

Stress and Reproduction in Birds

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SUMMARY

There is intrinsic conflict between survival and reproduction. This conflict can be viewed from the perspective of the pace-of-life framework (an ultimate view), trading off many offspring per year over a short life against few offspring per year over a longer life; it can also be viewed from a resource-utilization perspective (a proximate view), increasing current reproductive effort vs. self-maintenance. The hypothalamic–pituitary–adrenal (HPA) axis controls the production of glucocorticoids (GCs) primarily responsible for mediating this proximate decision-making process. In field studies, GCs tend to decrease performance measures associated with reproduction, and increase measures associated with immediate survival. This chapter investigates the role of GCs in regulating reproductive effort (the proportion of available energy expended on reproduction—a proximate query), approaching this question from an ultimate pace-of-life framework.

1. INTRODUCTION

Animals face an intrinsic tradeoff between survival and reproduction. This tradeoff manifests both on ultimate (e.g. pace of life) and proximate (e.g. resource utilization) levels. From an ultimate or pace-of-life perspective, animals face tradeoffs between longevity and the number of offspring they produce, so that some animals produce few offspring over a long life and others produce many offspring over a shorter life. A proximate or resource-utilization view highlights the tradeoff in resource allocation; animals have a limited amount of resources that they must divide between self-maintenance and reproduction. Although the consequences of trading off survival and reproduction can be dampened when resources are not limited (as in high-quality individuals), the conflict between these two components of fitness is virtually ubiquitous. How is this conflict mediated within individuals? More specifically, what proximate physiological mechanisms translate external and internal cues into the decision-making process of reproductive effort?

Glucocorticoids (GCs) are primary candidates for mediating this decision-making process (Wingfield & Sapolsky, 2003). Glucocorticoids are normally maintained in the blood at relatively low levels that fluctuate on circadian and circannual cycles to regulate energy availability and use (Dallman et al., 1994). However, as the level of challenge increases, the hypothalamus upregulates the hormone cascade, resulting in further release of GCs from the adrenal gland into the plasma. Elevated GCs then act through receptors in target tissue to alter behavior and physiology in a variety of ways, including glucose mobilization through gluconeogenesis (Dallman, Darlington, Suemaru, Cascio, & Levin, 1989; Plaschke, Muller, & Hoyer, 1996), increased lipogenesis (Cherrington, 1999; Landys, Piersma, Ramenofsky, & Wingfield, 2004), and fat deposition (Dittami, Meran, Bairlein, Totzke, 2006; Yuan, Lin, Jiang, Jiao, & Song, 2008); reduction or abandonment of the reproductive effort (e.g., Silverin, 1986; Wingfield & Silverin, 1986; Love, Breuner, Vezina, & Williams, 2004); promotion of escape behavior (Breuner, Greenberg, & Wingfield, 1998; Wingfield et al., 1998; Breuner & Hahn, 2003); and increases in locomotor activity, foraging behavior, and food intake (see Landys, Ramenofsky, & Wingfield, 2006 for review). Altogether, elevated GCs are thought to appropriately redirect energy and behavior from noncritical energy expenditure (e.g., reproduction) towards self-maintenance, making them a good tool for the examination of tradeoffs between reproduction and survival.

1.1. Allostasis

Historically, the GC-driven stress response has been viewed as a response to unpredictable events, and distinct from the circadian rhythm in baseline GC levels (Wingfield et al., 1998). In the last five to ten years, McEwen and Wingfield (2003) have been promoting the movement away from 'stress' terminology towards the idea of allostasis, which they define as 'stability through change.' Generally, the argument behind allostasis rests on the concept that, as an animal faces challenge, there are homeostatic mechanisms

that regulate physiology and behavior to maintain homeostasis. Allostasis incorporates large and small challenges into this framework, so that basal homeostatic regulation and ‘responding to stress’ are put on a continuum instead of considered separately. Allostasis also incorporates the current state of the animal in defining the response, including large-scale differences such as breeding vs. wintering, as well as small-scale differences such as current parasite load.

This can be argued to be an elegant framework from which to evaluate GC physiology for two reasons. First, ‘stressors’ do not occur in a vacuum. One cannot expect that a decline in food availability will have similar physiological or behavioral outcomes whether an animal is feeding young or foraging in a flock. Accounting for the current state of the animal allows for greater refinement of predictions, and greater explanation for variation in response measured. Second, it is unclear whether a GC ‘stress response’ is a distinctly different beast from baseline changes in GCs. In field studies, we see incredible variation in what constitutes baseline (called ‘baseline’ and not basal because the GC axis is very rarely quiescent in free-living animals). We also see incredible variation in GC responses to challenge: presentation of a static predator has very little effect on GC secretion and presentation of a moving predator increases GC levels slightly (e.g., [Silverin, 1998](#)); food removal increases GC levels to about double baseline levels (e.g., [Lynn, Breuner, & Wingfield, 2003](#)); changes in weather can have very little effect ([Romero, Reed, & Wingfield, 2000](#)), intermediate activation ([Wingfield, Moore, & Farner, 1983](#)), or can maximally activate the hypothalamic–pituitary–adrenal (HPA) axis ([Smith, Wingfield, & Veit, 1994](#)). Which of these conditions represents ‘stress’? This semantic argument is avoided if one considers the response to challenges on a continuum, and not from a dichotomous viewpoint.

Three reviews postulate that baseline and stress-induced GC secretion are two entirely separate issues ([Romero, 2004](#); [Bókonyi et al., 2009](#); [Bonier, Martin, Moore, & Wingfield, in press](#)). This opinion is based on the fact that there are two GC receptors, high-affinity mineralocorticoid receptors (MRs) and low-affinity GC receptors (GRs). This author disagrees for several key reasons. First, as described above, hormone secretion in response to challenge varies continuously from slightly elevated to maximal HPA activation. Splitting baseline and stress-induced levels into two separate traits ignores much of the range of GC secretion. Second, while there are two separate intracellular receptors, separating GC secretion into two discrete traits is an unwarranted oversimplification. As GC levels rise above baseline, both MR and GR occupation increase. The inverted-U dose-response curve common to many GC-induced processes is explained through initial increases in GCs (above baseline) activating MR-driven processes, and

higher levels acting through GR, often having an opposite effect ([Hayden-Hixon & Ferris, 1991a](#); [1991b](#); [Diamond, Bennett, Fleshner, & Rose, 1992](#)). Hence, both MR and GR are active in driving processes regulated by elevated GCs. Lastly, MR cannot be considered independently of stress-induced levels of GCs, as it plays a major role in both tonic inhibition of GC levels (setting baseline and immediate GC reactivity to a stressor) and negative feedback on elevated levels of GCs after the stressor begins ([Dallman et al., 1987](#); [Sapolsky, Zolamorgan, & Squire, 1991](#)). Therefore, this author believes that it is important to consider baseline to stress-induced levels along a continuum, within the framework of allostasis.

1.2. Pace-of-life

This section discusses the role of GCs in regulating reproductive effort (the proportion of energy spent on reproduction). However, this proximate mechanism (GC secretion) will be shaped by life history (ultimate) differences among species. For example, GC responses should vary along a continuum, such that species with high survival rates and high residual reproductive value should pass the cost of a current stress challenge onto their offspring (they will respond to the stressor with elevated GCs and then reduce parental care), whereas species with low survival rates and therefore low residual reproductive value should take the cost of challenge on themselves (through suppression of GCs to maintain parental care) ([Ghalambor & Martin, 2001](#); [Martin, 2002](#)). Greater GC levels are thought to drive the reproduction/survival tradeoff towards survival, and so greater GC response should be associated with high survival and high residual reproductive value. This continuum is elegantly demonstrated through the ‘pace-of-life’ framework ([Ricklefs & Wikelski, 2002](#); [Martin, 2004](#); for discussion see [Hasselquist, 2007](#); [Martin, Weil, & Nelson, 2007](#); [Stutchbury & Morton, 2008](#); [Wiersma, Ro, & Williams, 2009](#)). This framework puts number of eggs per breeding season against survival probability for that species (see [Figure 5.1](#)). The ‘fast’-pace-of-life animals (those on the upper left of the continuum) have many offspring over a short lifespan, and so should optimize every reproductive opportunity, despite challenges experienced. The ‘slow’ species (those on the lower right of the continuum) have few offspring per year over a longer lifespan, and so should optimize self-maintenance and reduce reproductive effort in the face of challenge. This reiteration of the classic reproduction vs. survival tradeoff presents a valuable framework from which to formulate predictions regarding whether, during challenge, GCs will move an animal away from the current reproductive bout towards survival. For example, fast species from that clade should bear the cost of the challenge to ensure success of the

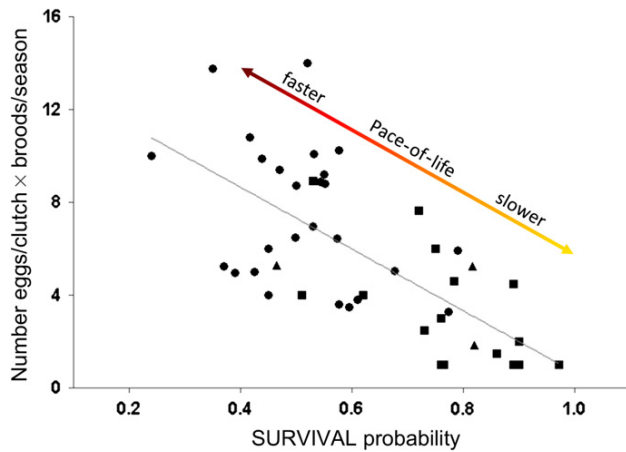


FIGURE 5.1 Pace-of-life framework for visualizing reproduction/survival tradeoffs. Each point is a single species. The group consists of 47 species for which we have data on corticosterone, survival probability, and number of eggs/breeding season. Circles, passerines; triangles, raptors, including two Strigiformes and one Accipitriformes; squares, 'other,' including Anseriformes, Charadriiformes, Procellariiformes, Sphenisciformes, Pelicaniformes, and Ciconiiformes.

current reproductive effort; hence, the slow species would be expected to suppress GC secretion. Alternatively, slow species within a clade should pass the cost of current challenge onto their offspring, and so would be expected to have a robust GC response to challenge, moving energy expenditure away from current reproduction towards self-maintenance.

