to the original site and resume the normal sequence of LHSs. These dramatic changes in behavior and physiology can occur within minutes to hours of exposure to a LPF and have been the subject of many experiments to determine the hormonal mechanisms underlying them (Wingfield and Ramenofsky, 1999).

THE EMERGENCY LIFE HISTORY STAGE AND ITS CONTROL: STRESS OR ANTI-STRESS HORMONES?

Vertebrates generally undergo marked activation of the hypothalamo-pituitary adrenal (HPA) axis that is remarkably similar across taxa (Greenberg and Wingfield, 1987). In all tetrapods, LPFs in the environment result in release of adrenocorticotropin (ACTH) from the precursor molecule pro-opiomelanocortin in the anterior pituitary. ACTH release is regulated by corticotropin releasing hormone (CRH). Arginine vasotocin (AVT) and mesotocin (MT) also may be potent secretagogues of ACTH in birds (Gorbman *et al.*, 1983; Norris, 1997). ACTH acts primarily on the adrenocortical cells to promote synthesis and secretion of glucocorticosteroids (Carsia, 1990). The hypothalamic-pituitary-adrenal (HPA) axis of vertebrates, particularly Aves, has many of the same feedback controls as in mammals (Carsia, 1990; Harvey and Hall, 1990).

There is massive evidence that chronic elevation of glucocorticosteroids over weeks or longer, has dramatic and debilitating effects including: inhibition of the reproductive system, suppression of the immune system, promotion of severe protein loss from skeletal muscle, disruption of second cell messengers, particularly the arachidonic acid cascade, neuronal cell death, and suppression of growth (*e.g.*, Munck *et al.*, 1984; Sapolsky, 1987; McEwen *et al.*, 1993; Sapolsky *et al.*, 2000). Although it is clear that elevated secretion of glucocorticosteroids allows an animal to survive many "stressful" events, there is a severe cost of prolonged high blood glucocorticoid levels. Therefore it is possible that the "stress" response system only increases fitness during relatively short-term responses (hours to days) to LPFs, and is detrimental to the animal during protracted challenges to homeostasis (days to weeks).

Rapid effects of glucocorticosteroids in response to LPFs have received much less attention. Accumulating experimental evidence in birds and mammals indicates

that corticosterone has a number of behavioral and physiological effects that promote fitness at least in the short term. These have been reviewed extensively by Sapolsky *et al.* (2000); Wingfield and Romero (2000) and include: suppression of reproductive behavior without inhibiting the reproductive system; regulation of the immune system (*e.g.*, Dhabhar, 1998); increased gluconeogenesis; increase foraging behavior—a permissive role rather than direct; promotion of escape (irruptive) behavior during day; promotion of night restfulness; facilitation of recovery on return to normal life history stage. These short term effects of corticosterone during a response to LPFs suppress "unnecessary" physiological and behavioral functions, activate alternate behavioral and physiological patterns that promote survival (*i.e.*, temporary emergency behavior) and collectively serve to avoid the long-term, detrimental effects of stress-induced high levels of corticosterone.

The basic principles of the ELHS and its control may be widespread among vertebrate taxa, and many aspects of the stress response are nearly stereotypical. Nonetheless, there are large differences in the responses of individuals to the same LPF (*e.g.*, Sapolsky, 1988; Meaney *et al.*, 1993a, b). Some of this variation is based on genetic differences among individuals (*e.g.*, Flaherty and Rowan, 1989; Satterlee and Johnson, 1988; Carsia and Weber, 1986; Gross and Siegel, 1985), whereas other variation is associated with differences in physiological condition and/or sub-stages within a LHS, *e.g.*, reproductive status in the breeding LHS (Wingfield *et al.*, 1994a, b).

Given that the short-term responses to elevated corticosterone induced by a LPF are highly adaptive, then it is pertinent to re-define stress. LPFs can trigger an increase in adrenocortical secretions, but may not be stressful per se. They certainly have the potential to be stressors, but if the animal is able to compensate by activating the ELHS, then the deleterious effects associated with chronic stress are avoided. When in an ELHS, the individual is not stressed but in a transitory stage maximizing chances of survival in best condition possible (Wingfield and Ramenofsky, 1999; Wingfield and Romero, 2000).

