



Glucocorticoid hormone levels increase with group size and parasite load in cliff swallows

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Animals often cope with adverse events by releasing glucocorticoid hormones, which in turn promote increased energy assimilation. In captive animals, crowding also leads to increased glucocorticoid activity, probably because of increased levels of social competition. We investigated how group size and ectoparasite infestations affected endogenous levels of the glucocorticoid hormone, corticosterone, in colonial cliff swallows, *Petrochelidon pyrrhonota*, in southwestern Nebraska, U.S.A. Parasites were removed from some colonies by fumigating nests. Baseline levels of corticosterone in breeding adults varied significantly with whether parasites were present, colony size (measured by total number of active nests at a site) and nesting stage. Across all analyses, birds from fumigated colonies averaged significantly lower baseline levels of corticosterone. These levels in adults increased with colony size at nonfumigated sites, especially during the period when nestlings were being fed, but no relation or the opposite one was found for birds in fumigated colonies. Baseline corticosterone levels were unrelated to sex, age, body weight or testosterone levels in adults. Corticosterone concentrations tended to increase during a bad-weather event when food was scarce. Patterns in nestling and recently fledged juveniles were consistent with those in adults. The increased baseline levels of corticosterone in birds of larger colonies appear related to the larger number of parasites there. Higher levels of corticosterone probably facilitate increased allocation of time and energy to foraging and greater energy assimilation during challenging events such as bad weather, parasitism by blood-feeding bugs in large colonies and the period when young are becoming independent of their parents.

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One way that animals cope with challenging events in their environment is through activation of the hypothalamic–pituitary–adrenal axis, typically resulting in the release of glucocorticoid hormones. In free-living animals, high levels of these hormones are often associated with adverse events, such as severe weather that restricts food supply, exposure to deleterious parasites or pathogens or increased likelihood of encountering a predator (Wingfield et al. 1983, 1994b, 1995; Dunlap & Schall 1995; Romero et al. 2000; Romero 2002). The short-term benefits of increased glucocorticoid activity are thought to include increased foraging and energy uptake (perhaps in part

through changes in behaviour) in attempts to survive the challenging event(s). In many birds, for instance, endogenous levels of the glucocorticoid hormone, corticosterone, track directly energetic requirements across the annual cycle, usually being highest during the breeding season when individuals have the greatest energy demand (reviewed in Romero 2002).

However, if circumstances lead to chronically elevated levels of glucocorticoid hormones, reproductive function or cognitive abilities can be impaired (e.g. Moore & Miller 1984; Sapolsky 1985; Orr & Mann 1992; DeNardo & Licht 1993; Knapp & Moore 1995; Cameron 1997; Fox et al. 1997; Kitaysky et al. 2003) and immune function suppressed (Grossman 1990; Fowles et al. 1993; Saino et al. 2003). In captive animals, adrenocortical activity can rise in crowded conditions (e.g. Brown & Grunberg 1995; Bugajski et al. 1995; Chapman et al. 1998; McEwen &

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Wingfield 2003), presumably from increased rates of social interaction and competition. In most studies of crowding in captivity, however, the animals cannot escape social confinement and they may experience exaggerated social stress (e.g. van Dijken et al. 1993; Creel et al. 1996, 1997; Smith & John-Alder 1999). Surprisingly, we know relatively little about how glucocorticoid hormone levels vary among free-living animals that actively choose to live in groups of different sizes or densities. If animals in larger groups in the wild have elevated levels of glucocorticoids, either because of a greater need to mobilize energy and/or because of intensified social competition, this could represent a cost of group living and one with potentially major effects on fitness.

Colonially breeding animals often show great variation in colony size within even a single population (Brown et al. 1990). This variation gives researchers a natural framework for studying both the costs and benefits of coloniality in free-living animals (e.g. Hoogland & Sherman 1976; Wiklund & Andersson 1994; Brown & Brown 1996, 2001). Although some studies have measured glucocorticoid levels in cooperatively breeding species that live in relatively small groups (e.g. Sapolsky 1985; Creel et al. 1997; Wingfield & Lewis 1993; Schoech et al. 1997; Rogovin et al. 2003; Goymann & Wingfield 2004; Muller & Wrangham 2004), field work has focused mostly on how levels of these hormones are influenced by social status or cooperative behaviour within kin-based groups. To our knowledge, no studies have measured how glucocorticoid hormone levels in birds vary among individuals in large versus small colonies.

We investigated how endogenous levels of the glucocorticoid hormone, corticosterone, vary among cliff swallows, *Petrochelidon pyrrhonota*, nesting in colonies of different sizes. Cliff swallows breed in colonies that vary in size over several orders of magnitude, and we studied birds in colonies ranging from 22 to approximately 3400 nests. Higher levels of corticosterone in larger colonies could indicate that birds there have a higher energetic demand, perhaps through greater competition for food or higher levels of ectoparasitism, or that they may experience increased social competition in larger colonies (Brown & Brown 1996). To distinguish between these possibilities, we experimentally removed blood-feeding ectoparasites from some colonies, thus reducing energy demand at those sites for both adult and nestling birds while presumably maintaining typical levels of social competition. Ectoparasites tend to increase with group size in cliff swallows and represent a serious cost of coloniality (Brown & Brown 1986, 1996). We also examined how corticosterone levels changed among birds exposed to a severe weather event, during which foraging opportunities and thus energy intake were reduced.