Are GCs primary mediators of the tradeoff between avian reproduction and survival? Does increasing GCs during the reproductive life-history stage necessarily lead to a decline in reproductive success that season? This chapter approaches this question from a 'pace-of-life' viewpoint, to evaluate how the above relationships may differ between slow- and fast-pace-of-life species. This

chapter considers relationships between environment, GC physiology, reproductive output, and survival in birds.

1.3. Categorization of Glucocorticoid (GC) Studies

The field of comparative GC physiology has expanded rapidly since the early 1990s. An evaluation of those studies shows a straightforward categorization (Figure 5.2). The majority of papers evaluate physiological, behavioral, or environmental correlates of GC secretion, either examining baseline GC levels or GC response to capture and handling stress (Figure 5.2, light gray arrows). Other studies evaluate the relationship between endogenous or experimentally manipulated GCs and performance (Figure 5.2, dark gray arrow). Performance measures range from behavior (e.g., parental feeding rates, song production, territory defense) to immune function, and can be categorized as physiological, behavioral, or morphological changes resulting from altered GC level. The least common, but potentially most important, category evaluates the effect of GC level on direct fitness measures, such as reproductive output or survival (Figure 5.2, black arrow). A recent review highlighted the commonalities of studies within each category, noting the need for more direct fitness measures in studies of stress physiology (Breuner, Patterson, & Hahn, 2009). This chapter is structured using these categories, evaluating relationships from a pace-of-life perspective.

1.4. Pace-of-life and Brood Value

For the purposes of this chapter, approximately 120 references dealing with avian GC physiology were used to measure interactions with the internal/external environment (category one), intermediate performance

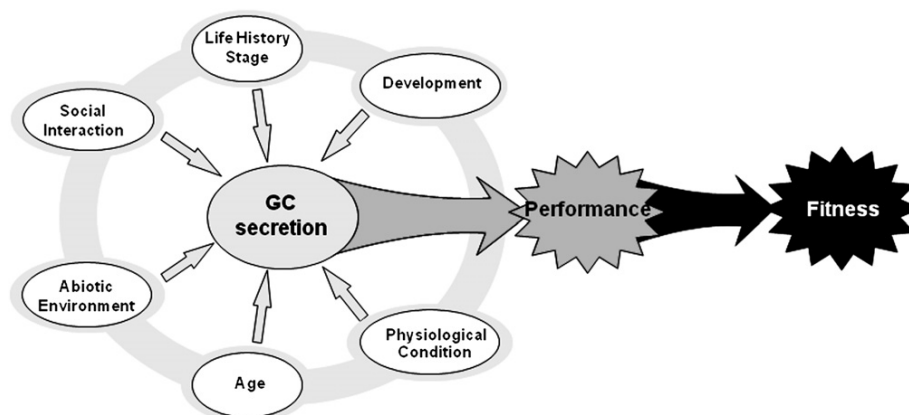


FIGURE 5.2 Framework illustrating the relationships between environment, glucocorticoid (GC) secretion, intermediate performance measures, and fitness.

(performance measures that do not measure reproductive output or survival; category two), and direct fitness measures (measures of reproductive output or survival; category three). Demographic information from each species was obtained in order to determine pace-of-life (Table 5.1): average clutch size, number of broods per season, and annual adult survival probability (preferably

calculated using MARK (a model estimating survival using mark-recapture data)) (White & Burnham, 1999). If there were multiple populations for which data were available, the population was chosen that was closest to the one for which GC data was available.

The pace-of-life framework offers a visualization of relationships among species (Figure 5.1). However, there is

TABLE 5.1 Demographic data for pace-of-life and brood value

Common name	Species	Clutch size	Broods per season	Total eggs per season	Survival probability ^a	Brood Value ^b	References
Adelie penguin	<i>Pygoscelis adeliae</i>	1	1	1	0.76	0.38	Jenouvrier et al. (2006)
American tree sparrow	<i>Spizella arborea</i>	4.96	1	4.96	0.39	0.79	Naugler (1993)
Barn owl	<i>Tyto alba</i>	5.28	1	5.28	0.465	0.73	Marti et al. (2005)
Barn swallow	<i>Hirundo rustica</i>	6.875	2	13.75	0.35	0.51	Brown and Brown (1999)
Black-browed albatross	<i>Thalasarche melanophris</i>	1	1	1	0.765	0.37	Nevoux et al. (2007)
Black-legged kittiwake	<i>Rissa tridactyla</i>	1.5	1	1.5	0.86	0.15	Saether (1989); Hatch et al. (2009)
Blue tit	<i>Cyanistes caeruleus</i>	10.8	1	10.8	0.416	0.77	Martin and Clobert (1996)
Blue-footed booby	<i>Sula nebouxii</i>	2	1	2	0.9	0.00	Nelson (2006)
Cactus wren	<i>Campylorhynchus brunneicapillus</i>	3.45	2.54	8.73	0.5	0.30	Proudfoot et al. (2000)
Cliff swallow	<i>Petrochelidon pyrrhonota</i>	3.5	1	3.5	0.595	0.61	Brown and Brown (1995; 1998)
Common eider	<i>Somateria mollissima</i>	4.5	1	4.5	0.89	0.04	Hanssen et al. (2003); Descamps et al. (2009)
Common murre	<i>Uria aalge</i>	1	1	1	0.89	0.04	Ainley et al. (2002); Lee et al. (2008)
Common redpoll	<i>Carduelis flammea</i>	5	1	5	0.425	0.76	Knox and Lowther (2000)
Common tern	<i>Sterna hirundo</i>	2.5	1	2.5	0.73	0.43	Saether (1989); Knox and Lowther (2000)
Curve-billed thrasher	<i>Toxostoma curvirostre</i>	2.7	2.2	5.94	0.79	-0.02	Twit (1996)
Dark-eyed junco	<i>Junco hyemalis</i>	4	1	4	0.45	0.74	Nolan et al. (2002)
Dusky flycatcher	<i>Empidonax oberholseri</i>	3.6	1	3.6	0.577	0.63	Pereyra and Wingfield (2003)
Eurasian tree sparrow	<i>Passer montanus</i>	4.95	2	9.9	0.439	0.45	Martin and Clobert (1996)
European blackbird	<i>Turdus merula</i>	4.04	2.5	10.1	0.531	0.27	Martin and Clobert (1996)
European starling	<i>Sturnus vulgaris</i>	4.71	2	9.42	0.47	0.42	Cabe (1993); Martin (1995)
Florida scrub-jay	<i>Aphelocoma coerulescens</i>	4.5	1	4.5	0.774	0.35	Martin (1995); Woolfenden and Fitzpatrick (1996); Mumme et al. (2000)

TABLE 5.1 Demographic data for pace-of-life and brood value—cont'd

Common name	Species	Clutch size	Broods per season	Total eggs per season	Survival probability ^a	Brood Value ^b	References
Greylag goose	<i>Anser anser</i>	6	1	6	0.75	0.40	Saether (1989)
Harris' hawk	<i>Parabuteo unicinctus</i>	3.5	1.5	5.25	0.817	0.09	Bednarz (1995)
Herring gull	<i>Larus argentatus</i>	3	1	3	0.76	0.38	Pierotti; Saether (1989)
House finch	<i>Carpodacus mexicanus</i>	4.4	2	8.8	0.552	0.35	Hill (1993); Martin (1995)
House sparrow	<i>Passer domesticus</i>	4.6	2	9.2	0.55	0.35	Martin and Clobert (1996)
Lapland longspur	<i>Calcarius lapponicus</i>	5.06	1	5.06	0.677	0.51	Custer and Pitelka (1977); Martin (1995)
Mallard	<i>Anas platyrhynchos</i>	8.91	1	8.91	0.53	0.67	Saether (1989); Krapu et al. (2004)
Mountain chickadee	<i>Poecile gambeli</i>	7	2	14	0.52	0.38	McCallum et al. (1999)
Northern pintail	<i>Anas acuta</i>	7.66	1	7.66	0.72	0.45	McCallum et al. (1999); Krapu et al. (2004)
Northern spotted owl	<i>Strix occidentalis caurina</i>	1.83	1	1.83	0.82	0.26	Gutierrez et al. (1995); Seamans and Gutierrez (2007)
Pied flycatcher	<i>Fidicula hypoleuca</i>	6.5	1	6.5	0.499	0.70	Martin and Clobert (1996)
Red-footed booby	<i>Sula sula</i>	1	1	1	0.9	0.00	Schreiber et al. (1996)
Red-winged blackbird	<i>Agelaius phoeniceus</i>	3.49	2	6.98	0.53	0.37	Martin (1995)
Semipalmated sandpiper	<i>Calidris pusilla</i>	4	1	4	0.62	0.58	Gratto-Trevor (1992); Rice et al. (2007)
Smith's longspur	<i>Calcarius pictus</i>	3.8	1	3.8	0.61	0.59	Briskie (2009)
Snow bunting	<i>Plectrophenax nivalis</i>	5.23	1	5.23	0.37	0.80	Lyon and Montgomerie (1995); Martin, (1995)
Snow petrel	<i>Pagadroma nivea</i>	1	1	1	0.9	0.00	Barbraud et al. (2000)
Song sparrow	<i>Melospiza melodia</i>	4.1	2.5	10.25	0.576	0.23	Arcese et al. (2002)
Wandering albatross	<i>Diomedea exulans</i>	1	1	1	0.972	−0.55	Weimerskirch (1992)
Western sandpipers	<i>Calidris mauri</i>	4	1	4	0.51	0.69	Wilson (1994); Fernandez et al. (2004)
White stork	<i>Ciconia ciconia</i>	4.6	1	4.6	0.784	0.33	Nevoux et al. (2008)
White-crowned sparrow	<i>Zonotrichia leucophrys pugetensis</i>	3.56	2.5	8.9	0.544	0.26	Martin (1995)
Willow warbler	<i>Pyhloscopus trochilus</i>	6	1	6	0.45	0.74	Peach et al. (1995)
Yellow warbler	<i>Dendroica petechia</i>	4.3	1.5	6.45	0.573	0.45	Martin (1995)
Yellow-eyed penguin	<i>Megadyptes antipodes</i>	1	1	1	0.9	0.00	Ratz et al. (2004)
Zebra finch	<i>Taeniopygia guttata</i>	5	2	10	0.24	0.58	Zann and Runciman (1994)

