STEROID HORMONE LEVELS ARE RELATED TO CHOICE OF COLONY SIZE IN CLIFF SWALLOWS

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Abstract. One hypothesis to explain the extensive variation in colony size seen in most taxa is that individuals sort themselves among groups based on phenotypic characteristics that correlate with their performance in groups of different sizes. We investigated how baseline levels of the steroid hormones, corticosterone and testosterone, were associated with choice of colony size and the likelihood of moving to a different site in later years in colonially nesting Cliff Swallows (*Petrochelidon pyrrhonota*) in southwestern Nebraska, USA, in 2000–2004. We sampled hormone levels of birds caught at colonies and, using mark–recapture, monitored their movement and choice of colony size through subsequent years in the study area. Maximum likelihood estimation and multistate model fitting (with program MARK) revealed that birds with baseline corticosterone levels above the average for the colony and time of sampling were less likely to choose a colony of the same size or larger in a later year than were birds with corticosterone levels below the average. This result held for Cliff Swallows in both fumigated (parasite-free) sites and colonies naturally infested with ectoparasites. Relative baseline corticosterone level was unrelated to the likelihood of movement between different colony sites, and corticosterone level measured after birds were held for 60 minutes was unrelated to either colony-size choice or the probability of movement. Males whose testosterone levels were above the average for the colony and time of sampling were more likely to choose a colony of the same size or larger in a later year than were ones whose testosterone levels were below the average, but the opposite pattern was found for females. The results indicate that steroid hormone level is a predictor of whether a Cliff Swallow will settle in a relatively small or large colony, and support the hypothesis that variation in colony size reflects, in part, a distribution of birds with inherently different neuroendocrinological characteristics.

Key words: Cliff Swallow; coloniality; corticosterone; dispersal; habitat selection; multistate mark–recapture; Petrochelidon pyrrhonota; *social behavior; steroid hormone levels; testosterone.*

INTRODUCTION

Most animals that breed in colonies show extensive variation in colony size, often over a range of several orders of magnitude (Brown et al. 1990). What causes variation in group size is poorly understood, however, with explanations often involving extrinsic constraints such as the amount of available breeding space at a given site (Lack 1968, Wittenberger 1981, Brown and Brown 1996). More recently, a few studies on birds have suggested a possible genetic basis to an individual's choice of colony size (Brown and Brown 2000, Møller 2002, Brown et al. 2003), with, for example, cross-fostered birds later settling to breed in colonies more similar in size or density to those of their birth than those where they were reared. Presumably, in such cases, there are inherent differences among individuals

that make them more or less successful in groups of different sizes, and their performance in these different social settings has selected for their sensitivity to group size in making settlement decisions (Brown and Brown 2000). No studies to date have identified the nature of the differences among individuals that might influence choice of colony size, and we know essentially nothing about the phenotypic characteristics that promote success in large vs. small groups.

One possible way that individuals in large and small groups may differ is in their propensity to mount neuroendocrinological responses to environmental stimuli. Many animals rely on steroid hormones such as testosterone and corticosterone to modulate their behavior in various ways, and inherent differences in either the sensitivity to these hormones' effects or the ability to produce them may correlate with how well an individual copes with a particular social environment. For example, the sex hormone, testosterone, stimulates aggression and mate acquisition, and many studies have shown that testosterone concentrations rise during the

time of the annual cycle when animals are most active at defending territories and courting mates (Wingfield et al. 1990, 2000). Consequently, individuals that experience higher intensities of competition for territories or mates (such as in large groups) might benefit from having either higher sensitivity to the effects of testosterone or higher endogenous levels of it. On the other hand, individuals in less competitive environments (e.g., small colonies) might be selected to have lower levels of the hormone, in part to reduce the possible costs associated with higher testosterone (e.g., Folstad and Karter 1992, Hillgarth and Wingfield 1997, Brown and Brown 2003, Roberts et al. 2004).

Another steroid hormone, in birds the glucocorticoid corticosterone, is associated with energy acquisition, increasing the assimilation of stored energy (muscle, fat), and causing changes in foraging behavior or locomotor activity to promote food consumption and movement (Wingfield et al. 1983, 1994, 1995, Romero et al. 2000, Romero 2002, Suorsa et al. 2003). In situations that require more effort at energy acquisition (such as in large colonies where there is greater local competition for food, or alternatively, in small colonies where there is less information available from conspecifics on where food can be found) individuals with higher endogenous levels of corticosterone could be favored because they might more readily modulate their behavior or physiology to cope with the challenging conditions. In contrast, in social situations in which food is more available, birds with inherently lower levels of corticosterone would benefit because they might more readily devote time and effort to reproductive activities rather than hormone-mediated foraging. Furthermore, because certain social environments themselves (e.g., crowded conditions) may cause birds to increase their baseline levels of glucocorticoids, and high levels of these hormones can be detrimental to survival (Brown et al. 2005), individuals predisposed to inherently higher concentrations should be selected to avoid social situations that would elevate their circulating corticosterone to harmful levels.