METHODS

Study Animal and Study Site

Cliff swallows are highly colonial passerines that breed throughout most of western North America (Brown &

Brown 1995). They build gourd-shaped mud nests and attach them to the vertical faces of cliff walls, rock outcrops, or artificial sites such as the eaves of buildings or bridges. Their nests tend to be stacked closely together, often sharing walls, and breeding at a site is highly synchronous (Brown & Brown 1996). Cliff swallows are migratory, winter in southern South America, and have a relatively short breeding season in North America. They begin to arrive at our study site in late April or early May and depart by late July. They generally raise only one brood. Cliff swallows are associated with a variety of ectoparasites, endoparasites and viruses throughout their range (Monath et al. 1980; Scott et al. 1984; Brown & Brown 1995; Brown et al. 2001). The ectoparasites, in particular the haematophagous swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*), are responsible for much of the nestling mortality and nest failures that occur in our study area (Brown & Brown 1986, 1996).

Our study site is centred at the Cedar Point Biological Station (41°13'N, 101°39'W) near Ogallala, in Keith County, southwestern Nebraska, U.S.A., along the North and South Platte Rivers, and also includes portions of Deuel, Garden, and Lincoln counties. There are approximately 160 cliff swallow colony sites in the 150 × 50-km study area, with about one-third of these not used in a given year. Colony size varies widely; in our study area, it ranges from 2 to 6000 nests, with some birds nesting solitarily. Over a 23-year period, mean ± SE colony size ($N = 1629$) was 385 ± 15 nests. Each colony site tends to be separated from the next nearest by 1–10 km, but in a few cases by 20 km or more. Birds nest on both natural cliff faces and artificial structures such as bridges, buildings and highway culverts. Cliff swallows have been studied at this site since 1982, and the site is described in detail by Brown & Brown (1996).

Hormone Sampling

Circulating hormone levels were measured for cliff swallows during the 2000 and 2001 breeding seasons. As part of a long-term mark–recapture project, we mist-netted thousands of adult cliff swallows at the study colonies at intervals throughout each nesting season. Nets were placed either across one end of a culvert containing nests, with birds caught as they exited the colony, or were dropped from the top of a bridge, such that the swallows would be caught as they flushed from their nests (Brown 1998). All birds were banded with U. S. Fish and Wildlife Service bands upon initial capture, and were weighed and sexed on each capture. Blood samples were taken from a subset of the adults caught; we tried to select this subset as randomly as possible. The principal criterion for inclusion was knowing exactly when a given bird first hit the net. All baseline measures of corticosterone (and for one analysis, testosterone) were from birds bled within 3 min of initial contact with a net to avoid the effects of handling stress on glucocorticoid response. Blood samples were taken with heparinized capillary tubes after brachial vein puncture with a 26-gauge needle or lancet. Samples were initially stored on ice in a cooler, then transported

back to a laboratory at the Cedar Point Biological Station, where plasma was separated by microhaematocrit centrifugation and harvested with a Hamilton syringe. Plasma samples were stored at -20°C until analysis. Corticosterone and testosterone concentrations were measured by radioimmunoassay (Wingfield et al. 1992). Blood samples were not collected from all of our study colonies; we chose colony sites for inclusion either (primarily) to maximize the range in colony sizes studied or (in some cases) to pair fumigated and nonfumigated colonies of roughly equivalent size.

In 2001, we collected data on baseline corticosterone for nestling and recently fledged juvenile cliff swallows at selected colonies. Juveniles were ones capable of flight that were caught in nets as they entered and exited nests at a colony site. Because juveniles move between different colonies after fledging (Brown & Brown 1996), we sampled only juveniles that were still relatively small (e.g. wing length < 100 mm) and thus ones that had likely fledged from nests at the site where they were caught. Nestlings were birds 10–12 days old, judged by their extent of feather development (C.R.B., personal observation). Each nestling sampled at a colony came from a different nest, to minimize problems with nonindependence of broodmates. Baseline samples from juveniles and nestlings were also collected within 3 min of capture (or, for nestlings, within 3 min of when we first touched them).

Because our arrival at a colony site usually resulted in an initial agitation of the colony residents, with many birds swirling around us and alarm calling, our presence alone may have led to higher glucocorticoid levels among the birds at a site. Although to some degree, any effect of our presence was constant among colony sites (because by definition we were physically present at any colony where birds were sampled), we examined this potential factor by evaluating whether the duration of the disturbance to a site might have affected corticosterone levels. This was done by noting the time of our arrival at each site on a given day and when each bird was caught, enabling us to calculate the elapsed colony disturbance time at a site for each individual that was blood-sampled.