This concept is worth formalizing in a more theoretical sense. It has long been known that baseline levels of glucocorticosteroids are essential for energy and salt management and without this absolute baseline (*e.g.*, in adrenalectomized animals), the individual will die (Gorbman *et al.*, 1983; Norris, 1997). We have called this baseline level A (Fig. 2, Wingfield *et al.*, 1997, 1998). Blood levels of glucocorticosteroids also change predictably over the day and also in relation to seasons. Again, it is thought that these fluctuations are involved in metabolism and osmoregulatory processes as the individual changes physiology and behavior from one LHS to the next (Fig. 1). These we have called level B (Fig. 2). Examples include increases of baseline corticosterone in breeding birds, and surges of cortisol in salmonids migrating from fresh to salt

Levels of Hormone Secretion

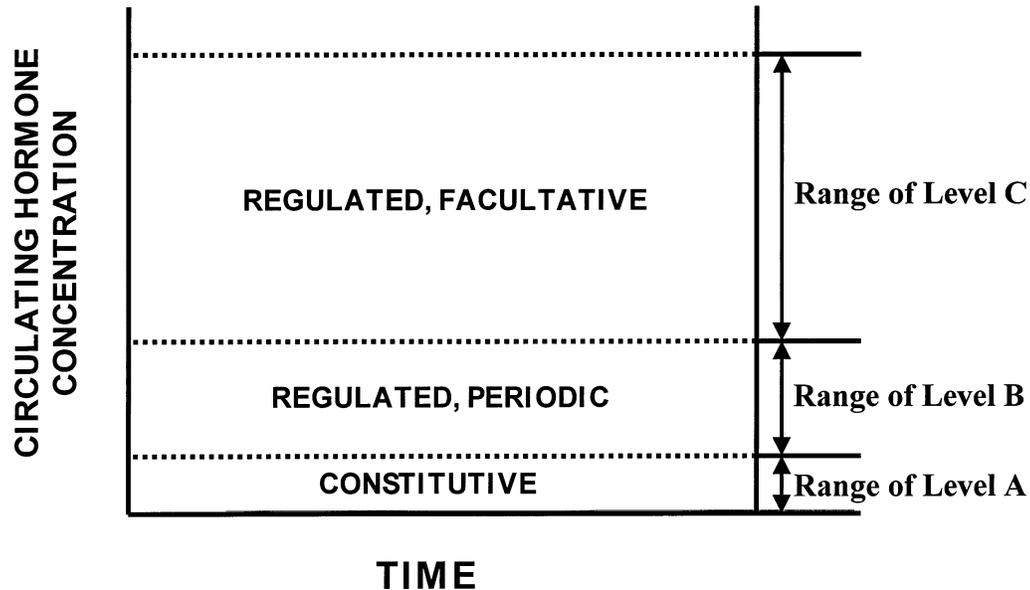


FIG. 2. A theoretical view of different levels of hormone secretion according to the levels of physiological and behavioral response. Level A is the absolute baseline required for existence of the individual. In the case of corticosterone, below this level is typical of adrenalectomy and the individual will die because it cannot manage glucose and salts. Secretion of hormone at this baseline may be constitutive, but some regulation may also occur (*e.g.*, when negative feedback set points change seasonally). Level B is the range of circulating concentrations of corticosterone that occur on a daily basis (or tidal rhythm in marine species) and in relation to seasons. These changes are part of the predictable life cycle and are regulated periodically by responses to environmental cues such as photoperiod. Changes in secretion at levels A and B make up the predictable life cycle of individuals in relation to glucose management, salt regulation, and associated behaviors. Superimposed on this predictable life cycle are transient increases in circulating levels of corticosterone to level C. This marked increase is triggered by a labile perturbation factor (LPF), thus is regulated facultatively, and if prolonged will trigger the emergency life history stage (ELHS, Fig. 1). If the individual is unable to combat the LPF there is potential for chronic stress and the debilitating effects of chronically high levels of glucocorticosteroids. If the ELHS can be triggered, then plasma levels of corticosterone decline to within level B. From Wingfield *et al.* (1997).