In this study of colonially nesting Cliff Swallows (*Petrochelidon pyrrhonota*), we tested the hypothesis that a bird's annual colony choice was related to its baseline level of testosterone and corticosterone in a prior year. We sampled birds for hormones and monitored where they settled in later years, allowing the estimation of formal transition probabilities between colonies for birds with different hormone levels. Although seasonal fluctuations in testosterone and corticosterone are thought to correlate with dispersal behavior in some animals (Holekamp et al. 1984, Silverin 1997, Belthoff and Dufty 1998), no previous study has looked at how annual choice of a colony size is related to hormonal profiles of individuals. We examine how choice of both a colony site and a colony size is potentially influenced by corticosterone and testosterone, and we do this by estimating multistate transition prob-

abilities for individuals moving both between sites in space and between groups of different sizes relative to their previous colony size. Because average levels of both corticosterone and testosterone are known to be greater in Cliff Swallows occupying larger colonies (Smith et al. 2005, Raouf et al., *in press*), we designed our analyses to account for movement by individuals relative to the hormone levels of other birds occupying the same colony at the same time, and thus tested the hypothesis that baseline hormone levels influence future colony choice. The results offer potential insight into phenotypic differences between Cliff Swallows occupying large vs. small colonies and why these differences may occur.

METHODS

Study animal and study site

Cliff Swallows are highly colonial passerines that breed throughout most of western North America (Brown and 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 (see Plate 1). Their nests tend to be stacked closely together, often sharing walls, and breeding at a site is highly synchronous (Brown and Brown 1996). Cliff Swallows are migratory, wintering 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, and individuals (rarely) live up to 12 years of age. Cliff Swallows are associated with a variety of ectoparasites, endoparasites, and viruses throughout their range (Monath et al. 1980, Scott et al. 1984, Brown and Brown 1995, Brown et al. 2001). The ectoparasites, in particular the hematophagous swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*), are responsible for much of the nestling mortality and nest failures that occur in our study area (Brown and Brown 1986, 1996).

Our study site is centered at the Cedar Point Biological Station (41°13′ N, 101°39′ W) near Ogallala, in Keith County, along the North and South Platte Rivers, and also includes portions of Deuel, Garden, and Lincoln counties, southwestern Nebraska, USA. We have studied Cliff Swallows there since 1982. The 150 × 50 km study area contains ~160 Cliff Swallow colony sites, with about one-third of them 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, colony size was 385 ± 16 nests (mean ± SE; N = 1363). Each colony site tends to be separated from the next nearest by 1–10 km, but in a few cases by ≥20 km. In our study area, the birds nest on both natural cliff faces and artificial structures such as bridges, buildings, and highway culverts. The study site is described in detail by Brown and Brown (1996).

PLATE. 1.　Cliff Swallows at a Nebraska (USA) breeding colony. Photo credit: C. R. Brown.

Field methods

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 either were placed 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, with the principal criterion for inclusion being knowing exactly when a given bird first hit the net. All baseline measures of corticosterone used here were from birds bled within 3 minutes of initial contact with a net, to avoid the effects of handling stress on glucocorticoid response. Most of the birds for which testosterone was measured were also bled within 3 minutes of initial contact with a net; however, some individuals were sampled for testosterone up to 11 minutes after initial contact with a net. The interval between capture and blood sampling had no significant effect on testosterone levels in Cliff Swallows (Smith et al. 2005). Some individuals were sampled for both corticosterone and testosterone, and others for only one hormone or the other. In 2000–2001, we sampled birds for hormones at 39 colonies in total, ranging in size from 22 to 3400 nests (Brown et al. 2005, Smith et al. 2005, Raouf et al., *in press*). Blood samples were not collected from

all of our study colonies; we chose colony sites for inclusion primarily to maximize the range in colony sizes studied.

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, and then were transported to a laboratory at the Cedar Point Biological Station where plasma was separated by microhematocrit centrifugation and harvested with a Hamilton syringe. Plasma samples were stored at −20°C until analysis. Corticosterone and testosterone concentrations were measured by radioimmunoassay as described by Wingfield et al. (1992).

In 2001, some adult Cliff Swallows were held for 60-minute periods in order to measure their response to handling. Birds whose time of initial capture was known were held in mesh bags attached to the inside of coffee cans for an hour, and then were bled. Cliff Swallows show a stress response typical of small passerines, with corticosterone level increasing rapidly from 3 to 10 minutes, and then more slowly to reach a maximum within 60 minutes (C. Brown, M. Brown, and J. Wingfield, *unpublished data*).

At the time hormone samples were taken at each colony, we designated the colony's stage as either early, mid, or late. The early stage was when more than half of the birds in a colony were building nests; mid was when more than half of the colony was incubating; and late was when more than half of the colony was feeding nestlings. These periods were designated separately for each colony, and 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

TABLE 1. Models describing Cliff Swallow survival (φ) and recapture (*p*) probabilities, and transition probabilities (ψ) for individuals moving to the same or a different colony site or to a smaller or larger colony size.

Model number and notation†	Model description
(1) $\phi_{(c)} p_{(t)} \psi_{(s)}$	Survival constant for all classes of birds; recapture varying with time (year); transitions separate for birds moving to a different vs. staying at the same site or colony size, yet treating birds with hormone levels above and below the mean as the same.
(2) $\phi_{(c)} p_{(t)} \psi_{(g-s)}$	Survival constant for all classes of birds; recapture varying with time (year); transitions separate for birds moving to a different vs. staying at the same site or colony size, while also separate for birds with hormone levels above vs. below the mean.
(3) $\phi_{(g)} p_{(t)} \psi_{(s)}$	Survival separate for birds with hormone levels above vs. below the mean when moving vs. not moving to a different site or colony size; recapture varying with time (year); transitions separate for birds moving to a different vs. staying at the same site or colony size, yet treating birds with hormone levels above and below the mean as the same.
(4) $\phi_{(g)} p_{(t)} \psi_{(g-s)}$	Survival separate for birds with hormone levels above vs. below the mean when moving vs. not moving to a different site or colony size; recapture varying with time (year); transitions separate for birds moving to a different vs. staying at the same site or colony size, while also separate for birds with hormone levels above vs. below the mean.
(5) $\phi_{(c)} p_{(t)} \psi_{(c)}$	Survival constant for all classes of birds; recapture varying with time (year); transition constant for all classes of birds.