^aAnnual survival probability of adults.^bBrood value = $\log_{10}(\text{clutch size} \times (\text{clutch size} \times \text{broods per year} \times (1/1 - \text{adult survival probability}))) + 1$.

no absolute value associated with each point, to enable numerical comparisons between species. [Bókonyi et al. \(2009\)](#) used the demographic data to calculate a 'brood value' for the current brood:

$$\log_{10}(\text{clutch size}/(\text{clutch size} \times \text{broods per year} \times \text{average reproductive lifespan}))$$

where reproductive lifespan represents the inverse of adult mortality probability ($1/1$ -adult survival probability). This calculation represents the value of current reproductive output relative to the lifetime reproductive output of a species. The majority of values resulting from this calculation range from -1 and 0 , which can be confusing to assess. To simplify evaluation of brood value, $+1$ has been added to each value so that the numbers range from $0-1$. Higher brood values are found in species where the current brood represents a larger proportion of the total number of young produced in a lifetime. Hence, the fast-pace-of-life individuals (upper left in [Figure 5.1](#)) would have higher brood values and slow-pace-of-life individuals (lower right in [Figure 5.1](#)) would have lower brood values.

2. REGULATION OF GLUCOCORTICOID (GC) SECRETION

This chapter asks how stress affects reproduction, or, how the GC response to stress mediates the allocation of resources between current and future reproductive events. As such, one would expect this chapter to focus solely on how GCs regulate reproductive function. However, the majority of literature on stress and reproduction concerns factors explaining variation in GC secretion. The authors of these papers approach this topic with a view to understanding how GCs will affect reproductive output, but ties to actual performance or fitness measures used are few. None-the-less, after 30 years of study, several strongly supported hypotheses elucidating how external (e.g., environment/social) and internal (e.g., body condition/immune status) factors affect GC reactivity, and, therefore, how animals will respond to stressors under varied conditions, have emerged. This section (1) briefly reviews how GC levels relate to annual seasonality, length of breeding season, and body condition and (2) goes further in depth on how GC levels change within the breeding cycle, especially in relation to parental care and pace-of-life differences.

The discussion of these studies rests on the assumption that greater hormone levels measured during challenge will reflect greater change in physiology and behavior. This primary assumption drives the fitness expectations discussed in most of the 'regulation of secretion' studies. There is evidence to support this assumption. For example,

corticosterone (CORT) contained within silastic tubing and implanted into pied flycatchers reduced parental visits to the nest, while CORT implants with a hole punched in the side of the tubing caused nest desertion ([Silverin, 1986](#)). However, several studies in both birds and rats have demonstrated significant changes downstream of total CORT secretion in terms of binding globulins, intracellular degradatory enzymes, and receptor number ([Dhabhar, McEwen, & Spencer, 1993](#); [Spencer et al., 1996](#); [Breuner et al., 2003](#); [Love et al., 2004](#)). A study evaluating nest abandonment rates within 12 hours of sampling determined that free (unbound to corticosteroid-binding globulin (CBG)) CORT levels predict female starling nest abandonment, whereas total CORT does not ([Lakshmi, Sakai, McEwen, & Monder, 1991](#); [Love et al., 2004](#)). Unfortunately it is exceedingly difficult to obtain measures of these downstream regulators, especially at the tissue level.

The 'greater hormone = greater output' hypothesis rests solidly on the assumption that hormone-behavior dose-response curves are linear or monotonic in nature. There is very little evidence for this, and in fact overwhelming evidence exists for alternative dose-response curves, such as inverted-U-shaped or threshold-dependent curves ([Hayden-Hixon & Ferris 1991a; 1991b](#); [Diamond et al., 1992](#); [Breuner & Wingfield, 2000](#)). Hence, we expect total plasma hormone levels to offer an estimate of organismal effects during challenge, but one that lacks the fine-tuning of downstream regulators or consideration of a nonlinear dose-response curve.

2.1. Parental Care and Within-breeding-season Regulation

How does brood value affect the GC response to stress? [Bókonyi et al. \(2009\)](#) reviewed the relationship between parental care and brood value across 64 species, incorporating data from 104 studies. Based on the brood value hypothesis, they predicted that (1) GC reactivity should be lower in species with a higher brood value and (2) sex-biased investment in parental care should be inversely related to sex differences in GC levels. They found that baseline CORT levels were strongly positively associated with brood value, while maximal CORT levels (corrected for changes in baseline and breeding latitude) were negatively associated with brood value ([Figure 5.3](#)). This author interprets this to mean that, when brood value is high, baseline levels are upregulated, allowing for greater flexibility in energy expenditure ([Sapolsky, Romero, & Munck, 2000](#); [Romero, 2002](#)). Therefore, stress reactivity is suppressed, decreasing the likelihood of lower feeding rates or nest abandonment. The relationship shown in [Figure 5.3](#) may be dependent on three data points, two from extremely long-lived sea birds (upper left) and one from a species that shows an incredibly small increase in

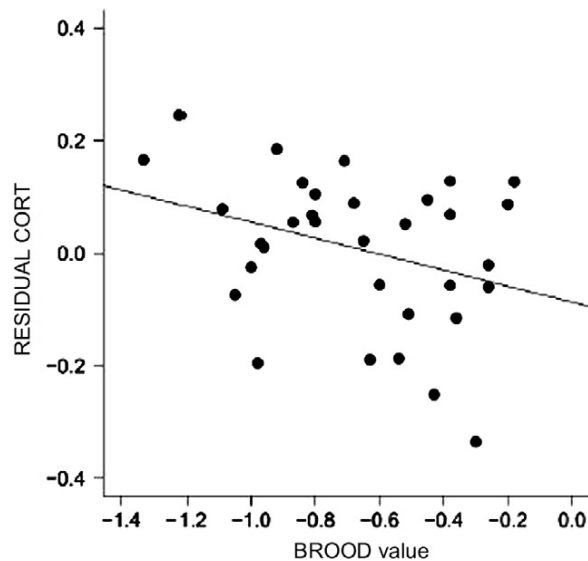


FIGURE 5.3 Regression of brood value against maximal corticosterone (CORT) levels corrected for variation in baseline CORT and latitude of population. Brood values reported here are all one unit lower than brood values in this chapter, as they were not corrected upward for ease of evaluation. Reproduced from Bókonyi et al. (2009), with permission.

stress-induced CORT (~10% increase to maximal stress levels). However, these data reflect patterns seen in several smaller studies, where expected brood value correlates with GC secretion. The first is described in detail in Section 2.3 (Breuner & Hahn, 2003), where three subspecies with different amounts of time to breed, and therefore a different brood value for each individual clutch, show a direct relationship between number of clutches and stress-induced free CORT (unbound to CBG). Specifically, as estimated clutch value increases

(fewer clutches per season), maximal CORT levels decrease. This relationship shows up repeatedly in latitudinal studies, where populations further north, with higher expected brood value, show suppression of the stress response (Silverin, Arvidsson, & Wingfield, 1997; Silverin & Wingfield, 1998; O'Reilly & Wingfield, 2001; Wilson & Holberton, 2004; however, see Section 2.3; Martin, Gilliam, Han, Lee, & Wikelski, 2005; Goymann et al., 2006).

According to Bókonyi et al. (2009), sex-biased investment relates to maximal CORT levels in females. Specifically, as relative investment of male care increases, female maximal CORT levels increase but male CORT levels are unaffected. Hence, when females are responsible for the majority of care, they suppress CORT levels, increasing the likelihood of brood survival. Alternatively, when care is equal or primarily male-driven, female maximal levels rise, allowing the female to invest in self-maintenance. This effect in females is illustrated well by a study on several species of shorebird (O'Reilly & Wingfield, 2001) that exhibit three mating systems representing three different strategies for parental care: the polygamous pectoral sandpiper (*Calidris fulicaria*), the monogamous semipalmated sandpiper (*Calidris pusilla*), and the polyandrous red phalarope (*Calidris fulicaria*). The authors predicted—as did Bókonyi et al. (2009)—that the sex responsible for the majority of parental care would suppress GC reactivity during incubation and nestling phases. Their predictions were supported, as GC response is suppressed in female pectoral sandpipers, equal in male and female semipalmated sandpipers, and suppressed in male red phalaropes (Figure 5.4).