water (see Wingfield and Romero, 2000). Superimposed on these predictable changes in glucocorticosteroids at levels A and B, are further surges in circulating levels to much higher and usually transitory peaks that we have called level C (Fig. 2). These transitory surges are what we propose activate the ELHS. Only if they become prolonged because of repeated LPFs, or because the individual is not able to move away, do typical symptoms of stress become apparent (Wingfield *et al.*, 1997, 1998). Thus, transitory elevation of corticosterone to level C, above levels A and B for the predictable life cycle, (Fig. 2) may be integrating physiological and behavioral strategies that maximize fitness in the face of unpredictable environmental events. Not only may the HPA axis be an integrator of mechanisms maximizing fitness, it may also be a subject of on-going selection.

GLUCOCORTICOSTEROIDS: INTEGRATORS OF FACULTATIVE BEHAVIORAL AND PHYSIOLOGICAL RESPONSES TO THE UNPREDICTABLE

The growing evidence that early effects (minutes to hours) of rising glucocorticosteroid levels in response to LPFs trigger an ELHS to avoid severe stress, suggests an integrating role for behavioral and physiolog-

ical responses to these unpredictable events. The generalized ELHS allows a consistent and adaptive suite of responses regardless of time of year and LHS, and is flexible enough to orchestrate different combinations of behavioral strategies and energy mobilization according to the type of perturbation the individual experiences. Particularly intriguing is the ability to customize the response not only to different LPFs (physical and social), but also integrate them with individual traits such as body condition, disease and social status. Next, we outline several very different examples of corticosterone integration of life history strategies that allow individuals to cope with unpredictability without becoming stressed.

The "leave it" strategy

It has long been known that severe weather and other LPFs result in abandonment of nests by birds (*e.g.*, Elkins, 1983). However, this abandonment occurs very quickly after onset of a severe LPF, *i.e.*, well before adults become debilitated trying to forage to feed growing young when trophic resources are declining ("leave-it" strategy). This strategy appears to be cease breeding immediately, despite young being present, and survive the LPF in the best condition possible so