† Model number and notation are as used in Tables 2 and 3.

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 and Brown 1996) ensured that most individuals could be classified accurately based on the status of the colony as a whole. We found significantly higher corticosterone levels among birds during the late stage than during the early and mid stages (Raouf et al., *in press*). However, birds sampled during the early and mid stages were combined because there was no difference in average corticosterone levels between those two periods.

We continued mark–recapture at colonies in the study area in 2002–2004, but without sampling for hormones. During these years, we mist-netted adult Cliff Swallows at 27–31 colonies annually, all near the center of our study area within a 35-km radius of the Cedar Point Biological Station. Colonies of all sizes were sampled. The total number of bird captures during each of the five years of this study was 18 717, 16 401, 19 087, 20 309, and 19 815, respectively. This enabled us to determine whether individuals sampled for hormones in 2000–2001 were recaptured in the study area in a subsequent year, and an encounter history over the five years (indicating whether a bird was caught in a given season) was created for each individual for whom corticosterone or testosterone was measured.

Each year, 2–4 colonies were fumigated to remove ectoparasites as part of other work (e.g., Brown and Brown 2004*a*). Nests within these colonies were sprayed with a dilute solution of an insecticide, Dibrom, which was highly effective in killing swallow bugs (Brown and Brown 1996, 2004*a*). Nests were fumigated weekly to remove any bugs brought into the colony by transient birds. Each colony was sprayed in its entirety. Because the presence of ectoparasites may influence the likelihood of between-year dispersal in

Cliff Swallows (Brown and Brown 1992, 1996), we separated most analyses by fumigation status of the site where blood was initially sampled for an individual.

Cliff Swallow colony size was defined as the maximum number of nests at a site to contain one or more eggs. Active nests were counted at some sites by periodically checking the nest contents with a dental mirror and flashlight, whereas the colony size at other sites was estimated by counting the number of nests in active sections of the colony. Full details on these methods of determining colony sizes are given in Brown and Brown (1996).

Statistical analysis of survival

We estimated between-year movement probabilities using the general methods of Lebreton et al. (1992) and Burnham and Anderson (2002). Program MARK (White and Burnham 1999) was used to assess the fit of different models to a given data set (and thus the support of different hypotheses) and to generate maximum likelihood estimates of survival, recapture, and movement probabilities. We identified a priori a set of models that were fit to the data for nonfumigated and fumigated colonies separately (Table 1). All models incorporated time dependence (different parameters for different years) in recapture probability, in part reflecting varying netting effort over the years. Survival and movement probabilities, however, were time constant in all cases; preliminary analyses showed that models with time-dependent survival or movement would not converge, probably due to the many parameters relative to sample size in these multistate models.

Model fit was assessed by the Akaike Information Criterion (Burnham and Anderson 2002), corrected for sample size (AIC$_c$), as provided by MARK. In theory, the model with the lowest AIC$_c$ is the so-called best model. The currently accepted convention (Burnham

and Anderson 2002) is that models with AIC_c values that differ by less than 2.0 are indistinguishable statistically. In these cases, one can use the "AIC_c weight" provided by MARK as a measure of a model's relative probability of being the best model for the data compared to the others tested. Because our models also specifically estimated annual recapture probability, any differences among years in the likelihood of recapturing birds (due to sampling effort or number of sites netted) were accounted for in estimating annual movement probability.

Before comparing the fit of the candidate models, we performed a goodness-of-fit test for each data set using program RELEASE (Burnham et al. 1987). This evaluated how well the data met the variance assumptions inherent in the binomial distribution used in mark–recapture analysis. When a data set does not meet the assumptions, it is usually because the data are overdispersed, reflecting lack of independence or some heterogeneity among observations, and often brought about by the presence of transients or trap dependence. We assessed the goodness of fit for the classical Cormack-Jolly-Seber (CJS) model (time-dependent survival and time-dependent recapture) by calculating a combined χ^2 value based on Tests 2 and 3 in RELEASE (Pradel et al. 2005). We used a single-state goodness-of-fit test, because no tractable multistate tests are currently available (Lebreton and Pradel 2002). However, data sets that meet the single-state assumptions are probably appropriate for multistate analysis (J.-D. Lebreton, *personal communication*). Tests 2 and 3 in RELEASE showed acceptable goodness of fit for the data sets containing all birds sampled for corticosterone in nonfumigated colonies ($\chi^2_5 = 5.45$, $P = 0.36$) and in fumigated colonies ($\chi^2_4 = 1.09$, $P = 0.90$), for corticosterone among birds held for 60 minutes ($\chi^2_4 = 0.00$, $P = 0.99$), and for males ($\chi^2_5 = 8.17$, $P = 0.15$) and females ($\chi^2_4 = 2.13$, $P = 0.71$) sampled for testosterone in nonfumigated colonies. Thus, no variance inflation adjustments were needed for these analyses.

Multistate parameter designations

Because of the large number of parameters inherent in even relatively simple multistate models (Lebreton and Pradel 2002), we did not attempt to estimate movement probabilities separately for different colony sites, nesting stages, or absolute hormone levels (cf. Brown et al. 2005). Instead, for each colony, we calculated the average baseline corticosterone level for birds sampled there in a given nesting stage (early, mid, and late), and designated each bird as either above or below the mean for that site at that stage. We did a similar calculation and designation for all birds sampled for testosterone over daily or two-day intervals throughout the season (see Smith et al. 2005); this allowed us to control for the pronounced date-related variation in testosterone levels over the season and made it possible to compare birds with relatively high vs. relatively low

levels of testosterone, regardless of when in the season the samples were taken. All birds were thus coded as "A," above the mean for corticosterone or testosterone, or "B," below the mean, on their initial capture in the multistate encounter histories. For birds held for 60 minutes, we used the same designations for maximum corticosterone level.