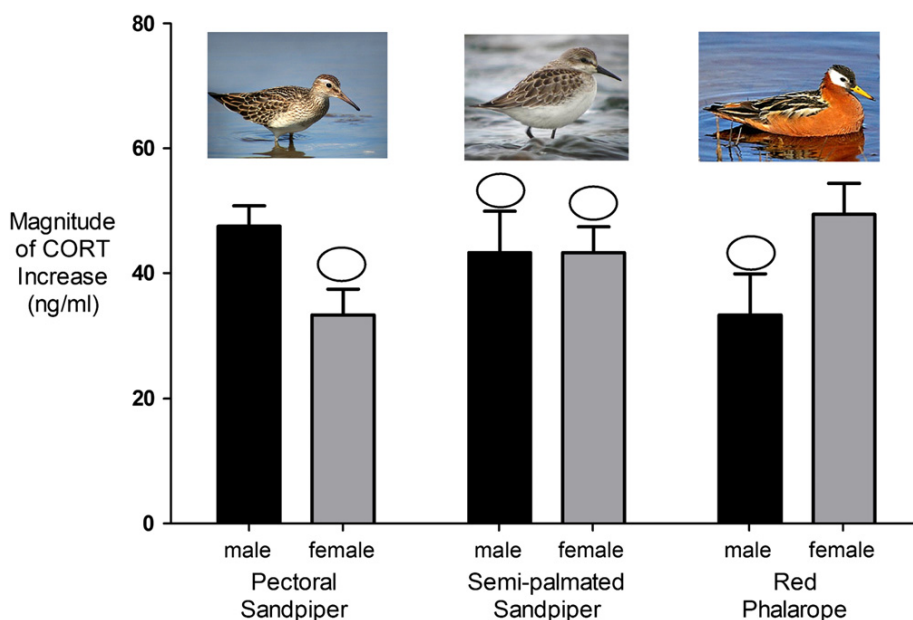


FIGURE 5.4 Three species of shorebird, each with different roles for males and females in raising the young. In the polygynous pectoral sandpiper (*Calidris melanotos*), the female raises the brood; in the monogamous semipalmated sandpiper (*Calidris pusilla*), parental care is shared; in the polyandrous red phalarope (*Phalaropus fulicaria*), the male raises the brood (parental care denoted by egg above bar). Stress-induced corticosterone secretion is inversely related to the load of parental care in each species. Redrawn from O'Reilly and Wingfield (2001), with permission. See color plate section.

2.2. Annual Regulation of Glucocorticoids (GCs)

Most seasonal species regulate GC secretion over the annual cycle. Romero (2002) reviewed baseline and stress-induced CORT levels across seasons, comparing prebreeding, breeding, and postbreeding data (the last was often represented by winter sampling). In birds (29 separate studies, 14 species), baseline CORT is upregulated during breeding compared to winter, whereas stress-induced CORT is static over the cycle except for a marked decline during molt. On average the species show no change in the GC response to stress, but that average is a result of eight species that increase GC response during breeding compared to winter, 13 species that decrease, and one that does not change.

However, evaluation of these data from a pace-of-life perspective does not produce clear patterns. Based on the slow-to-fast continuum, we would expect that fast birds, taking the cost of challenge on themselves, would show a reduced response to stress during breeding (as compared to winter, when brood value is not a selective factor), whereas slow birds, passing the cost of challenge onto their offspring, would have equal or greater response to stress between breeding and winter. This author estimated brood values for most of the bird species reviewed by Romero (2002) (where data were available), also including 17 studies completed since 2002. All studies evaluated stress-induced GC levels during breeding and winter in a species for which clutch size, number of broods per season, and annual survival probability were known. This analysis ended up with 30 studies represented by only 11 species (Wingfield, Vleck, & Moore, 1992; Wingfield, Suydam, & Hunt, 1994; Astheimer, Buttemer, & Wingfield, 1995; Breuner & Orchinik, 2001; O'Reilly & Wingfield, 2001; Lindstrom, Hawley, Davis, & Wikelski, 2005; Romero, Cyr, & Romero, 2006; Lynn & Porter, 2008; Rubenstein, Parlow, Hutch, & Martin, 2008; Fokidis & Deviche, 2009; Newman & Soma, 2009). These data show no relationship between brood value and seasonal fluctuations of the GC response to stress. In fact, the data are completely overlapping (species with lower GCs during breeding have a brood value of 0.29 ± 0.08 ; species with higher or equal GCs during breeding have a brood value of 0.33 ± 0.04 ; brood values averaged across species from Table 5.1). To rigorously explore the relationship between brood value and seasonal change in GCs, one would need many more species represented—enough to perform a phylogenetic comparison of results. At present, those studies are not available.

2.3. 'Latitudinal' Regulation of Glucocorticoids (GCs)

In the temperate and subtropical zones, there is an inverse relationship between latitude and time available to breed.

With less time to produce young (less opportunity for a second brood), each brood becomes more valuable. Hence, stress-induced GCs may be differentially regulated across species or populations with similar lifespans that breed at different latitudes, with higher GC secretion expected in populations at lower latitudes and lower GC secretion expected in populations at higher latitudes. However, the relationship between latitude and GCs is complicated by elevation and hemisphere differences. First, elevation complicates the relationship because higher elevation shortens available breeding time independently of latitude. As an extreme example, Eurasian woodcocks (*Scolopax rusticola*) breeding in the Himalayas (31°N; up to 3500 m elevation) will have a much shorter breeding season than Eurasian woodcocks breeding further north, around the Mediterranean (36°N; sea level). Second, climate changes more slowly through the southern latitudes than it does through the Northern latitudes. Therefore, a 7° shift north in the northern hemisphere (e.g., O'Reilly & Wingfield, 2001) will have a much more dramatic effect on the length of the breeding season than a similar shift in the southern hemisphere. For these reasons, it is best to avoid a scale of absolute latitude; one way towards that is to simply use the number of broods possible. In passerines and other short-lived species, number of broods represents the length of the breeding season, which is the relevant factor, independent of latitude, altitude, or hemisphere.

Five subspecies of white-crowned sparrows (*Zonotrichia leucophrys*) breed from above the arctic circle down to southern California. Breuner et al. (2003) determined GC responses to stress in three separate populations, representing three of the five subspecies. The *Z. l. gambelii* population, breeding north of the Brooks Range (68°N; 720 m elevation) is severely limited in the amount of time in which to raise a clutch, and is therefore obligatorily single-brooded. *Z. l. oriantha*, breeding in the high Sierras (38°N; 2940 m), is somewhat less limited and may have years where two full broods are possible. *Z. l. pugetensis*, breeding in the Puget Sound area (47°N; 275 m), can raise up to three broods per season (Chilton, Baker, Barrentine, & Cunningham, 1995). Breuner et al. (2003) collected baseline and stress-induced GCs from males during the nesting period in all three populations, comparing total and free GC levels. The expectation was that stress-induced GC levels would be highest in the *Z. l. pugetensis* population (with a lower brood value) and lowest in the *Z. l. gambelii* population (with the highest brood value). Surprisingly, total stress-induced GC levels were similar among the three populations; however, binding-globulin affinity and capacity changed, so that estimations of free GC levels were highest in *Z. l. pugetensis*, intermediate in *Z. l. oriantha*, and lowest in *Z. l. gambelii*. Hence, the level of free stress-induced GCs is inversely correlated with the length of the current breeding effort (Figure 5.5). In this