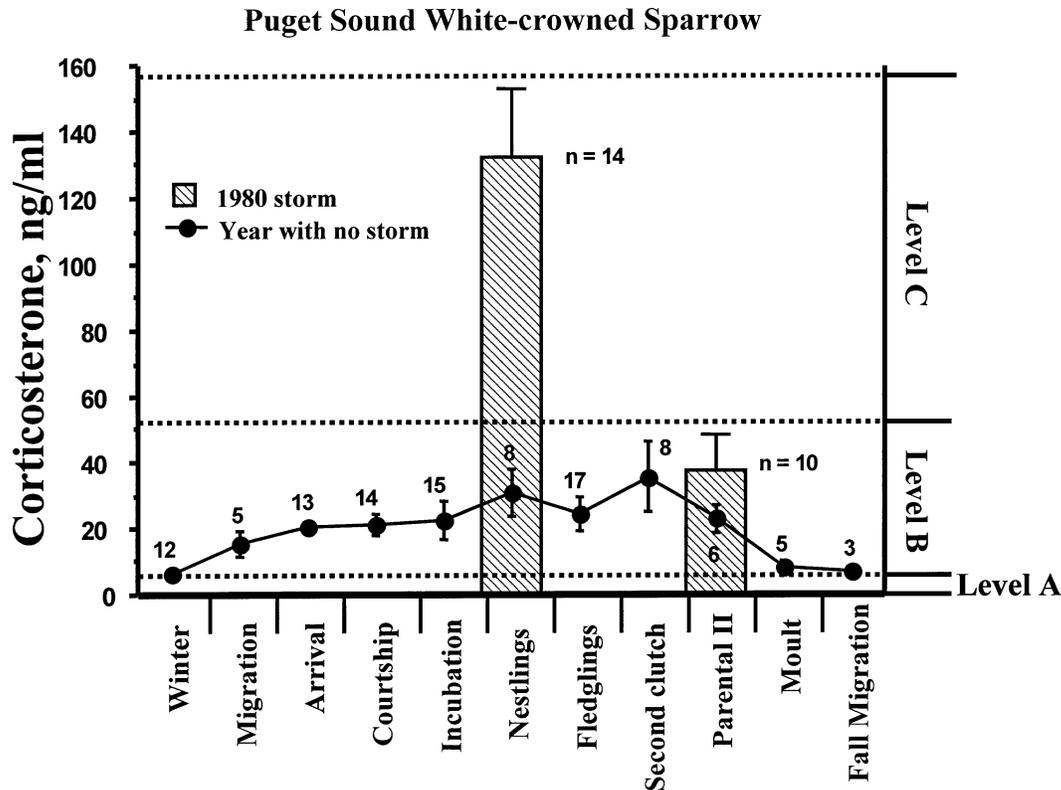


FIG. 3. An example of the effects of a labile perturbation factor (LPF in this case severe weather), in breeding male white-crowned sparrows, *Zonotrichia leucophrys pugetensis*. Changes in plasma levels of corticosterone are arranged in relation to stages and sub-stages in the life cycle (x axis). The circles connected by solid lines represent changes in corticosterone levels in the blood of males breeding normally (*i.e.*, levels A and B) and with no exposure to LPFs (*e.g.*, Wingfield and Farner, 1978). The vertical bars (cross hatched) represent plasma levels of corticosterone in a year (1980) when severe weather interrupted breeding resulting in males abandoning their nests and territories. At this time corticosterone levels (left hand bar) were significantly elevated and in the range of level C. Later in the season the weather ameliorated and these birds returned to their territories and re-nested. Note that by this time plasma levels of corticosterone returned to the range of level B (right hand bar). It is useful here to compare with Figure 4. In this figure, the different theoretical levels of secretion fit well with an actual response to an LPF. Redrawn from Wingfield *et al.* (1983).

that individuals can return to breeding and re-nest promptly after the LPF passes and trophic resources return to normal. In this way reproductive success may be maximized over the alternate strategy of feeding young despite declining resources and depleting energy stores of the parents (Wingfield *et al.*, 1983). However, this tactic is only likely to succeed if the breeding season is long enough and provides flexibility in timing so that re-nesting, or multiple broods, are possible.

Evidence from field studies shows that birds abandoning territories and nests have high levels of corticosterone in blood (Fig. 3, Wingfield *et al.*, 1983). Over the breeding season of white-crowned sparrows, *Zonotrichia leucophrys pugetensis*, there is an increase in plasma levels of corticosterone within level B (Fig. 3) that is associated with actual onset of nesting and feeding young. During a severe storm, however, circulating levels of corticosterone are much higher (level C) and birds abandon their territories and nests and range over a large area in loose flocks. Corticosterone titers return to level B once the LPF passes and birds are re-nesting (Fig. 3). Moreover, plasma levels of re-

productive hormones such as luteinizing hormone and testosterone are not affected. Thus, high concentrations of plasma corticosterone (level C) redirect these birds away from breeding but the reproductive system remains functional, just behaviorally suppressed. When the LPF subsides and corticosterone concentrations return to level B, re-nesting could begin immediately and is not delayed by a period of recrudescence that would have been necessary if the gonads had been suppressed and regression had occurred (Wingfield *et al.*, 1983).

Exactly how elevated corticosterone may trigger abandonment of the nest remains to be clarified. A role of CRF has been implicated because injection of this peptide into the third ventricle of *Z. l. gambelii* rapidly increases perch hopping activity in a dose dependent manner (Maney and Wingfield, 1998). Furthermore, non-invasive treatment of white-crowned sparrows with corticosterone (via ingestion of hormone-treated meal worms) results in a rapid increase in blood levels (within minutes) and an increase in activity (within 15 min, Breuner *et al.*, 1998). The loci of these behavioral actions and the receptors involved are currently under investigation.