We then performed two types of analysis. One was to examine whether birds with hormone levels above or below the mean at a given time or site tended to be more or less likely to move to a different colony site in a later year. All birds recaptured in later years were coded as "S" if they used the same colony where they had been initially sampled for hormones in a particular year, or "D" if they moved to a different physical location. In the second analysis, all birds recaptured in later years were coded as "S" if they used a colony smaller in size than the one where they had been initially sampled for hormones in a particular year, or "L" if they used a colony of the same size or larger, irrespective of the colony's physical location. This allowed us to estimate formal transition (i.e., movement) probabilities for birds with different relative hormone levels, and the multistate analysis accounted in the estimation for cases in which birds were missed in a given year, but later reappeared at a colony. Transition probabilities that were impossible, given our parameter designations (e.g., going from S or L back to A or B, going from A to B) were fixed at 0.00 using the Fix Parameters utility in MARK. For baseline corticosterone, we did separate analyses for birds sampled at nonfumigated vs. fumigated sites, given that between-year movement may be affected by parasite load (Brown and Brown 1992, 1996). For testosterone, we used only nonfumigated data because relatively few birds were sampled for testosterone in fumigated colonies. For birds held (for which sample sizes were smaller), data from all colonies were combined because fumigation had no effect on corticosterone levels measured after 60 minutes (Raouf et al., *in press*). The sexes were separated for analyses of testosterone, given the differences between males and females in average testosterone level (Smith et al. 2005), but they were combined for corticosterone because there were no intersexual differences in levels of that hormone (Raouf et al., *in press*).

RESULTS

Movement between sites

Corticosterone.—For Cliff Swallows sampled for baseline corticosterone ($N = 784$) in nonfumigated colonies, a model treating between-year movement probabilities the same among birds that were above and below the mean for their colony and nesting stage was the best fit (Table 2). This model estimated the combined movement probabilities (mean ± SE) for both classes of birds as 0.467 ± 0.095 for going to a different

TABLE 2. Models to estimate movement probabilities (ψ) to a different or the same colony site in a later year in relation to whether a Cliff Swallow had a hormone level above vs. below the mean for the colony and time of sampling, and the models' degree of fit to the data.

Model	AIC_c	ΔAIC_c	AIC_c weight	No. parameters
Baseline corticosterone, nonfumigated colonies				
(1) $\phi_{(c)} p_{(t)} \psi_{(s)}$	1896.201	0.00	0.63041	8
(2) $\phi_{(c)} p_{(t)} \psi_{(g-s)}$	1898.105	1.90	0.24342	10
(3) $\phi_{(g)} p_{(t)} \psi_{(s)}$	1900.114	3.91	0.08913	10
(4) $\phi_{(g)} p_{(t)} \psi_{(g-s)}$	1901.870	5.67	0.03705	12
(5) $\phi_{(c)} p_{(t)} \psi_{(c)}$	2021.095	124.89	0.00000	6
Baseline corticosterone, fumigated colonies				
(1) $\phi_{(c)} p_{(t)} \psi_{(s)}$	982.339	0.00	0.77181	8
(5) $\phi_{(c)} p_{(t)} \psi_{(c)}$	984.866	2.53	0.21817	6
(3) $\phi_{(g)} p_{(t)} \psi_{(s)}$	991.029	8.69	0.01001	10
Corticosterone after 60 minutes, all colonies				
(5) $\phi_{(c)} p_{(t)} \psi_{(c)}$	652.603	0.00	0.84974	5
(1) $\phi_{(c)} p_{(t)} \psi_{(s)}$	656.303	3.70	0.13366	7
(2) $\phi_{(c)} p_{(t)} \psi_{(g-s)}$	660.602	8.00	0.01558	9
(3) $\phi_{(g)} p_{(t)} \psi_{(s)}$	666.294	13.69	0.00090	10
(4) $\phi_{(g)} p_{(t)} \psi_{(g-s)}$	670.375	17.77	0.00012	12
Testosterone, males				
(4) $\phi_{(g)} p_{(t)} \psi_{(g-s)}$	1088.225	0.00	0.52881	13
(2) $\phi_{(c)} p_{(t)} \psi_{(g-s)}$	1088.645	0.42	0.42860	11
(1) $\phi_{(c)} p_{(t)} \psi_{(s)}$	1094.385	6.16	0.02430	9
(3) $\phi_{(g)} p_{(t)} \psi_{(s)}$	1094.952	6.73	0.01830	11
(5) $\phi_{(c)} p_{(t)} \psi_{(c)}$	1148.575	60.35	0.00000	6
Testosterone, females				
(2) $\phi_{(c)} p_{(t)} \psi_{(g-s)}$	959.838	0.00	0.39711	10
(3) $\phi_{(g)} p_{(t)} \psi_{(s)}$	960.976	1.14	0.22482	11
(4) $\phi_{(g)} p_{(t)} \psi_{(g-s)}$	961.201	1.36	0.20093	13
(1) $\phi_{(c)} p_{(t)} \psi_{(s)}$	961.453	1.61	0.17714	8
(5) $\phi_{(c)} p_{(t)} \psi_{(c)}$	1025.377	65.54	0.00000	6