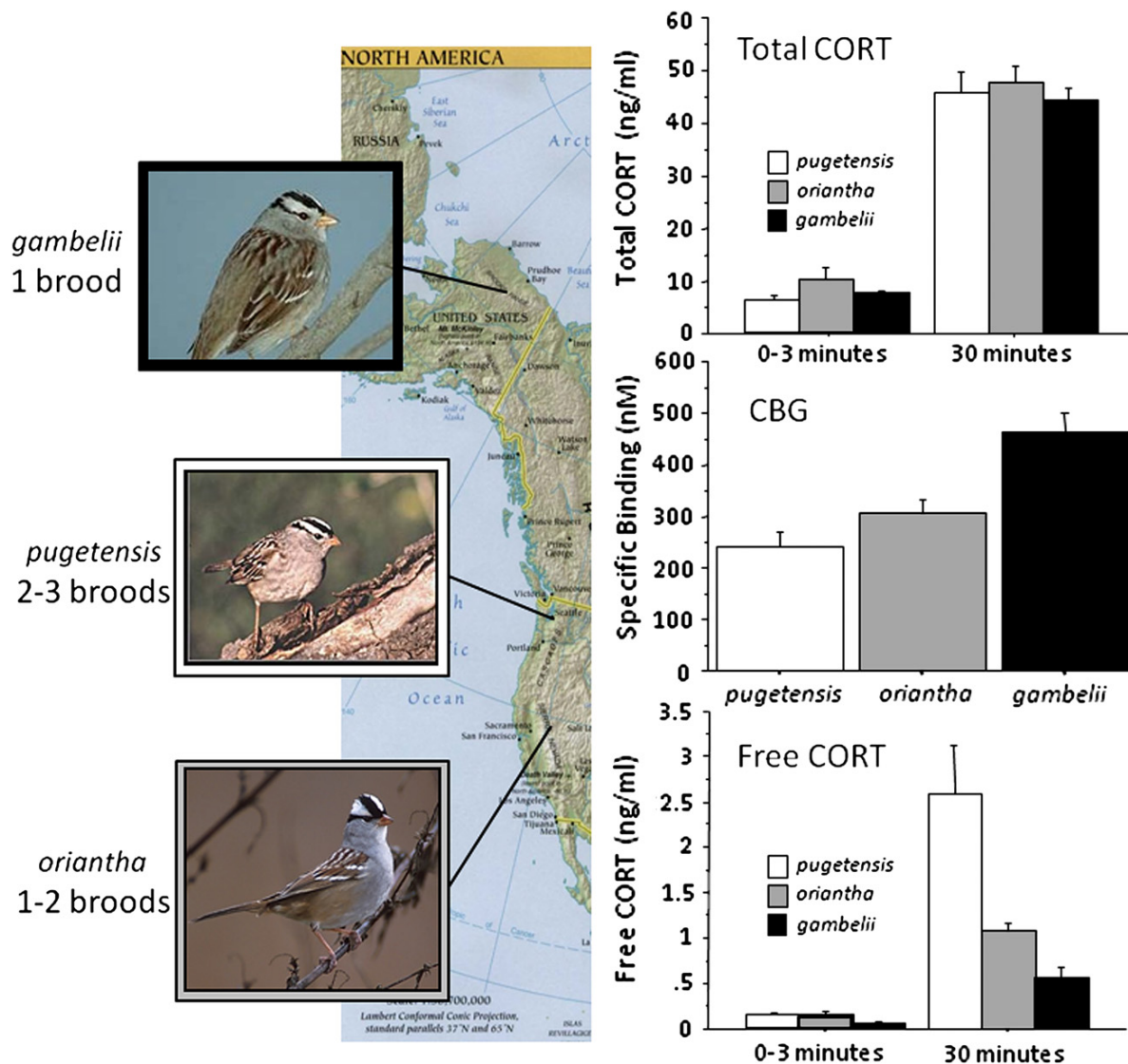


FIGURE 5.5 Population location and total corticosterone (CORT), corticosterone-binding globulin (CBG), and free CORT levels in three populations of white-crowned sparrows with varied amounts of time to breed. Blue, *Zonotrichia leucophrys gambelii*; green, *Zonotrichia leucophrys pugetensis*; black, *Zonotrichia leucophrys oriantha*. Redrawn from Breuner et al. (2003), with permission. See color plate section.

study, by using brood number instead of latitude, the relationship between GCs and each reproductive attempt could be evaluated more clearly.

A review of the studies published on latitude over the last 10 years provides marginal support for the effects of latitude on GC reactivity. Across 10 passerines and two seabirds, six species show suppressed GC reactivity at more northern latitudes, three show no difference, and two show higher GC reactivity in the north (Wingfield, Kubokawa, Ishida, Ishii, & Wada, 1995; Silverin et al., 1997; O'Reilly & Wingfield, 2001; Wilson & Holberton, 2004; Lindstrom et al., 2005; Martin et al., 2005; Goymann et al., 2006). However, one of these two counterexamples is from male bush warblers (*Cettia diphone*), the only polygynous

species represented; if a male is not involved in parental care, one would not expect a suppression of GC reactivity—see above. In contrast to this, Bókony et al. (2009) found the opposite pattern when the latitude of each population of 64 species was added as a covariate in the analysis. Surprisingly, GC reactivity was directly related to latitude, and so increased as one moved away from the equator; Akaike's Information Criterion identified latitude as the prominent explanatory variable in determining elevated GC levels. Can this be explained by difference in scale? Most of the studies on individual species are carried out over a 7–15° change, usually within one climate zone (though see Breuner et al., 2003; Goymann et al., 2006). The Bókony study covers a range of species from –66 to 82°N,

with a fairly good representation of tropical populations. It is possible that the small differences in elevated GCs measured over short distances are overwhelmed by large-scale hormonal differences due to tropical vs. temperate habitat; hormone patterns are often less dynamic in the tropics (Hau, Gill, & Goymann, 2008). To clarify this, it would be helpful to use length of breeding season instead of latitude, in order to avoid confounding elevation and hemisphere, to determine whether the pattern persists.

2.4. Body Condition and Glucocorticoids (GCs)

Glucocorticoid reactivity is often inversely related to body condition. Greater energetic reserves during challenge are thought to lessen the volume of GCs released, since the animal can often wait out whatever challenge occurs and move on to find more resources once the challenge has passed. Animals with fewer endogenous reserves secrete more GCs during a challenge, and so are more likely to redirect behavior away from the current reproductive effort towards survival. For example, low food availability in an income breeder (fueling reproduction from available food in the environment) may cause an increase in GC levels. Animals in good condition may only have a slight increase in GCs, and therefore spend less time feeding young and more time searching for food. In contrast, animals in poor condition may have a larger GC increase, inducing nest abandonment to ensure energy availability for the parent.

However, there is incredible variation in the relationship between energetic reserves and GC elevation, with many studies showing no relationship at all. The pace-of-life hypothesis would predict that fast species would keep GC levels low, despite low body condition, to enable continuation of the current brood. Alternatively, slow species would be expected to vary GC elevation according to body condition, so that self-maintenance is prioritized over current reproduction. In terms of brood value, we then expect that animals with high brood value (high relative value of the current brood) would suppress the GC response, in spite of low energetic reserves, while animals with low brood value would allow for GC response to vary inversely with body condition. Of the 17 avian studies that include measures of body condition and GC reactivity during the breeding season, only 12 of them are in species with survival data (Wingfield et al., 1994; Schoech et al., 1997; Wingfield, Ramos-Fernandez, La Mora, & Drummond, 1999; Pravosudov, Kitaysky, Wingfield, & Clayton, 2001; Breuner & Hahn, 2003; Pereyra & Wingfield, 2003; Lindstrom et al., 2005; Moe, Angelier, Bech, & Chastel, 2007; Muller et al., 2007). Surprisingly, the results are exactly opposite to those predicted. Species with low brood value sort into the group that does not modulate GCs with

body condition, while species with high brood value do modulate GCs inversely to body condition (mean brood values: 0.18 ± 0.09 vs. 0.54 ± 0.07 , respectively). Certainly, this relationship is complicated by the dichotomous strategies represented by income vs. capital breeders. Capital breeders fuel reproduction from endogenous stores, and so go through predictable fasts with radical change in body condition. If we remove the capital breeders from the relationship (leaving 10 species, all passerines), any directional relationship disappears, and species that vary GC secretion with body condition have similar brood values to those that do not.

In the world of avian endocrinology, lower body condition is thought to be bad, while higher body condition is thought to be good. So, the greater the energetic reserves, the better. This is incredibly oversimplified. As body mass increases in a given skeletal size, it can significantly hamper maneuverability, increasing the risk of predation. In many bird species, chicks grow to be larger than adults and must lose weight to fledge. In both of these situations, lighter is better. Walsberg (2003) published a commentary on the use of energetics in stress physiology. His main point revolves around energy balance as only a small representation of what an animal may need, ignoring a wealth of other resources necessary for survival. He also argues that 'energy balance' is a temporally variable thing, wherein animals have periodic energy intake but constant power output. Hence, the timing of 'balance' will vary given the size and metabolic rate of the animal. Altogether, Walsberg argues for less attention to be spent on body condition and energy balance, as the saliency of the measure is not clear for the field of stress physiology.

3. INTERMEDIATE PERFORMANCE MEASURES

In the evaluation of stress effects on reproduction, most measures fall short of direct fitness measures (e.g., nestling success or integration into the reproductive population in the next season). The majority of studies focus on intermediate measures of performance; i.e., measures that are expected to enhance or restrict reproductive success. This section covers morphological, physiological, and behavioral examples of intermediate performance measures that are known or thought to influence reproductive success.

3.1. Morphology

Male morphological characteristics are thought to play an important role in female mate choice; hence, sexually selected characteristic development can have significant repercussions for reproductive success (Ferns & Lang,

2003). Stressors have long been known to affect feather quality (King & Murphy, 1984; Murphy, King, & Lu, 1988), and recent experimental evidence has supported this finding. In male barn owls (*Tyto alba*), CORT implants reduced the level of pheomelanin (yellow to red coloration) of feathers growing while the implant was in place (Roulin et al., 2008). In white-crowned sparrows (*Z. leucophrys*), GC implants slowed individual feather growth (Romero, Storchlic, & Wingfield, 2005), while repeated acute bursts of GCs delayed the onset of molt (Busch, Sperry, Wingfield, & Boyd, 2008). In European starlings (*S. vulgaris*), GC implants slowed individual feather growth rate (Romero et al., 2005) and decreased feather quality, reducing coloration and increasing interbarb distance (DesRochers et al., 2009).

There is also evidence for GCs reducing other sexually selected morphological traits in birds. In barn swallows, lower GC levels are associated with longer tails, a trait that is under current directional selection in this species (Saino, Incagli, Martinelli, Moller, 2002). In selected lines of the zebra finch (*Taeniopygia guttata*), males selected for higher GC reactivity had lower ultraviolet (UV) reflectance in both legs and cheek patches (Roberts, Buchanan, Hasselquist, Bennett, & Evans, 2007). Both structures are thought to be signals used by females to ascertain male quality.

3.2. Physiology

3.2.1. Body composition

Glucocorticoids were named for their hyperglycemic properties. Gluconeogenesis is one pathway through which GCs increase blood glucose. Prolonged elevation of GCs reduces energetic stores across the body. In fasting mammals, elevated GCs reduce both muscle and fat. However, when elevated GCs are accompanied by nutrient intake, so that insulin and GCs are elevated at the same time, the nutrients are preferentially deposited as fat (Dallman et al., 1993), resulting in low muscle mass but incredibly high fat stores. This situation is similar in birds (Figure 5.6). Prolonged and repeated intermittent GC application results in a decline in muscle mass (Gray, Yarian, & Ramenofsky, 1990; Astheimer, Buttemer, & Wingfield, 2000; Bauchinger & Biebach, 2001; Busch et al., 2008), while GC implants increase fat stores in free-living birds (Wingfield & Silverin, 1986; Wingfield, 1988; Gray et al., 1990). However, a recent study in captive white-crowned sparrows (*Z. leucophrys*) showed no change in fat scores with repeated transient GC application compared to control birds (Busch et al., 2008). This may be because either (1) captive birds are already so overfed that further increase in fat level is difficult to detect or (2) repeated

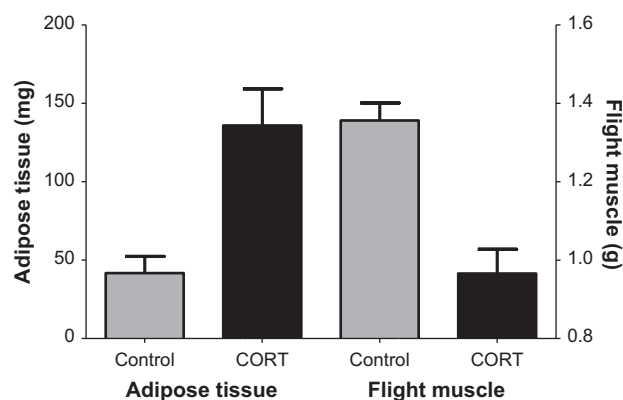


FIGURE 5.6 The change in adipose tissue and flight muscle after prolonged corticosterone (CORT) treatment in male dark-eyed juncos (*Junco hyemalis*). Reproduced from Gray, Yarian, and Ramenofsky (1990), with permission.

elevation does not raise GC levels high enough to increase fat load.