Designating Colony Size, Stage and Bird Age

Cliff swallow colony size was defined as the maximum number of nests at a site to have contained one or more eggs. Active nests were counted at some sites by periodically checking the nest contents with a dental mirror and flashlight, and the colony size at other sites was estimated by counting the number of nests in active sections of the colony (Brown & Brown 1996). The density of nests in cliff swallow colonies covaries positively with colony size, meaning that larger colonies also tend to be denser. We used colony size in all analyses, because it is more intuitive and does not involve certain assumptions about the suitability of nesting substrate necessary for density calculations (Brown & Brown 1996), but many of our conclusions would apply equally to colony density as the independent variable.

At the time each colony was sampled, we designated the colony's stage as either early, mid or late. The early stage was when over half of the birds in a colony were nest building, mid stage was when over half of the colony was incubating, and late stage was when over half of the colony was feeding nestlings. These periods were designated separately for each colony, so different colonies active at the same time may have been at different stages, depending on when they started. These three stages, however, corresponded broadly to the early, middle and latter parts of the breeding season. The exact nesting stage was not known for any of the adult birds sampled, because none were caught at their nests. However, the high degree of synchrony within cliff swallow colonies (Brown & Brown 1996) ensured that most individuals could be classified accurately based on the status of the colony as a whole. We had more data for the mid stage than for the early or late stages, in part because the early stage was short at most sites and often included periods of bad weather that prevented mist netting, and because cliff swallows at many sites became much harder to catch (especially by our dropping nets over the side of a bridge) once they began feeding nestlings. In a few cases, the same colony was sampled at two different stages. For corticosterone analyses of adults, we used only colonies with at least 10 birds sampled in a given stage; in many cases, our sample size was 20 or more (at least 10 males and at least 10 females) per colony per stage.

We designated age of adult birds in two ways. We knew the exact ages of those birds first banded as nestlings or juveniles in a past year. The oldest bird of exact age in our sample was 7 years old. For birds first banded as unknown-aged adults, we designated the minimum age as the number of years elapsed since banding. Thus, the minimum age of a bird first banded in the year of hormone sampling was 1 year, a bird first banded the previous year was 2 years, and so forth. This gave us a relative measure of a bird's age, with some individuals having a minimum age of up to 10 years. We believe that minimum age was a relatively accurate indicator of exact age, because many of the unbanded adults in our study area in a given year are probably yearlings, given the large number of adult birds ($\sim 10\,000$) banded each season.

Potential Effects of Transient Birds

One potentially confounding factor in interpreting steroid hormone levels is the presence of transient birds at some colonies. Large numbers of transients pass through some colonies (Brown & Brown 2004a), many of them apparent nonbreeders. Transients, for a variety of reasons, might have higher or lower corticosterone levels than resident birds at a site. To investigate this possibility, we identified the colonies in 2000 and 2001 where transients were suspected to occur by fitting a series of within-season survival and recapture models to the daily capture data for all birds at each site each year (Brown & Brown 2004b). Some models contained an effect of transients and others did not (see Pradel et al. 1997). Models with an effect of transients had the best fit (Brown &

Brown 2004b) for sites where transients might have confounded measurements of hormone levels. For those nine colonies, we examined the seasonal capture histories of all birds whose hormones were measured. Those caught only once at a colony during the season were considered transients and those caught at least twice were considered residents. Although this test was conservative, because some of the individuals classified as transients may have been residents that never happened to get caught again, it did allow us to determine any obvious differences between known colony residents and birds that might not have lived at the site.

For all nine colonies combined, in the early stage, known residents ($N = 25$) had a mean \pm SE of 4.15 ± 0.95 ng/ml corticosterone versus 4.34 ± 0.55 ng/ml for potential transients ($N = 34$). In the mid stage, the comparison was 3.94 ± 0.48 ng/ml for residents ($N = 64$) and 5.74 ± 0.84 ng/ml for transients ($N = 54$), and in the late stage, it was 8.23 ± 1.02 ng/ml for residents ($N = 66$) and 6.04 ± 0.91 ng/ml for transients ($N = 55$). These differences were not significant at any stage (Wilcoxon tests: $P \geq 0.13$ on all). Thus, capture history at a site was not related to corticosterone level, so we combined data from all individuals caught at a colony and did not designate residents and transients separately in subsequent analyses. We found a similar result when comparing testosterone levels of birds designated as residents versus transients (Smith et al. 2005).