Notes: See Table 1 for model descriptions. Models also contained parameters for annual survival (ϕ) and recapture (p) probabilities. Model numbers not shown in a given category were those not reaching convergence. Differences in the number of estimable parameters between categories reflected differences in the way data were distributed within categories.

colony site in a later year and 0.059 ± 0.017 for staying at the same site (with a 0.474 probability of not being encountered again due to death or permanent emigration). However, a model that had separate movement probabilities for birds above vs. below the mean was (barely) within 2.0 in AIC_c of the best model (Table 2). This model estimated movement probabilities for birds above the mean corticosterone as 0.472 ± 0.107 for going to a different colony site and 0.036 ± 0.018 for staying at the same site, and for birds below the mean corticosterone, as 0.466 ± 0.101 for going to a different site and 0.075 ± 0.023 for staying at the same site.

For Cliff Swallows sampled for baseline corticosterone ($N = 261$) in fumigated colonies, no models with separate movement probabilities for birds above and below the mean for their colony and nesting stage would reach convergence (Table 2). This prevented a formal test of the effect of corticosterone on movement for birds from fumigated sites; however, that convergence could not be reached suggests little support in the existing data for any corticosterone-related pattern. The best-fitting model that would converge (Table 2)

estimated movement probabilities for birds both above and below the mean as 0.263 ± 0.114 for going to a different colony site and 0.454 ± 0.195 for staying at the same site.

For Cliff Swallows whose corticosterone levels were measured after 60 minutes of being held ($N = 218$), a model with a constant movement probability for all possible transitions was the best fit (Table 2). The next best model with separate movement probabilities for birds above vs. below the mean corticosterone ranked well below in the degree to which it fit our data (Table 2).

Testosterone.—For both male ($N = 436$) and female ($N = 428$) Cliff Swallows sampled for testosterone in nonfumigated colonies, a model with separate between-year movement probabilities for birds above vs. below the mean at the time of sampling was the best fit (Table 2). This was strongly the case for males; the next best model with birds above and below the mean treated the same differed by more than 6.0 in AIC_c (Table 2). Among females, the next best alternative that combined birds above and below the mean differed by only 1.14 in AIC_c (Table 2), although the AIC_c weights indicated

TABLE 3. Models to estimate transition probabilities (ψ) of choosing larger or smaller colonies in a later year in relation to whether a Cliff Swallow had a hormone level above vs. below the mean for the colony and time of sampling, and the models' degree of fit to the data.

Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	No. parameters
Baseline corticosterone, nonfumigated colonies				
(4) $\phi_{(g)} p_{(t)} \psi_{(g-s)}$	2032.084	0.00	0.56161	11
(2) $\phi_{(c)} p_{(t)} \psi_{(g-s)}$	2033.862	1.78	0.23094	9
(3) $\phi_{(g)} p_{(t)} \psi_{(s)}$	2034.835	2.75	0.14191	13
(1) $\phi_{(c)} p_{(t)} \psi_{(s)}$	2036.381	4.30	0.06553	11
(5) $\phi_{(c)} p_{(t)} \psi_{(c)}$	2060.457	28.37	0.00001	6
Baseline corticosterone, fumigated colonies				
(2) $\phi_{(c)} p_{(t)} \psi_{(g-s)}$	952.320	0.00	0.84022	9
(1) $\phi_{(c)} p_{(t)} \psi_{(s)}$	955.640	3.32	0.15978	11
(5) $\phi_{(c)} p_{(t)} \psi_{(c)}$	979.929	27.61	0.00000	6
Corticosterone after 60 minutes, all colonies				
(1) $\phi_{(c)} p_{(t)} \psi_{(s)}$	634.294	0.00	0.74157	8
(2) $\phi_{(c)} p_{(t)} \psi_{(g-s)}$	637.475	3.18	0.15120	10
(3) $\phi_{(g)} p_{(t)} \psi_{(s)}$	638.721	4.43	0.08107	11
(4) $\phi_{(g)} p_{(t)} \psi_{(g-s)}$	640.984	6.69	0.02615	13
(5) $\phi_{(c)} p_{(t)} \psi_{(c)}$	656.763	22.47	0.00001	5
Testosterone, males				
(2) $\phi_{(c)} p_{(t)} \psi_{(g-s)}$	1149.233	0.00	0.72149	11
(1) $\phi_{(c)} p_{(t)} \psi_{(s)}$	1151.137	1.90	0.27851	9
(5) $\phi_{(c)} p_{(t)} \psi_{(c)}$	1179.665	30.43	0.00000	6
Testosterone, females				
(2) $\phi_{(c)} p_{(t)} \psi_{(g-s)}$	1020.620	0.00	0.68384	11
(4) $\phi_{(g)} p_{(t)} \psi_{(g-s)}$	1022.908	2.29	0.21786	14
(3) $\phi_{(g)} p_{(t)} \psi_{(s)}$	1025.797	5.18	0.05139	12
(1) $\phi_{(c)} p_{(t)} \psi_{(s)}$	1026.016	5.40	0.04606	9
(5) $\phi_{(c)} p_{(t)} \psi_{(c)}$	1033.984	13.36	0.00086	6

Notes: See Table 1 for model descriptions. Models also contained parameters for annual survival (ϕ) and recapture (p) probabilities. Model numbers not shown in a given category were those not reaching convergence. Differences in the number of estimable parameters between categories reflected differences in the way that data were distributed within categories.

that the top model with an effect of testosterone for females was 1.77 times more likely than the next best alternative. The best-fitting model indicated that males above vs. below the mean testosterone level for a given sampling interval had probabilities of 0.866 ± 0.004 and 0.328 ± 0.085 for going to a different colony site in a later year, respectively, and probabilities of 0.134 ± 0.004 and 0.114 ± 0.039 for staying at the same site, respectively. For females above vs. below the mean, the best-fitting model estimated probabilities of 0.312 ± 0.096 and 0.571 ± 0.165 for going to a different site in a later year, respectively, and probabilities of 0.066 ± 0.034 and 0.055 ± 0.027 for staying at the same colony site, respectively.