Three recent captive studies show an overall loss of body mass in response to elevated GCs or chronic stress (El-Lethey, Huber-Eicher, & Jungi, 2003; Martin et al., 2005; Rich & Romero, 2005). However, this pattern does not hold for animals with endogenously higher GC response. Zebra finches selected for greater GC reactivity had the highest body mass index measured from all three groups (selected high, control, selected low) (Roberts et al., 2007a).

3.2.2. Immune function

The interaction of immune function and stress physiology is currently one of the most exciting areas in environmental endocrinology. With the onset of ecoimmunology, studies into relationships between hormones and immune function have proliferated (Martin, 2009). These studies have primarily focused on the immunosuppressive effects of GCs, which are interpreted as either (1) a brake on immune function in order to prevent autoimmune disease (Munck, Guyre, & Holbrook, 1984; Raberg, Grahn, Hasselquist, & Svensson, 1998; Sapolsky et al., 2000) or (2) a tradeoff of energy mobilization, such that costly behaviors during reproduction, or a shift in energy utilization during stress, cannot coexist with immune activity (Folstad & Carter, 1992; Lochmiller & Deerenberg, 2000; Martin et al., 2007). However, it is misleading to characterize GCs as solely immunosuppressive. In the mammalian literature, the enhancing vs. suppressive effects of GCs depend on the time frame of reference as well as the specific arm of the immune system (reviewed by Martin, 2009).

The vertebrate immune system has both innate and adaptive arms, and each arm has humoral and cellular components. The innate arm is a rapid general defense

against pathogens. It is composed of many cell types, such as macrophages, granulocytes, and natural killer cells. These cells fight infection directly and also secrete substances to fight pathogens extracellularly, such as complement, antimicrobial peptides, and destructive enzymes. The adaptive arm consists of the cells and antibodies generated to fight specific antigens of invading cells or organisms. The adaptive arm requires upregulation of helper T cells, killer T cells, or antibody-producing B cells specific to the pathogen present; mobilization of this arm of the immune system takes longer, but the arm is more potent once fully activated. At the base of the adaptive arm are helper T cells, which release cytokines to activate either the cellular or humoral components of the adaptive arm. Additionally, differential activation within the adaptive or the innate arm can subsequently alter the activation of the other arm. Hence, the vertebrate immune system is incredibly complex, with tradeoffs within and between arms. As a result, the strongest tests of GC-immune interactions assess multiple arms of the immune system, and illuminate possible tradeoffs between activation and suppression of cellular and humoral components in the innate and adaptive arms.

Although studies of GC-immune interactions have been most common in mammals (because of their obvious medical applications), we can draw on this vast literature to direct our appraisal of GC-immune studies in birds. Two poignant examples of GC-immune interactions from mammalian systems highlight this application. First, it has long been apparent that stress causes a decline in the cellular component of the adaptive arm, measured as a decline in leukocytes in the blood (up to 50% loss within two hours of stress). However, [Dhabhar and McEwen \(1997\)](#) reviewed mammalian studies demonstrating a *redistribution* of leukocytes to the skin, as opposed to an overall loss. In fact, the inflammatory response in the skin increased when accompanied by moderate stress, and almost doubled when accompanied by severe stress. This enhancement of the cell-mediated inflammatory response (regulated through Th1 helper cells) is time-sensitive. Two hours of restraint or shaking stress enhanced the inflammatory response, while three weeks of chronic stress reduced the same response ([Dhabhar & McEwen, 1997](#)). The second example focuses on the GC-induced tradeoff between the humoral and cell-mediated components of the adaptive arm. Over extended time periods (days to weeks), GCs inhibit the activity of mammalian Th1 cells and enhance the activity of Th2 cells, thereby suppressing the cell-mediated response while enhancing the humoral (antibody) response (see [Elenkov, 2004](#) for review). Both of these examples illustrate that variation in GC effect is dependent on the time course and branch of immune response measured; they also support the need for a robust experimental approach when studying GC-immune interactions.

These studies, however, can be extremely difficult to carry out in free-living birds, especially the adaptive studies that require the investigator to repeatedly capture the same animal. As a result, the majority of avian studies in this area have associated GC treatment with one specific component of the immune system, such as measuring the secondary antibody response (adaptive/humoral), bactericidal activity (complement), or wing-web swelling (adaptive/cellular when given in a two-injection treatment). With only one component tested, it is difficult to truly assess tradeoffs within the immune system and to discern whether GC effects on the immune system are total or isolated to one specific component. Additionally, the bird immune system is not identical to the mammalian system, which limits our ability to extrapolate from mammalian systems. Birds lack lymph nodes (a key site of upregulation of the adaptive immune response), and they have a different set of inflammatory cytokines and different types of white blood cells (see [Kaiser & Staheli, 2008](#) for a helpful review).

Despite these limitations, a good number of avian studies address GC interaction with both cellular and humoral components of the immune system. The most in-depth studies have been done in chickens (*Gallus domesticus*). [S. Shini, Kaiser, A. Shini, and Bryden \(2008\)](#) demonstrated the temporal divergence of GC action on humoral immune function. Experimentally increased GC initially enhanced primary antibody response (after one hour) but decreased the response to below that of controls after three and 24 hours ([Figure 5.7](#)). Glucocorticoid increase also resulted in a decrease in immune tissue weight. In free-living birds, the results are much more

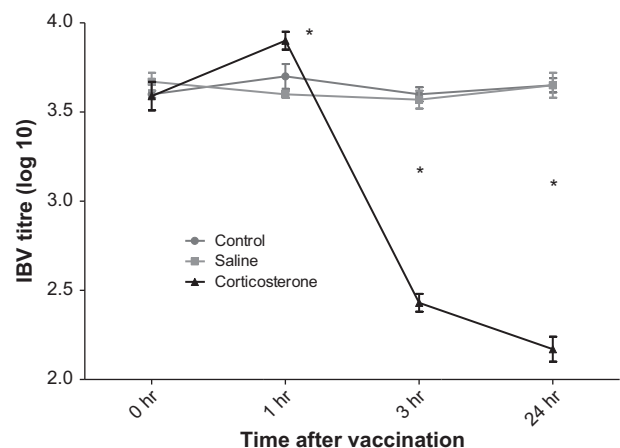


FIGURE 5.7 Primary antibody response to infectious bronchitis virus (IBV) vaccine in chickens given control (1 ml ethanol in 1 L) or corticosterone (20 µg in 1 ml ethanol in 1 L water) water to drink over 10 days before blood was drawn for assay. The saline group received plain water to drink and a saline injection on day one as a control for a different experiment. Redrawn from [S. Shini, Kaiser, A. Shini, and Bryden \(2008\)](#), with permission.

variable. Study of general immunity in house finches (*Carpodacus mexicanus*) showed that birds with higher maximal CORT in response to capture and handling are more likely to contract mycoplasma infection (Lindstrom et al., 2005). In fasting, incubating common eiders (*Somateria mollissima*), CORT implant reduced general immunoglobulin levels compared to control implanted females (Bourgeon & Raclot, 2006). Cutaneous immunity was measured in zebra finches (*T. guttata*) by injecting a foreign antigen—e.g., phytohemagglutinin (PHA)—into the wing web and quantifying swelling 24 hours later. In individuals selected for greater GC reactivity, there was no line effect on PHA response, but endogenous stress-induced CORT levels were directly related to PHA response (greater GC levels indicate greater response) (Roberts et al., 2007a; Roberts, Buchanan, Hasselquist, Evans, 2007). In north temperate house sparrows (*Passer domesticus*), CORT implants reduced the PHA response, but there was no effect in tropical house sparrows (Martin et al., 2005). There was no effect of CORT implants on the PHA response in barn swallows (*Hirundo rustica*) (Saino et al., 2002) or in fasting common eiders (*S. mollissima*) (Bourgeon & Raclot, 2006). In zebra finches, stress-induced CORT levels were positively related with secondary antibody response against diphtheria, but negatively related to primary antibody response to tetanus (among individuals, not among selected lines; Roberts et al., 2007a; 2007b). In white-laying hens (*Gallus gallus domesticus*), GC treatment reduced the primary antibody response to both sheep red blood cells and tetanus toxoid, but not to human serum albumin (all three injected into hens eight days before primary antibody sampling) (El-Lethey et al., 2003).