Fumigation

In 2000 and 2001, three and four colonies, respectively, were fumigated to remove ectoparasites as part of other work (e.g. Brown & Brown 2004a, b). Nests within these colonies were sprayed with an insecticide, Dibrom, that is highly effective in killing swallow bugs (Brown & Brown 1996, 2004a). The active ingredient in Dibrom (also known as naled) is 1,2-dibromo-2,2-dichloroethyl dimethyl phosphate, which acts as a cholinesterase inhibitor. We diluted the insecticide in water (1:150) and applied it as a light mist directly to the outsides of nests and the adjacent substrate. It served primarily as a contact insecticide. Nests were fumigated weekly to remove any bugs brought into the colony by transient birds. Each colony was sprayed in its entirety. We did not spray inside any active nest, and in over 20 years of using this chemical, we have not detected any adverse effects on cliff swallows (Brown & Brown 1996).

Dibrom has no documented endocrinological effects (Cox 2002). However, because of the possibility that the fumigant might have endocrine-blocking properties, we tested it by running five separate corticosterone assays (and one blank) containing the diluted concentration of Dibrom used in the field. Dibrom showed no interaction with the antiserum in these assays; levels were undetectable in tubes with fumigant and identical to the blank. Further evidence that Dibrom, as applied to swallow nests in this study, has little or no effect on glucocorticoids is that there was no significant difference between maximal corticosterone levels of adult cliff swallows held for

60 min in fumigated versus nonfumigated colonies ($P = 0.80$; C. R. Brown, S. A. Raouf, L. C. Smith, M. B. Brown & J. C. Wingfield, unpublished data).

Bad-weather Event

We studied changes in baseline corticosterone of cliff swallows in response to a period of adverse weather in 2001, during which a 5-day period of extremely windy weather occurred from 20 to 24 May. Daytime high temperatures during this period were slightly below normal, and the extreme wind made foraging difficult for these aerial feeders; many birds spent most of these days foraging away from their colonies. On 24 May, we mist-netted some adults foraging low among juniper trees at the Cedar Point Biological Station, and compared their baseline corticosterone levels with those of birds caught at a nonfumigated colony site 5.5 km away on 18–19 May (before the bad weather) and with those of birds caught at a nonfumigated colony site 1.5 km away on 30 May (after the bad weather). Recaptures of banded birds have shown that swallows from these colony sites routinely feed at Cedar Point during bad weather (C. R. Brown & M. B. Brown, unpublished data).

Statistical Analysis

The set of corticosterone values obtained was not normally distributed, and no transformations successfully normalized it. We thus used nonparametric tests for most of our statistical analyses. To assess the separate effects of several independent variables on corticosterone levels, we ranked the corticosterone values and used the ranked values (Montgomery 2001) in a parametric ANCOVA using Proc GLM in SAS (SAS Institute 1990). Mean \pm SE corticosterone levels are reported.

RESULTS

Baseline Corticosterone of Adults

Using all adults for which baseline corticosterone was measured ($N = 1042$), an ANCOVA identified the independent variables that potentially affected baseline corticosterone levels in cliff swallows (Table 1). Sex, date of sampling and elapsed disturbance time to the colony had no significant effects; thus, we combined the sexes for subsequent analyses and did not consider date or disturbance time further. Baseline corticosterone varied significantly with year, whether a colony was fumigated, nesting stage and colony size, and the effect of each variable was independent of the others (Table 1). Year, however, disappeared as a significant effect ($\alpha = 0.05$) with a sequential Bonferroni correction for multiple table-wide comparisons (Rice 1989), so we do not consider the effect of year further.

Baseline corticosterone was significantly lower for adult birds occupying fumigated (parasite-free) colonies than for birds exposed to natural levels of ectoparasites during each

Table 1. Analysis of covariance (ANCOVA) to detect effects of variables potentially affecting baseline corticosterone levels of adult cliff swallows in 2000–2001*

Variable	F	df	P
Year	4.05	1, 1041	0.044
Site fumigated or not	47.89	1, 1041	<0.0001
Sex	0.96	1, 1041	0.33
Nesting stage (early, mid or late)	5.87	2, 1040	0.003
Colony size	10.57	1, 1041	0.001
Date	1.35	1, 1041	0.24
Elapsed colony disturbance time	0.64	1, 1041	0.42

*Includes all birds for which corticosterone was sampled within 3 min of capture (N = 1042).

nesting stage (Fig. 1). Corticosterone levels were highest during the late stage (while birds were feeding nestlings) among birds from both fumigated and nonfumigated colonies. There appeared to be little difference in corticosterone levels between the early and mid stages for either class of birds (Fig. 1).