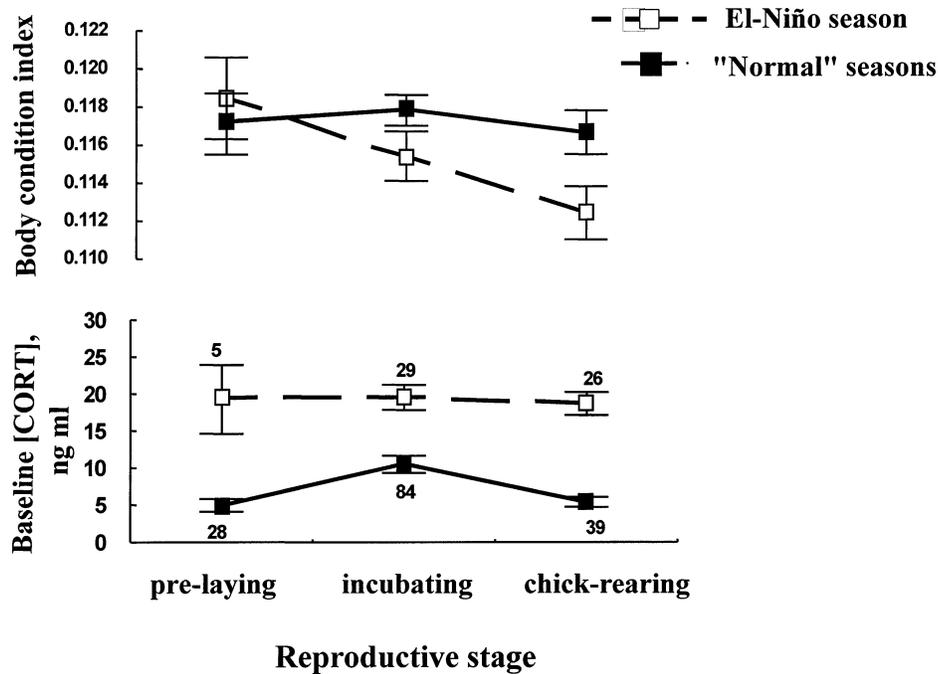


FIG. 4. Comparison of the seasonal dynamics of body fat reserves (calculated as body condition index, upper panel) and baseline levels of corticosterone (low panel) in breeding common murrelets, *Uria aalge*, between "normal" seasons and an El-Niño in the Low Cook Inlet, Alaska (A. S. Kitaysky *et al.*, unpublished).

Another example of LPFs redirecting birds away from breeding involves the effects of an El-Niño southern oscillation event of 1997–1998 that decreased abundance of food resources in the vicinity of breeding colonies of seabirds in the Lower Cook Inlet, Alaska (J. F. Piatt *et al.*, unpublished). Body fat reserves of common murrelets, *Uria aalge*, appear to be normal at the pre-egg laying stage of reproductive cycle, but deteriorated during the incubating and chick-rearing stages (Fig. 4). This decrease in body condition coincided with moderately elevated baseline levels of corticosterone (level B) and abandonment of eggs and young chicks (Fig. 4). The results of experimental manipulations with corticosterone in breeding common murrelets suggest that parents with elevated baseline corticosterone leave breeding colonies (A. S. Kitaysky *et al.*, unpublished). Thus, it is likely that food-shortages during the El-Niño of 1997–98 resulted in an increase in corticosterone secretion that directly caused the abandonment of eggs and young chicks by murrelets. Though increased baseline levels of corticosterone were detected in most of examined birds, a large variability in corticosterone secretion in response to acute stress was also detected. At the same time, not all murrelets abandoned their eggs and/or chicks. Furthermore, higher adrenocortical stress response was negatively correlated with current reproductive success. Finally, re-sighting data of breeding common murrelets at the same colonies during subsequent years show that parents that had higher adrenocortical responses to acute stress during the current reproductive attempt were more likely to reproduce at the same colonies in

the future than parents that had had lower stress response (A. S. Kitaysky *et al.*, unpublished). This example demonstrates that the elevation of baseline and acute stress-induced levels of corticosterone reflects current environmental conditions but by no means is a sign of physiological stress. Instead, the elevation of corticosterone secretion during food shortages is a part of the ELHs, that allows common murrelets to avoid stress. These results also provide a clue that under current conditions, choosing the most appropriate ELHs might be a product of on-going selection.