Taken together, it is difficult to synthesize any overall effects of GCs on immune system function in birds. Based on mammalian studies, we expect extended GC application to enhance humoral immune function, but the evidence supports this in some species (e.g., zebra finches) and not in others (e.g., laying hens). In contrast, GC application should inhibit cell-mediated immune function, but, once again, support for this is equivocal. Additionally, a common immune test (PHA injection) in mammals is supposed to measure cell-mediated immunity, but in birds the tests all measure 24-hour responses to initial PHA injection, not the 24-hour response to the second PHA injection 8–12 days after the first. Hence PHA data do not truly measure a full cell-mediated adaptive immune response and so we cannot apply these measures to our expectations as outlined by mammalian studies. The way forward may lie in testing multiple aspects of immune function (innate, adaptive with humoral, and cell-mediated) within one species. Roberts et al. (2007a; 2007b) have obtained the most complete look at immune function in zebra finches. However, these

results are based on selected lines, not direct GC application, so the results are all correlational.

While the results presented above are mixed, it is clear that GCs can have significant effects on immune function. This interaction is thought to have driven the evolution of CBGs, enabling delivery of GCs directly to sites of immune activity (Pemberton, Stein, Pepys, Potter, & Carrell, 1988). Corticosteroid-binding globulin is a glycoprotein present in the plasma with high affinity for GCs. It is thought to limit access of GCs to tissues, in that only free GCs can cross capillaries and enter tissues (Hammond, 1995; Breuner & Orchinik, 2002; Malisch & Breuner, 2010). This prevents approximately 95% of circulating GCs from accessing tissues and, hence, effecting a change in immune function. However, mammalian CBG is a member of the serine protease superfamily; this family of proteins is cleaved by elastase secreted by activated neutrophils. Hence, at sites of inflammation, CBG can be cleaved, resulting in a local increase in free CORT from 5 to 100% of total CORT in the plasma. If avian CBG is also a member of this family, immune activation could be highly regulated by CBG in the plasma.

3.3. Behavior

3.3.1. Singing and territorial behavior

Several studies link GCs to reduced song performance. Greater CORT secretion as adults is correlated with lower song rates (Owen-Ashley, Turner, Hahn, & Wingfield, 2006; Wada et al., 2008), and food restriction (known to increase endogenous CORT levels (Lynn et al., 2003)) reduces undirected song in zebra finches by 67% (Johnson & Rashotte, 2002). Additionally, developmental nutritional stress is associated with poor song performance as adults. While CORT levels were not measured in these studies, nutritional stress increases endogenous CORT levels in several species (Kitaysky, Piatt, Wingfield, & Romano, 1999; Kitaysky, Kitaiskaia, Wingfield, & Piatt, 2001; Kitaysky, Romano, Piatt, Wingfield, & Kikuchi, 2005). As a result of early nutritional stress, there is a reduction in song repertoire (Nowicki, Searcy, & Peters, 2002; Spencer, Buchanan, Goldsmith, & Catchpole, 2004), number of song bouts, length of song bouts, and total time spent singing (Buchanan, Spencer, Goldsmith, & Catchpole, 2003). One song performance study experimentally increased CORT during development, resulting in a decrease in song complexity in adults (Spencer et al., 2004), similar to the results found with nutritional stress described above.

Wingfield and Silverin (1986) examined GC effects on aggressive responses to simulated territorial intrusion (STI), which is a standardized method for obtaining unbiased measures of territorial behavior. Only three of the ten CORT-implanted males responded to STI at all; those three

spent less time within 5 m, took fewer flights over the decoy, and sang fewer songs as compared to control males.

Surprisingly, this study has only been replicated and published three times, all within arctic passerines. As described above, arctic breeding seasons are necessarily shorter, limiting the number of broods a species can have. In fact, all three species studied (white-crowned sparrow (*Z. leucophrys*), Lapland longspur (*Calcarius lapponicus*), and tree sparrow (*Spizella arborea*)) are obligatorily single brooded when breeding in the arctic. Hence, the brood value of each individual brood should be higher for the three arctic populations as compared to the temperate song sparrow. Of the three, the Lapland longspur and the tree sparrow male responses to STI are insensitive to CORT (Astheimer et al., 2000; Meddle, Owen-Ashley, Richardson, & Wingfield, 2003). This indicates that the current brood is of high enough value that males have evolved behavioral insensitivity to CORT, making it less likely that they will abandon the current brood if circumstances deteriorate. Surprisingly, white-crowned sparrows are sensitive to CORT implant and show a reduction of aggressive behavior in response to STI when CORT is present (Meddle et al., 2002).

From a pace-of-life perspective, we would expect calculated brood values for temperate song sparrows to be lower than those for Lapland longspurs and American tree sparrows because the latter two species have repressed their response to CORT during breeding. Brood values fall out as expected: song sparrow with the lowest at 0.23 and longspurs and tree sparrows higher at 0.59 and 0.79, respectively (see Table 5.1). In this case, brood value does predict behavioral response to CORT, in that two species with little time to breed, and thus high brood value, repress their response to stress and take the cost of stressors onto themselves (instead of passing it onto their young).

3.3.2. Foraging/feeding young

Elevated GCs are thought to increase self-maintenance behavior at the cost of parental care. For example, parents may increase foraging without increasing food delivery to the young. This increase in foraging time usually results in a reduction of time spent with the young, which is especially important for altricial chicks before they reach thermoregulation. Subsets of this paradigm have been demonstrated in several studies. Chronic and transient CORT administration increases both foraging and food intake measures (Saldanha, Schlinger, & Clayton, 2000; Koch, Wingfield, & Buntin, 2002; Lohmus, Sundstrom, & Moore, 2006; Angelier, Clement-Chastel, Gabrielsen, & Chas, 2007). Higher endogenous CORT is linked to greater time spent away from the nest and greater weight gain while feeding young (Angelier et al., 2007a; Angelier, Shaffer, Weimerskirch, Trouve, & Chastel, 2007; Lendvai

& Chastel, 2008). Corticosterone implants increase time spent away from the young (Silverin, 1986; Kitaysky, Wingfield, & Piatt, 2001). Lastly, elevated CORT (endogenous or experimental) is associated with a reduction in chick feeding rate (Silverin, 1986; Almasi, Roulin, Jenni-Eiermann, & Jenni, 2008).

A few recent studies have, however, challenged the idea that CORT reduces offspring feeding rate. In common murre (*Uria aalge*) and Adelie penguins (*Pygoscelis adeliae*), elevated endogenous CORT levels are associated with behaviors that should benefit the young. First, common murre usually time breeding with the spawning period of capelin fish, matching food availability to the increased food requirement of their young. However, one year there was a mismatch, and the young hatched before the capelin spawned. As expected, average CORT levels were elevated in all of the parents that year; however, the birds who provisioned their young at higher rates were the individuals with higher endogenous CORT levels (Doody, Wilhelm, McKay, Walsh, & Storey, 2008). In Adelie penguins, preforaging CORT levels were compared to distance travelled. Individuals with higher pretrip CORT levels spent less time at sea, remained closer to the colony, and had lower mass gain over the trip (Angelier et al., 2008). These trip characteristics are usually associated with short trips made to feed young at the expense of self-maintenance (Weimerskirch et al., 2003). Both of these examples indicate that elevated CORT may be associated with an increase in provisioning to the young, and have led to the formation of a new hypothesis on the relationship between CORT, foraging, and provisioning: under ideal conditions, parents can forage and feed their young as required; however, slight elevations in CORT levels may initially increase parental feeding behavior, whether through mobilization of greater energy stores to meet costs of foraging, increasing nest attentiveness, or some undescribed pathway. This suggests that moderately elevated CORT may be a necessary and inherent part of reproduction (Angelier et al., 2008). However, when endogenous CORT levels are greatly elevated above baseline (as is the case for most of the implant studies mentioned above), foraging behavior will become more directed towards self-maintenance, at the cost of food delivery to the young.

4. DIRECT FITNESS METRICS

How does stress affect reproduction? Thus far, this chapter has covered the regulation of CORT secretion and the effect of CORT on intermediate performance measures, but has not directly addressed the effect of CORT on reproductive output. As stated throughout this chapter, CORT is thought to redirect physiology and behavior away from reproductive activities and toward self-maintenance, mediating the tradeoff intrinsic to limited budgets of energy and time.

If this idea is true, then elevated CORT should be associated with diminished reproductive output.

Bonier, Moore, Martin, and Robertson (2009) have addressed reproductive/survival issues with the CORT–fitness hypothesis. This hypothesis states that increased CORT will result in a decline in fitness, independently of whether that fitness metric is reproductive output or survival. Their argument stems from the concept that, when comparing two populations, the one facing challenge will have lower reproductive success or survival than the one under ideal conditions. This author agrees with this argument (which is supported by several avian studies — see Section 4.1), but feels that it oversimplifies CORT–fitness interactions by neglecting the tradeoff between allocation of resources towards current vs. future reproduction. Within the CORT–fitness hypothesis, there is no room for brood value, no consideration of tradeoffs, and no room for exploring selection for CORT reactivity as it modulates differential expression of physiology and behavior in individuals under similar conditions.

The CORT–fitness hypothesis was not well supported by previous work, possibly because variation among and within species is too great (Bonier et al., 2009). However, the example Bonier et al. use of the effect of CORT on reproduction and survival in side-blotched lizards (*Uta stansburiana*) (Lancaster, Hazard, Clobert, & Sinervo, 2008) actually supports the focus of this chapter: the utility of brood value. In side-blotched lizards, yellow slow-pace-of-life females have fewer larger young, while orange fast-pace-of-life females have many small young. Exogenous CORT elevation increases reproduction and decreases survival in orange females, while having the opposite effect in yellow females. This study is useful for a number of reasons. First, unlike most fitness studies, it measures *both* reproduction and survival, so it is possible to directly measure the tradeoff. Second, it demonstrates that alternative reproductive strategies (different brood values) show different sensitivity to CORT elevation, indicating the need for inclusion of brood value in further analyses.