Baseline corticosterone levels of adults increased with colony size for nonfumigated sites (Fig. 2). Because early and mid stages were so similar (Fig. 1), we combined data from those stages (Fig. 2a) and present the late-stage pattern separately (Fig. 2b). The univariate correlations between mean corticosterone per colony and colony size for the early/mid and late stages were both positive, and were significant for the late stage (Spearman correlation: $r_s = 0.79$, $N = 8$ colonies, $P = 0.028$; Fig. 2b) and tended towards significance for the early/mid stages ($r_s = 0.33$, $N = 28$ colonies, $P = 0.09$; Fig. 2a). When the P values were combined (Sokal & Rohlf 1969, page 623), the overall

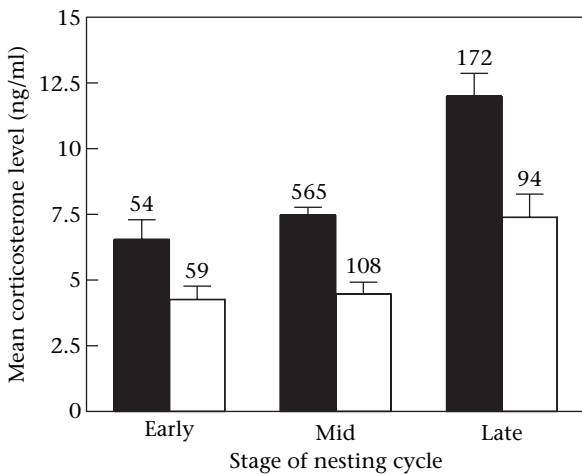


Figure 1. Mean + SE baseline corticosterone level (ng/ml) of adult cliff swallows in nonfumigated (■) and fumigated (□) colonies during the early (nest-building and egg-laying), mid (incubation) and late (nestling-feeding) stages of the nesting cycle. Corticosterone level varied significantly with fumigation status and nesting stage (Table 1). Sample sizes (number of birds sampled) are shown above the bars.

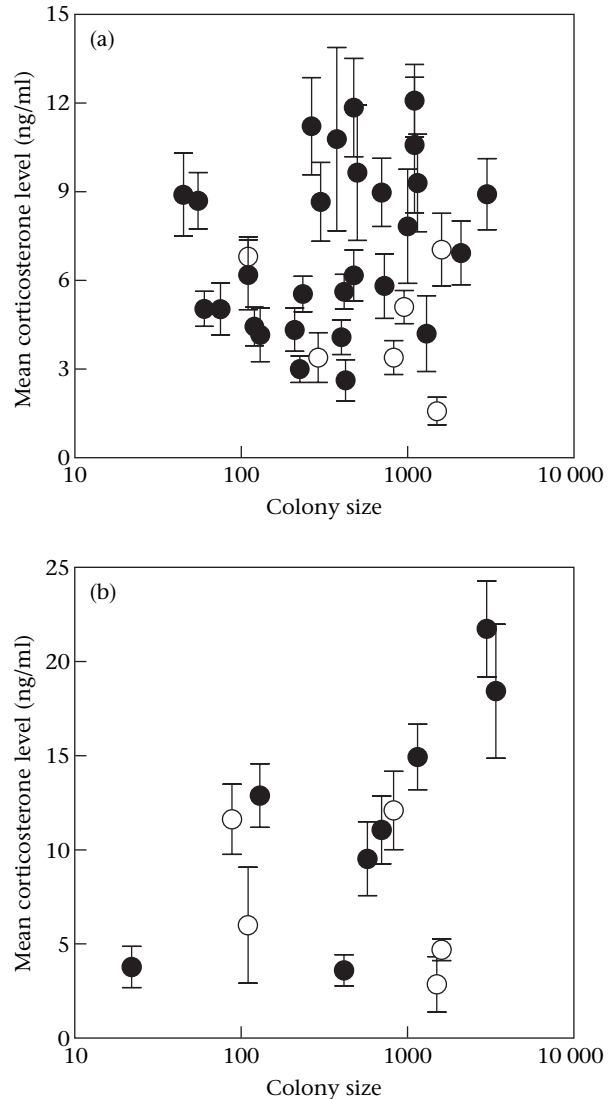


Figure 2. Mean ± SE baseline corticosterone level (ng/ml) of adult cliff swallows in relation to breeding colony site (number of active nests) for nonfumigated sites (●) and fumigated sites (○) during (a) the nest-building, egg-laying and incubation stages (i.e. early and mid stages) and (b) the period of feeding nestlings (late stage). Sample size (number of birds sampled) was 14–30 for each colony.

correlation was significant (chi-square test: $\chi^2_4 = 11.97$, $P = 0.018$; Fig. 2). Mean baseline corticosterone concentration in the late stage increased about four-fold across the range of colony sizes studied. We had data for only five to six fumigated colonies, but corticosterone levels appeared to decrease with colony size among fumigated colonies (Fig. 2).

For a subset of adults, we repeated the ANCOVA with the same variables (Table 1), as well as exact age, and found no significant effect of exact age on baseline corticosterone levels in adults ($F_{5,87} = 1.90$, $P = 0.10$). In similar analyses, we found no significant effect of minimum age ($F_{8,941} = 0.35$, $P = 0.94$), body mass during any stage (early: $F_{1,229} = 0.08$, $P = 0.77$; mid: $F_{1,744} = 1.15$, $P = 0.28$; late: $F_{1,391} = 1.37$, $P = 0.24$), or testosterone

concentration ($F_{1,694} = 0.17$, $P = 0.68$) on baseline corticosterone levels.