The "take-it" strategy

Not all individuals abandon the territory and adopt a leave-it strategy. Some may seek a refuge and ride out the LPF ("take-it" strategy, Wingfield and Ramenofsky, 1999). A "refuge" can be provided either by using a shelter (use of a micro-habitat) or by using an alternate set of "energy conserving" behavioral and physiological traits. For instance, during reproduction these traits will also depend on life-history stage. Thus juvenile traits are expected to be different from adults setting the stage for evolutionary interactions (*e.g.*, parent-offspring conflict), *e.g.*, in chicks, increases of begging and food delivery by parents, whereas in parents—accumulation of fat/protein reserves, brood reduction, decrease of chick-provisioning.

One form of refuge seeking is to go into torpor by decreasing body temperature. This has been studied in the rufous hummingbird, *Selasphorus rufus*, that enters nocturnal torpor to conserve energy in the face of environmental challenges, especially during spring mi-

gration when trophic resources may be particularly unpredictable. In this species, plasma levels of corticosterone rise in response to capture handling and restraint, and this rise is followed by an increase in urine (cloacal fluid) concentrations. Thus collection of cloacal fluid is a non-invasive way of measuring changes in corticosterone levels in these three gram birds (Hiebert *et al.*, 2000b). Corticosterone treatment via ingestion of cyclodextran in nectar resulted in hummingbirds going into torpor more frequently. However, although corticosterone levels rose in the evening regardless of whether the individual developed a torpid state, an additional factor is probably involved for regulation of this strategy (Hiebert *et al.*, 2000a).

Another form of the “take-it” strategy is to accumulate extra energy reserves in response to a LPF. Field observations have shown that during early stages of reproduction, black-legged kittiwakes, *Rissa tridactyla*, accumulate large fat deposits in response to a decline in food availability (Kitaysky *et al.*, 1999a). This accumulation of fat reserves was not associated with a change in baseline levels of corticosterone, that were still at level A. Interestingly, accumulation of fat reserves in response to food shortage was not found in kittiwakes raising young. Instead, a strong decline of fat reserves was observed, in parallel with an increase in baseline levels of corticosterone. However, elevated baseline levels were lower (*i.e.*, level B) than acute stress-induced levels of corticosterone (level C), suggesting that kittiwakes feeding young were not physiologically stressed but relied on stored energy reserves to fuel their activities.

At different LHSs birds are likely to be faced with different trade-offs and apparently might use different mechanisms allowing them to cope with the LPF. At early stages of the reproductive cycle, black-legged kittiwakes alternate long incubation shifts with long-duration foraging trips when they are able to accumulate large fat reserves to buffer declines in food availability. At the chick-rearing stage, kittiwakes have to commute frequently between foraging grounds and breeding colonies to feed their young. As a result, energy expenditure of chick-rearing kittiwakes increases during food shortages (Kitaysky *et al.*, 2000). This may preclude accumulation of extra fat reserves and parent kittiwakes partially rely on mobilization of stored energy reserves such as fat and proteins to fuel their increased activities (Kitaysky *et al.*, 1999a). Thus, moderate (level B) increases of baseline levels of corticosterone might represent yet another form of the “take-it” strategy—the mobilization of stored energy sources such as fat and proteins to ride out LPFs.

The “take it at first and then leave-it” strategy

Black-legged kittiwakes provide an example of an intriguing combination of ecological and physiological factors shaping emergency life history strategy. During prolonged food shortages breeding black-legged kittiwakes suppress their adrenocortical response to acute stress (Kitaysky *et al.*, 1999a). At early stages of re-