Transitions between colony sizes

Corticosterone.—For Cliff Swallows sampled for baseline corticosterone in both nonfumigated and fumigated colonies, a model treating colony-size transitions between years as different for birds above vs. below the mean corticosterone was clearly the best fit (Table 3). In each case, the next best model without an effect of corticosterone differed by more than 2.0 in AIC$_c$. For birds initially sampled in nonfumigated colonies, those above vs. below the mean had transition probabilities of 0.380 ± 0.014 and 0.471 ± 0.016 to

a colony of the same size or larger in a later year, respectively, and transition probabilities of 0.245 ± 0.093 and 0.202 ± 0.080 to a smaller colony, respectively. For those in fumigated colonies, birds above vs. below the mean had transition probabilities of 0.601 ± 0.017 and 0.826 ± 0.004 to a colony of the same size or larger in a later year, respectively, and transition probabilities of 0.203 ± 0.090 and 0.173 ± 0.004 to a smaller colony, respectively.

For Cliff Swallows sampled for corticosterone after being held for 60 minutes, a model with colony-size transition probabilities the same for birds above and below the mean was the best fit (Table 3). A model with an effect of corticosterone differed by 3.18 in AIC$_c$, indicating little support.

Testosterone.—For both male and female Cliff Swallows sampled for testosterone in nonfumigated colonies, a model treating colony-size transition probabilities between years as different for birds above vs. below the mean was the best fit (Table 3). The next best alternative model without an effect of testosterone differed by 5.18 in AIC$_c$ for females and 1.90 in males, but even in the latter case, the AIC$_c$ weights indicated that the top model with an effect of testosterone was 2.59 times more likely (Table 3). Among males, those with testosterone levels above vs. below the mean had

transition probabilities of 0.754 ± 0.004 and 0.405 ± 0.080 to a colony of the same size or larger in a later year, respectively, and transition probabilities of 0.244 ± 0.004 and 0.153 ± 0.049 to a smaller colony, respectively. Among females, those with testosterone levels above vs. below the mean had transition probabilities of 0.148 ± 0.062 and 0.427 ± 0.141 to a colony of the same size or larger in a later year, respectively, and transition probabilities of 0.236 ± 0.088 and 0.194 ± 0.066 to a smaller colony, respectively.

DISCUSSION

The analyses in this study provide evidence for an apparent association between an individual's endogenous levels of corticosterone and testosterone and its selection of a relative colony size in a later year. For corticosterone in the sexes combined in both parasite-free sites and colonies naturally infested with ectoparasites, birds with relatively lower levels of baseline corticosterone were more likely to settle subsequently in larger colonies. For testosterone, this same pattern held for females but was reversed in males, and testosterone also seemed to be associated with dispersal to new breeding sites between years in both sexes. In contrast, there was little evidence for an effect of corticosterone on dispersal to new sites, and the relative extent of an individual's maximum corticosterone response (after being held for 60 minutes) was unrelated to either colony-size choice or dispersal to new sites. To our knowledge, no previous studies on other taxa have looked for a relationship between endogenous levels of these steroid hormones and choice of group size in the wild.

Advantages and limitations of multistate mark–recapture

Our demonstration of an effect of steroid hormones on colony choice may be related, in part, to the use of multistate statistical methods. Because the detection of a transition (between colony sizes or colony sites) will be related to both the likelihood of recapturing an individual in a given year and whether an individual survives to make a transition, it is necessary to include survival and recapture probabilities in movement models. We evaluated different models for survival and recapture in both our candidate set and in preliminary analyses, and those used here were the most appropriate biologically. They are also consistent in structure with past single-state analyses of Cliff Swallow survival (Brown and Brown 2004b, Brown et al. 2005). The movement and transition probabilities estimated here thus take potential variation in survival and recapture into account. However, a full exploration of how survival per se is related to steroid hormone levels in Cliff Swallows was done in another study (Brown et al. 2005), in which we used single-state techniques that treated hormone level as a covariate and thus allowed

a more detailed examination of the effect of hormones on survival. Unfortunately, similar methods cannot be used with movement analyses because there is as yet no way to model covariates when states (i.e., the colonies occupied) change over an individual's lifetime.

As with most mark–recapture studies, two general caveats are in order. One is that we estimated local movement only. Cliff Swallows that permanently emigrated from the study area between years would be counted as dead in our analyses and would not figure into estimation of movement probabilities. This problem also applies to survival analyses, but because study areas are finite, there is no good way to deal with it (Barrowclough 1978, Payne 1990, Marshall et al. 2004). However, the conclusions reported here on relative tendency to use different sites or different colony sizes will be unaffected by long-distance, permanent emigration, as long as this emigration does not covary with corticosterone or testosterone levels. This seems likely, at least for corticosterone: within the study area, corticosterone had no major effect on whether birds dispersed to a different site or stayed at the same one.