Mean corticosterone level was higher for cliff swallows during the bad-weather event (Fig. 3), but did not differ significantly between the three classes of birds (Kruskal-Wallis ANOVA: $\chi^2_2 = 4.80$, $P = 0.09$).

Baseline Corticosterone of Nestlings and Juveniles

Nestlings were sampled at two pairs of colonies, a small nonfumigated one (90 nests) and a small fumigated one (110 nests), and a large nonfumigated one (3400 nests) and a large fumigated one (1600 nests). Baseline corticosterone levels of nestling cliff swallows were generally similar to those of adults measured at the same nesting stage (late). For the small-colony pair, there was no significant difference in baseline corticosterone levels of nestlings from the fumigated versus nonfumigated site (Wilcoxon signed-ranks test: $Z = 0.27$, $P = 0.79$; Fig. 4). However, for the large-colony pair, nestlings at the fumigated site had significantly lower corticosterone concentrations than did those at the nonfumigated site ($Z = -2.61$, $P = 0.009$; Fig. 4). For the nonfumigated sites, there was no significant difference in baseline corticosterone levels between nestlings in the small and large colonies ($Z = 1.09$, $P = 0.27$; Fig. 4), although the pattern was similar to that seen for adults (Fig. 2b). For the fumigated sites, nestlings in the large colony had significantly lower corticosterone levels than nestlings in the small colony ($Z = -2.32$, $P = 0.02$; Fig. 4), also consistent with the pattern for adults (Fig. 2b).

Recently fledged juveniles were sampled at three non-fumigated colonies of 860, 1100 and 3400 nests, and at one fumigated colony of 1600 nests. Thus, we considered

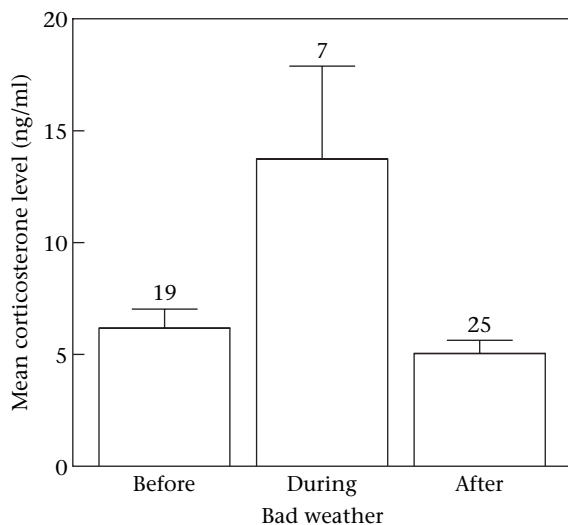


Figure 3. Mean + SE baseline corticosterone level (ng/ml) for adult cliff swallows before, during and after a bad-weather event in 2001. Before and after the event, birds were caught at colony sites; during the event, birds were caught while foraging away from the sites. Sample sizes (number of birds sampled) are shown above the bars.

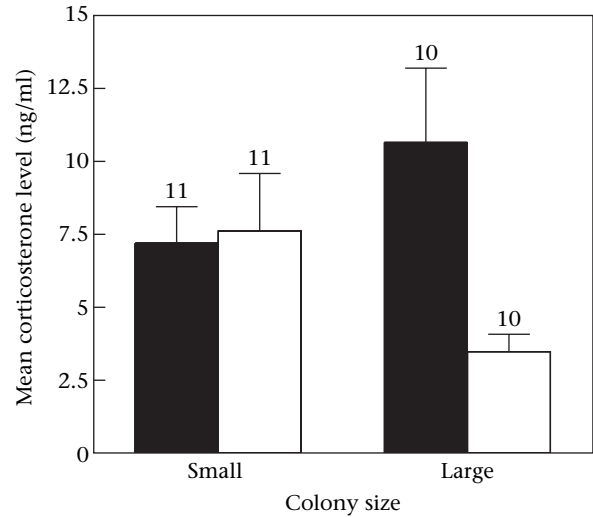


Figure 4. Mean + SE baseline corticosterone level (ng/ml) for nestling cliff swallows at a pair of small and large colonies, each of which contained one nonfumigated site (■) and one fumigated site (□). Sample sizes (number of birds sampled) are shown above the bars.

these data as exclusively from large colonies, and combined data from the three nonfumigated colonies because of the small per-colony sample sizes. As with adults and nestlings, baseline corticosterone levels were significantly lower for juveniles from the fumigated site (12.88 ± 1.89 ng/ml) than for ones from the nonfumigated colonies (27.15 ± 2.46 ng/ml; $Z = -3.78$, $P < 0.001$).