production, a suppressed stress response is associated with increased fat deposits and normal (at level A) baseline corticosterone. At the chick-rearing sub-stage, however, a suppressed stress response coincides with depleted energy reserves and an increased (level B) baseline corticosterone. These physiological changes during reproduction under poor foraging conditions are associated with changes in kittiwakes’ behavior. Specifically, in response to food shortages, parent kittiwakes allocate more time to foraging and less time to guarding/brooding their chicks (Kitaysky *et al.*, 2000). Recent experimental studies have shown that a moderate elevation (within level B) of baseline corticosterone directly causes this change in the resource allocation by parent kittiwakes (Kitaysky *et al.*, 2001). The change in resource allocation results in a considerable increase of the amount of time that kittiwake chicks are unattended by parents and usually those chicks succumb to predators. However, this loss of offspring during food shortages increases post-breeding survival of parent kittiwakes (Golet *et al.*, 1998). Thus, modulation of stress response by parent black-legged kittiwakes in response to LPFs is a part of the ELHS strategy that increases life-time fitness.

Black-legged kittiwakes with experimentally elevated levels of corticosterone increase foraging at the expense of brooding/guarding their chicks, but do not alter their chick provisioning rate and may suffer long-term effects of chronically-elevated levels of corticosterone as a result (Kitaysky *et al.*, 2001). The functional importance of the food-provisioning strategy of black-legged kittiwakes is not known. Several explanations seem possible. First, the food-provisioning strategy of parent black-legged kittiwakes maybe phylogenetically determined. Although pelagic-foraging kittiwakes rely on more variable food resources compared to their inshore foraging counterparts, chick-provisioning behavior of kittiwakes is still similar to that of other species of gull (*e.g.*, Harris, 1970; Henderson, 1975; reviewed in Ydenberg and Bertram, 1989). Second, kittiwake chicks are physiologically sensitive to variations in daily food intake and respond to moderate food shortages by a chronic elevation of corticosterone (Kitaysky *et al.*, 1999b). Timing of an increase in baseline levels of corticosterone (level B) in general reflects the point when energy demands of food-restricted chicks exceed their energy intake and a chronically elevated secretion of corticosterone (at dangerously high concentrations—level C) might persist over period of weeks (Kitaysky *et al.*, 1999b; Kitaysky *et al.*, 2001a). Chronic elevation of corticosterone during early development can have long-term deleterious effects (reviewed in Welberg and Seckl, 2001). Impaired physiological condition of black-legged kittiwake chicks under-nourished during early development might decrease their chances of survival. This would force their parents to provide food on chick demands. In fact, recent experimental studies have shown that high corticosterone levels increase chick begging rates and increase rates of food provisioning by parents (Ki-

TABLE 1. Corticosterone levels in relation to weather at Barrow, Alaska.

	Breeding		Molt	
	Baseline	Stress	Baseline	Stress
Lapland Longspur	No	Yes 37–39%	Yes 47–53%	Yes 41–73%
Snow Bunting	No	No	Yes 19%	Yes 25–30%
Common Redpoll	No	No	Yes 35–59%	Yes 36–60%

Figures represent percentage of the variation in corticosterone levels from breeding and molting passerines that could be explained by weather conditions 24 and 72 h preceding capture and sampling. From Romero *et al.*, 2000.

taysky *et al.*, 2001). Thus, the release of corticosterone in hungry kittiwake chicks represents an ELHS that allows them to restore depleted energy reserves by modifying the behavior of their parents and thereby avoiding nutritional stress.

Modulation of adrenocortical responses to LPFS

Facultative expression of behavior and physiology in an ELHS to combat LPFs is adaptive for many populations throughout their life cycle. However, there is growing evidence that the ELHS may not be adaptive in all cases. It has been postulated that birds breeding in severe environments in which the breeding season is brief may reduce the adrenocortical response to LPFs temporarily (Wingfield *et al.*, 1995, 1998). Indeed, several species of arctic birds breeding on the Alaskan tundra near Barrow (71°N) showed little or no correlation of baseline (*i.e.*, level B) and stress-induced (level C) corticosterone levels with snow storms accompanied by below freezing temperatures during the breeding season. After breeding had terminated, such storms resulted in a much stronger correlation with corticosterone concentrations in blood (Table 1; Romero *et al.*, 2000). It has also been shown that not only is the adrenocortical response to LPFs reduced in these birds, but the behavioral responses to experimentally implanted corticosterone levels (to mimic level C) were suppressed (Astheimer *et al.*, 2000). These data suggest that although behavioral insensitivity to elevated corticosterone levels develops, metabolic responses indicated by loss of protein in flight muscles are not affected. Thus in response to an LPF, energy can still be mobilized but the behavioral components of the ELHS that would redirect the individual away from breeding (resulting in zero reproductive success for that season) are turned off. Clearly, modulation of the stress responses and effects of corticosterone at level C indicate a high degree of integration of metabolic demands and behavioral strategies to maximize lifetime fitness.