4.1. Reproduction

The majority of studies evaluating the effects of GCs on reproduction do so at a population level, evaluating correlations between reproductive success in one population facing a more challenging environment against reproductive success in a population not facing that challenge. It is important to realize that reproduction *and* survival will be reduced in the face of challenge, compared to an ‘ideal’ stress-free population. Instead of population comparisons, we need within-population investigations evaluating fitness parameters across individuals that react to challenges with different CORT–behavior–physiology output.

We can, however, gain some initial insights from these population-level studies. The relationship between CORT and reproductive output between populations suggests that increased endogenous CORT predicts lower reproductive success (Wingfield et al., 1999; Scheuerlein, Van’t Hof, & Gwinner, 2001; Saino, Romano, Ferrari, Martinelli, & Moller, 2005; Ellenberg, Setiawan, Cree, Houston, & Seddon, 2007; Muller et al., 2007; Williams, Kitaysky, Kettle, & Buck, 2008). Further, experimentally increased CORT (implant) reduces breeding success in terms of number of young fledged, number of unhatched eggs, and nest abandonment (Silverin, 1986; 1998; Criscuolo et al., 2005; Almasi et al., 2008; Angelier & Chastel, 2009). Four other studies showed no relationship between endogenous CORT level and reproductive output (Beletsky, Orians, & Wingfield, 1992; Wingfield et al., 1999; Evans, Roberts, Buchanan, & Goldsmith, 2006; Almasi et al., 2008). In an interesting study, Cyr and Romero (2007) applied random, continuous acute stressors to female free-living starlings (*Sturnus vulgaris*). This treatment reduced CORT around 24 hours after completion of the last acute stressor; mothers experiencing chronic stress fledged fewer young compared to animals not receiving the treatment. Hence, it appears in this situation that a lower CORT level is associated with a loss of reproductive output. However, it is entirely possible that CORT levels were elevated during and immediately after the acute stressors were applied, but that the repeated elevation of the HPA axis downregulated overall CORT secretion, leading to lower CORT levels when measured the next day. Although we cannot evaluate overall CORT levels from this study, it does demonstrate that chronic stress lowers reproductive output in free-living starlings.

Over the last two years, the number of within-population studies assessing CORT–fitness relationships has increased significantly. Higher levels of endogenous CORT within a population predict lower reproductive success in six species (Love et al., 2004; Angelier, Weimerskirch, Dano, & Chastel, 2007; Bonier et al., 2007a; Bonier, Martin, & Wingfield, 2007b; Kitaysky, Piatt, & Wingfield, 2007). In one study, endogenous CORT levels predicted laying success, but not hatching or fledging success (Lancot, Hatch, Gill, & Eens, 2003), and in another study higher endogenous CORT levels predicted lower fledging success if elevated CORT was observed early in the breeding season, but higher fledging success if elevation occurred later in the season (Bonier et al., 2009).

4.2. Survival

Avian studies evaluating CORT relationship to survival in adults are still rare. In a declining colony of common murre (*U. aalge*), increased CORT level correlated with negative population growth, although this relationship was not

present in a growing colony (Kitaysky et al., 2007). In one colony of cliff swallows (*Petrochelidon pyrrhonota*), early CORT levels predicted lower survival rates to the next year (C. Brown, M. Brown, Raouf, Smith, & Wingfield, 2005).

4.3. Tradeoffs?

To properly evaluate the adaptive significance of CORT effects on fitness, one needs to evaluate the effect on both reproduction and survival. A decline in reproductive output in one year is only adaptive if it increases survival probability to the next year. This tradeoff is elegantly illustrated in a study by Love and Williams (2008). In European starlings (*S. vulgaris*), greater CORT levels in mothers are associated with lower reproductive output but higher survival to the next year; however, the relationship is fairly

complex. Mothers in poor body condition have elevated CORT levels. When this level of CORT is injected into eggs, the resulting brood has a higher proportion of females, and the males grow at a slower rate than control males. To test whether this type of brood benefits the mother in poor condition, Love and Williams produced four groups of European starlings: control mothers with control broods, control mothers with CORT-treated broods (fewer and smaller males), 'poor-condition' mothers (wing feathers clipped to reduce foraging ability) with control broods, and 'poor-condition' mothers with CORT-treated broods. The salient comparison here is the survival rates of mothers in poor condition with and without CORT-treated broods. The wing clipping reduced the ability of mothers to feed their young. However, the broods with CORT treatment required less food, and so matched the ability of the

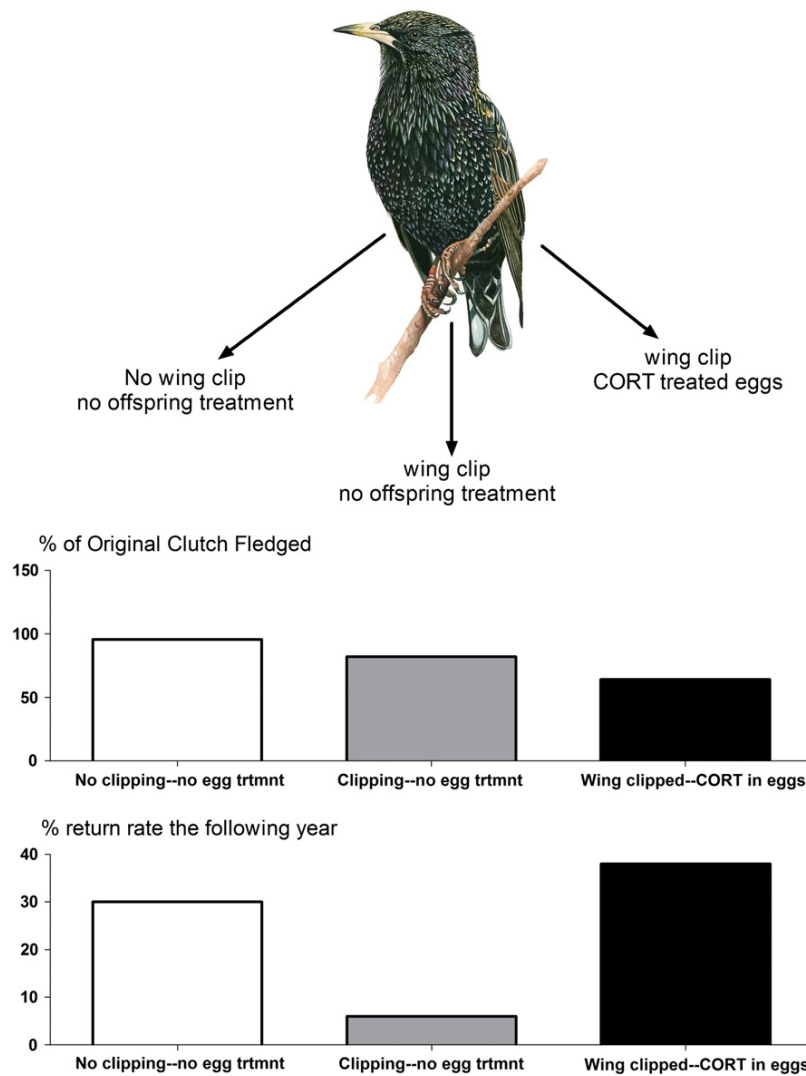


FIGURE 5.8 Matching clutch need to maternal ability: if a poor-condition mother (wing-clipped) produces a poor condition brood (corticosterone (CORT)-treated), she will raise fewer young that year (upper graph) but increase her survival probability 10-fold over poor-condition mothers raising a full brood (lower graph). Redrawn from Love and Williams (2008), with permission. See color plate section.

wing-clipped mothers. The reproductive output was lower for all poor-condition mothers, but survival to the next year was higher in those mothers whose brood matched their ability. That is, if a poor-condition mother produces a poor-condition brood, she will raise fewer young that year but increases her survival probability 10-fold over poor-condition mothers raising a full brood (Figure 5.8).

5. SUMMARY

How does stress affect reproduction in birds? We know that higher brood value predicts lower GC response, but does not predict seasonality of that response, and it appears that GC–latitude relationships vary by scale of enquiry (Section 2). There is strong evidence for a negative relationship between GCs and sexually selected traits (feather quality, song, and territorial defense); GCs may enhance attendance of young at low levels but suppress it at higher concentrations, and GC-immune interactions can depend on timing, arm of the immune system, species, and season (Section 3). Finally, populations with elevated GCs tend to have lower reproductive output and lower survival, but within-population studies produce much more complicated results (Section 4).

To truly evaluate the role of GCs in allocating resources between reproduction and survival, we need more studies directly evaluating reproduction and survival within a population. At present, there are very few studies measuring CORT–survival interactions in adult birds. Further, while there are more studies evaluating CORT–reproduction interactions, the majority look between populations, demonstrating that a population facing challenge (stress) will have lower fitness than a population ‘without’ challenge. Additionally, the majority of studies are correlative, offering much less power to determine what effect is due to CORT elevation and what may simply be a byproduct of individual quality or a nonadaptive association. Only one study to date has evaluated the tradeoff between reproduction and survival to assess the adaptive benefit of the CORT effect, and found that the decline in reproductive output resulting from elevated CORT did indeed increase survival to the next breeding opportunity (Love and Williams, 2008, Figure 5.8).

We have come a long way from measuring hormone–environment interactions, to directly assessing CORT–fitness measures. However, there is a long way to go before we can fully support any directional effect of stress on reproduction.

ABBREVIATIONS

CBG	Corticosteroid-binding globulin
CORT	Corticosterone
GC	Glucocorticoid
GR	Glucocorticoid receptor

HPA	Hypothalamic–pituitary–adrenal
MR	Mineralocorticoid receptor
PHA	Phytohemagglutinin
STI	Simulated territorial intrusion
Th1	T-helper cells-1
Th2	T-helper cells-2
UV	Ultraviolet

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