The other caveat, as in the earlier study of survival in relation to hormone level (Brown et al. 2005), is that levels of corticosterone and testosterone are not fixed for an individual, that is, they may change between days or years. Our analyses, as constructed, implicitly assume that hormone level is unchanging and that baseline levels measured are an accurate relative index of an individual's endogenous hormone profile. The ideal way to analyze movement would be to sample the same individuals for each hormone repeatedly (at least on each occasion that they are captured), and to model movement in relation to these changing covariates. Unfortunately, this is not practical in the field, at least on the scale necessary for mark–recapture, and tractable statistical methods for handling varying covariates in either single-state or multistate models do not exist at present (Bonner and Schwarz 2004, Kendall 2004). However, using a single classification for a potentially changing covariate represents a conservative analysis if one assumes that the covariate distribution is "polluted" by misclassifications (e.g., Lank et al. 1990, Brown and Brown 1998). In such cases, if differences are found (as in this study), they are probably of sufficient strength to overcome any error introduced by the changing covariates (Brown and Brown 2004c).

Corticosterone and colony choice

In Cliff Swallows, changes in corticosterone level appear to be associated with adverse events such as increased ectoparasitism or reduced foraging success (Raouf et al., in press). Higher corticosterone levels cause increased allocation of time and effort to foraging and greater energy assimilation during challenging conditions (such as bad weather that curtails insect availability, and when the birds are exposed to infestations of blood-feeding bugs). Absolute levels of base-

line corticosterone thus may vary with the extent of these conditions that a bird experiences at any given time (Raouf et al., *in press*). However, in this study, our measure of corticosterone for each individual was relative to others in the same colony at the same time, and we controlled for any variation among sites or time period in absolute corticosterone level. Consequently, our results presumably provide an index of individuals' inherent propensity to show glucocorticoid response to environmental events, independent of their circumstances at the time of sampling. Clearly, variation in levels of baseline corticosterone exists among Cliff Swallows at a given time in the season or at a given colony site (see Brown et al. 2005). The cause of the variability is unclear, but the results show that this variation is associated with settlement patterns.

Why would birds with higher levels of baseline corticosterone be more likely to choose a colony that was smaller in size in a later year, in contrast to birds with lower than average corticosterone levels? One possibility is that individuals with a propensity to maintain inherently higher baseline corticosterone levels would be disadvantaged by moving to colonies of greater size, where the presence of large numbers of blood-feeding swallow bugs (Brown and Brown 1986, 1996) causes seasonally elevated glucocorticoid responses (Raouf et al., *in press*). Because high baseline levels of corticosterone lead to lower annual survival (Brown et al. 2005), individuals could regulate their circulating levels of corticosterone (and thus potentially their survival prospects) by being sensitive to and selecting an appropriate colony size. Birds predisposed to lower baseline corticosterone levels would pay a lower price for settling in a larger colony because they could potentially better "afford" the expected increase in glucocorticoid response associated with such sites. The estimated transition probabilities to colonies of different sizes suggest more an avoidance of larger colonies by some birds with higher corticosterone levels and less an active selection of smaller colonies by those individuals, because the transition probabilities to smaller colonies were more similar for all birds, regardless of relative corticosterone level. That we found the same pattern among birds from fumigated colonies indicates that the propensity to select colony sizes is independent of widely varying conditions (e.g., level of ectoparasitism) and the extent of glucocorticoid response at the time of the initial corticosterone sampling. In an absolute sense, the higher colony-size transition probabilities for birds from fumigated sites indicate both greater site fidelity to less infested colonies and higher survival of individuals in fumigated colonies (Brown and Brown 1996, 2004b), making those individuals more likely to be encountered within the study area in a later year.

In contrast to selection of a colony size, we found little evidence for a strong effect of corticosterone on between-year dispersal among discrete colony sites.

Although corticosterone has been shown to rise during the dispersal phase of the life cycle in some organisms (Holekamp et al. 1984, Silverin 1997, Belthoff and Dufty 1998) and thus may cause movement, these cases all involve young animals dispersing for the first time. Adult dispersal rarely appears to be associated with levels of glucocorticoids, and our data are consistent with that pattern. Because relative corticosterone level did not correlate with extent of movement, our results seem to indicate that the colony-size transitions in relation to corticosterone level reflect sensitivity to group size per se, and cannot be explained by differential dispersal away from the initial sampling site or associations between physical movement and the likelihood of encountering a smaller or larger colony.

Cliff Swallow corticosterone levels measured after 60 minutes had no relationship with either choice of colony size or likelihood of dispersing to a different site in a later year. This is consistent with an earlier study (Brown et al. 2005) that showed no apparent effect of corticosterone levels after 60 minutes on annual survival. The maximum corticosterone level that a bird exhibits in response to handling stress thus does not seem to have any long-term consequences. Instead, it underscores the importance of natural phenotypic variation in baseline levels for studying life-history effects of steroid hormones such as corticosterone.

Testosterone and colony choice

As with corticosterone, our analyses provide an index of a bird's propensity to exhibit a low or high testosterone level, relative to other individuals at the same time and at the same site, and thus they control for seasonal variation or effects of social environment. Over the course of a nesting season, Cliff Swallows of each sex show a seasonal rise in levels of testosterone early in the nesting cycle, corresponding to the period when birds are establishing nest ownership and laying eggs, and then a decline as birds switch to parental duties (Smith et al. 2005). When we control for this date-related variation, both male and female Cliff Swallows in larger colonies tend to have higher average levels of testosterone, possibly reflecting greater competition for matings (often extrapair) and nest sites in the larger groups (Smith et al. 2005). Thus, the apparent effect of testosterone on subsequent colony-size choice in males is perhaps not surprising, with males with a propensity for higher endogenous levels (relative to others of the same colony) being more likely to settle in a larger colony in the next year. Individuals predisposed to higher testosterone levels (perhaps because they have bigger testes; Brown and Brown 2003) will be more successful in larger colonies, whereas in small colonies the same individuals would pay the potential costs of higher testosterone (such as immunosuppression; Roberts et al. 2004) without realizing any of the advantages. In contrast, individuals with inherently lower levels of testosterone would be at a disadvantage

in the greater competitive milieu of larger colonies and should be more likely to avoid such sites, as is apparently the case.