If storms in spring and summer become severe enough and prolonged (*e.g.*, 3–4 days), then at least some species, *e.g.*, Lapland longspurs, *Calcarius lapponicus*, will eventually abandon the nest and upregulate their adrenocortical response to stress by almost

an order of magnitude (Astheimer *et al.*, 1995). In other words it appears that suppression of the adrenocortical response to LPFs is only adaptive up to a point. If the individual's life is threatened by severe weather and the potential for starvation, then it is highly unlikely that young could be raised to independence that season. Abandonment of the breeding attempt and a return of the HPA axis to normal would then make sense. The mechanisms by which the adrenocortical response to LPFs are suppressed and then reinstated are currently under investigation. Particularly intriguing are the mechanisms by which behavioral responses to high circulating levels of corticosterone are turned off while metabolic responses in the periphery remain intact.

The role of corticosterone in the resolution of parent-offspring conflict

The regulation of begging through secretion of corticosterone might represent an evolutionary stable signaling system as a resolution of parent-offspring conflict in birds. The results of field experiments suggest that parent kittiwakes assess the physiological condition of their chicks by monitoring begging and provide food on chick demands. Chicks given implants of corticosterone beg more than controls resulting in parents foraging to bring more food (Kitaysky *et al.*, 2001). In such a system, a chick can misrepresent its requirements in order to acquire more food than it needs (Godfray, 1995). Cheating might be prevented if there is a cost associated with begging that is larger than the benefits of the extra food obtained. If continuous begging is associated with a prolonged secretion of corticosterone, then a cheating chick would suffer detrimental effects of chronically elevated levels of corticosterone. Thus, exaggerated begging might be costly and a cheating chick may endanger its future survival. However, this conclusion hinges on the assumption that incessant begging requires continuous secretion of corticosterone. Recent experimental studies of black-legged and red-legged, *Rissa brevirostris*, kittiwake chicks confirmed this prediction. Baseline levels of corticosterone are significantly elevated in chicks of both species within 10 min of presenting them with a food stimulus to trigger begging. These data suggest strongly that the actual act of begging, or perhaps anticipation of food, do indeed elevate secretions of the HPA axis (A. S. Kitaysky *et al.*, unpublished).

CONCLUSIONS

One of the most critical functions within an individual's life cycle is to respond to unpredictable events in the environment with appropriate behavioral and physiological adjustments. These strategies must integrate management of energy balance in relation to body stores and food available, changes in the physical and social environment that determine access to food and other resources such as shelter, and then trigger individual behavioral responses that will minimize the cost in terms of survival and future potential to repro-

duce. The emergency life history stage (ELHS) is a suite of such facultative behavioral and physiological responses that provides great flexibility to combat the effects of LPFs at any time of year and within normal LHSs. Plasticity of the ELHS occurs at both the population and individual levels. Secretions of glucocorticosteroids above the normal baseline levels in relation to season and LHSs (level C) integrate these facultative responses, probably in conjunction with many other hormones and paracrine secretions within the brain. The result is a highly customized individual response to LPFs regardless of time of year, LHS, and individual state.

The facultative responses may be as diverse as torpor in the face of reduced food resources at specific times of year, abandonment of a territory and nest resulting in extended movements over a large area, or altered behavioral interactions between parents and offspring that may have profound implication for survival of adults and young. The cellular and molecular mechanisms underlying these specific responses tailored for individual circumstances present a major challenge for the future. Currently it appears that glucocorticosteroids provide an initial integrating signal, and interactions with other hormones and paracrine secretions may determine specific behavioral and physiological responses in different environmental and social contexts.

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