DISCUSSION

Our results indicate that average endogenous corticosterone levels of adult cliff swallows were higher in larger breeding colonies under natural conditions, and the same pattern held for nestlings and juveniles. Haematophagous ectoparasites appeared to be a prominent influence in creating this pattern, because baseline corticosterone levels of birds in parasite-free colonies were lower and did not systematically increase with colony size. There was no obvious increase in baseline corticosterone in the larger colonies in the absence of parasites, which implicates ectoparasitism as a cause of the higher corticosterone levels in larger, nonfumigated colonies.

Of the various costs of grouping experienced by cliff swallows (Brown & Brown 1996), the most important is that of ectoparasitism. Infestations of blood-feeding swallow bugs increase with colony size. These ectoparasites reduce nestling survival and body mass, transmit an alphavirus to both adults and nestlings, and reduce both daily and annual survival probability for birds of all ages (Brown & Brown 1986, 1996, 1999, 2004a, b; Brown et al. 1995, 2001). They also have indirect effects, such as lowering haemoglobin levels and elevating white blood cell counts (Chapman & George 1991) and causing higher first-year dispersal and greater wing and tail feather asymmetry among juveniles (Brown & Brown 1992, 2002). Because most of these effects of ectoparasites are

energetically demanding, it is not surprising that birds exposed to infestations of parasites would show an increased glucocorticoid response. Increased corticosterone concentrations may allow the birds to better cope with the challenges of parasitism, probably by increasing energy uptake through increased foraging or energy assimilation from fat. With more parasites (and pathogens) per capita in larger cliff swallow colonies (Brown & Brown 1986, 1996, 2004a; Brown et al. 2001), the birds living there should be under greater energy demand, consistent with the observed increase in baseline corticosterone levels with colony size. Large, infested colonies thus represent lower-quality breeding sites, so our results are consistent with those in other species showing higher corticosterone levels for individuals in marginal or poor habitat (Dunlap & Wingfield 1995; Marra & Holberton 1998; Suorsa et al. 2003).

Although there are other potential costs of larger colonies for cliff swallows, such as increased competition for food under some circumstances and greater rates of attacks from predators (Brown & Brown 1996), our comparison of corticosterone levels between birds in fumigated and nonfumigated colonies suggests that these other costs did not cause a higher glucocorticoid response. If anything, baseline corticosterone levels seemed to decline in larger fumigated colonies, which may suggest that the birds there were not energetically challenged by food competition, having to travel further during foraging, being attacked more often by predators or engaging in more social interaction. In the absence of ectoparasites, cliff swallows may be under greater energy demand in smaller colonies, where, for example, they have fewer conspecifics with whom to forage and less information available on the whereabouts of food (see Brown & Brown 1996). Some of our evidence supports this hypothesis: corticosterone levels of nestlings from the small fumigated colony were higher than those from the large fumigated colony (Fig. 4) and the pattern was similar for adults (Fig. 2). Cliff swallows showed increased levels of corticosterone when food was scarce (in bad weather and while learning to catch prey as juveniles), which also supports the contention that the lower foraging success in the smaller colonies may explain the relatively higher corticosterone levels for birds at those sites when parasites were removed.

The corticosterone levels of nestling cliff swallows probably reflect their nutritional condition, because in work on other bird species, chicks release more corticosterone when deprived of food (Nunez-de la Mora et al. 1996; Kitaysky et al. 1999; Saino et al. 2003; Suorsa et al. 2003), perhaps to stimulate increased begging (Kitaysky et al. 2001). In our study, nestlings in the large fumigated colony had lower levels of baseline corticosterone than their counterparts in the small fumigated colony, which is consistent with the hypothesis that birds in the larger colonies (without parasites) were in better condition because of the foraging advantages that their parents enjoyed at those sites.

Our results suggest a possible trade-off associated with colony size in cliff swallows. In the presence of nest-based ectoparasites, birds in larger colonies averaged higher baseline corticosterone levels. From studies of captive

animals, one might conclude that the crowding inherent in large colonies increases glucocorticoid response. However, the results of the fumigation experiment show that blood-feeding bugs were the probable cause of the increased corticosterone levels, and that cliff swallows in large colonies did not have elevated glucocorticoid levels in the absence of bugs.

Corticosterone levels in other birds have been shown or have been suggested to vary with breeding stage, sex and age (Stein-Behrens & Sapolsky 1992; Wingfield et al. 1992; Astheimer et al. 1994, 2000; Sapolsky et al. 2000; Holberton & Wingfield 2003). In many species, differences in corticosterone secretion depend on the stage of the reproductive cycle, although these differences have usually been demonstrated using the stress-series protocol, in which animals are held for varying durations. We found systematic differences in baseline corticosterone levels between adult cliff swallows in the prelaying, laying and incubation periods compared to the time of nestling feeding. This result could have occurred for at least two reasons. First, by the late (nestling) stage, individuals would have been exposed to parasites for several weeks, and the parasites' cumulative effects by then would be greatest. Second, the period of feeding nestlings is itself demanding to adults, because they must find enough food for themselves and their brood. Increased corticosterone levels during such times may aid the birds' short-term ability to assimilate energetic resources that are then in high demand, or they may cause the birds simply to allocate more time to foraging. Cliff swallows in fumigated colonies also showed increased baseline corticosterone levels later in the season, which supports this second possibility.