The reverse pattern in females, however, is difficult to explain. Females also show higher average levels of testosterone in larger colonies (Smith et al. 2005), perhaps implying a competitive advantage for more aggressive individuals in those situations. Consequently, we would predict that females with higher relative testosterone levels should be more likely to settle in larger colonies. The evidence against this prediction is strong, however, with the best-fitting model being clearly superior to any alternative that might have suggested a different pattern. We can offer no plausible hypothesis for why females with lower levels of testosterone would prefer larger colonies, in which their reduced testosterone concentrations conceivably render them at a competitive disadvantage.

Unlike the case with corticosterone, relative levels of testosterone were also correlated with dispersal to new colony sites in later years. This was the case in both sexes, although again the patterns were reversed. Males with higher levels of testosterone were more likely to move to a different site in a later year, whereas those with lower levels were less likely to disperse. If higher testosterone leads to greater aggressiveness and competitive ability, such individuals might be more successful in establishing themselves at an unfamiliar site and securing a nest site there. However, this should also be the case for females, and we found no evidence for such a pattern. Our results on testosterone all came from birds sampled at nonfumigated colonies, and there is inherently more dispersal from these sites; thus, the relatively high movement probabilities in general for the testosterone data set are somewhat surprising and suggest that many of the birds in this analysis were encountered somewhere in the study area. The opposing patterns for males vs. females in both colony-size transitions and site-movement probabilities suggest some potential covariation between choosing a colony of a relative size and whether one moves elsewhere or stays at the same colony site, but the nature of this relationship, if any, has not been explored.

Phenotypic differences and coloniality

To our knowledge, these results are the first to show neuroendocrinological differences among birds choosing nesting colonies of different sizes. They presumably reflect the inherent propensity of individuals to respond hormonally to environmental conditions, and thus they suggest that Cliff Swallows sort themselves among colonies to some degree. Because there are clear survival consequences for individuals with different endogenous levels of these steroid hormones, especially corticosterone (Brown et al. 2005), and because baseline levels vary with colony size (Raouf et al., *in press*), selection should favor a link between an individual's inherent sensitivity to glucocorticoid hormones and psychological processes involved in choice of a breeding site. For testosterone, males with higher levels will be more effective competitors in larger colonies, and those who select larger colonies may thus have a net advantage over those with similar levels who ''waste'' them in less competitive small groups. Of course, other factors also influence an individual's expectation of success in groups of different sizes (Brown and Brown 1996), and basal hormone level is only one factor that may be linked to group-size choice. Nevertheless, the broad patterns reported here are generally consistent with how we would intuitively expect birds to sort themselves among group sizes, given the apparent fitness consequences of different hormone levels (Brown et al. 2005, Smith et al. 2005).

Choosing a colony size has a heritable component in Cliff Swallows (Brown and Brown 2000). Therefore, if the endocrinological characteristics of individuals reported here are a reason underlying heritable colony choice, these characteristics must also have a heritable basis. Relatively little work has been done on the heritability of circulating levels of either corticosterone or testosterone, especially in birds, although the evidence available suggests at least that basal level of corticosterone (or of the similar glucocorticoid, cortisol) has moderately high heritabilities in rats, humans, and some fish (Pottinger and Carrick 1999, Martin et al. 2000, Wüst et al. 2000, Tanck et al. 2001, Fevolden et al. 2002, Bartels et al. 2003). One study suggests that testosterone concentrations might have a partly genetic basis in Stonechats (*Saxicola torquata*; Rödl et al. 2004). If the same patterns apply to Cliff Swallows, genetic correlations between natural variations in hormone level and choice of colony size could be established and, given the survival consequences associated with different hormone levels and colony sizes (Brown et al. 2005, Raouf et al., *in press*), probably could be maintained by viability selection alone.

Studies of avian coloniality typically have neglected to consider that individuals who occupy colonies of different sizes may have very different phenotypic attributes (Brown and Brown 2001). Consequently, direct comparisons of reproductive success or other factors among birds in different groups may be confounded by differences in individual quality; this may be one reason that so few general patterns in the evolution of coloniality have emerged (Wittenberger and Hunt 1985, Brown and Brown 2001). Only recently, several studies of birds have provided indications that there are genetically based differences among individuals who choose different-sized colonies (Brown and Brown 2000, Møller 2002, Brown et al. 2003). The extensive range in colony size observed in Cliff Swallows may represent a series of polymorphisms, in which individuals are adapted to relatively small, medium, or large groups (Brown and Brown 2000). The only phenotypic difference identified among these individuals (until this study) was the greater likelihood that birds potentially

susceptible to parasitism by fleas (Siphonaptera) would settle in larger groups (Brown and Brown 1996). The data reported here on how relative hormone level correlates with subsequent colony choice are much stronger than the earlier work on parasitism, and they provide better evidence for phenotypic sorting among groups. Although ecological factors such as local food supply also undoubtedly influence colony size in Cliff Swallows (Brown et al. 2002), the evidence is mounting that coloniality in this species (and perhaps others) reflects clumped distributions of individuals that differ in phenotypic characteristics.

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