We found no sex differences in corticosterone levels. Intersexual differences are expected whenever, for example, the sexes invest differentially in the reproductive attempt and thus allocate resources differently to reproduction versus self-maintenance (Astheimer et al. 1994, 2000; Holberton & Wingfield 2003). In contrast, during the nonbreeding season, glucocorticoid levels are often the same between the sexes, reflecting similar energy demand (Wingfield et al. 1994a; Holberton et al. 1996; Holberton & Able 2000). Male and female cliff swallows invest roughly equally in reproductive activities: they both build the nest, incubate and feed the young. It is thus not surprising that they respond similarly to environmental challenges such as ectoparasitism, which affects both sexes the same. Although the number of studies that have measured corticosterone response as an explicit function of age in birds is still limited, life-history theory predicts that older individuals for whom the current reproductive attempt is more valuable should show lower glucocorticoid responses, so as not to divert resources to self-maintenance at the expense of reproduction (Astheimer et al. 2000; Ricklefs & Wikelski 2002). Using two indexes of age (exact and minimum), we found no support for this prediction.

There was no significant relationship between levels of corticosterone and testosterone in cliff swallows after controlling for date-related variation (Smith et al. 2005) in testosterone levels. Although in some species circulating

levels of these two hormones are correlated, a number of other studies have found no link between testosterone and corticosterone concentrations (reviewed in Roberts et al. 2004). Cliff swallows of both sexes show the highest testosterone levels during the period of nest establishment and pair formation (Smith et al. 2005), but apparently this phase of the annual cycle (our 'early' stage) is not energetically challenging enough to cause increased corticosterone and thus an association between levels of these steroid hormones.

Baseline corticosterone levels in recently fledged juvenile cliff swallows were markedly higher than in adults from the same colony site. For the three large non-fumigated colonies where juveniles were sampled, the mean baseline corticosterone level of juveniles was almost two-fold higher than that of the adults sampled at the same time from the same sites (27.1 versus 15.8 ng/ml); for the large fumigated colony, the difference was about 4.5 times higher (12.9 versus 2.9 ng/ml). The higher corticosterone levels of recently fledged juveniles may serve to direct juveniles' activities to foraging during the transition to independence, when they are in the process of learning to forage for themselves (Heath 1997). The increased baseline corticosterone for juveniles from nonfumigated nests (relative to fumigated ones) may also reflect their long-term exposure to parasites in the nests from which they had recently fledged.

The glucocorticoid response we found in cliff swallows exposed to a bad-weather event when food was scarce matches results found for Arctic and other high-latitude birds when exposed to severe spring weather (Wingfield et al. 1983, 1994b, 1995; Smith et al. 1994; Romero et al. 2000; O'Reilly & Wingfield 2001). During such times, higher levels of corticosterone may serve in part to redirect behaviour away from nesting activities and thereby increase foraging time, a critical reallocation of effort during impending periods of food scarcity. Cliff swallows routinely experience periodic bouts of cold and rainy weather during spring even at relatively low-latitude sites such as our Nebraska study area, and their flying-insect food is greatly reduced during such times. Most of these events are relatively brief (1–3 days), but occasionally prolonged events can result in massive mortality (Brown & Brown 1998). Almost immediately with the onset of bad weather, cliff swallows drastically reduce activity around nests and colony sites and begin foraging elsewhere. Corticosterone may help to modulate this switch.

In all analyses in this study, it appeared that glucocorticoid levels in cliff swallows directly tracked putative energy demand. Whether corticosterone acted primarily by modulating behaviour to increase foraging time or affected the physiology of energy assimilation was unclear; most likely, both processes are involved to various degrees. However, there was little evidence that the crowding inherent in larger colonies, per se, had any effect on levels of endogenous glucocorticoids and thus that increased rates of social interaction represented a major stressor.

Despite the different challenges that cliff swallows in different-sized colonies face, the net effect is higher corticosterone levels for those in the larger colonies,

especially late in the season. An outstanding question is whether the increased levels of baseline corticosterone in birds of larger colonies reach chronically high enough levels to be costly independent of the factors (e.g. ectoparasitism) that cause the increase. Chronically elevated corticosterone levels can be deleterious in various species (e.g. Moore & Miller 1984; Sapolsky 1985; Grossman 1990; Orr & Mann 1992; DeNardo & Licht 1993; Fowles et al. 1993; Knapp & Moore 1995; Cameron 1997; Fox et al. 1997), and there is evidence that very high baseline levels are associated with reduced annual survival in cliff swallows (Brown et al. 2005). The direct physiological consequences of increased corticosterone thus could represent a separate cost of coloniality distinct from the other negative effects of swallow bugs.

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