EFFECTS OF ENDOGENOUS STEROID HORMONE LEVELS ON ANNUAL SURVIVAL IN CLIFF SWALLOWS

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Abstract. The hormone corticosterone is an important part of animals' response to environmental stress, modulating short-term adaptive changes in behavior and physiology. The hormone testosterone is also critical, especially for males, in regulating the expression of sexual behavior and parental care. These hormones can have costly consequences, however, and within populations individuals show variation in endogenous levels of both corticosterone and testosterone. We studied how annual survival varied as a function of natural levels of these hormones in colonially breeding Cliff Swallows (*Petrochelidon pyrrhonota*) in southwestern Nebraska, USA, in 2000–2003. We sampled hormone levels of birds caught at colonies and using mark–recapture, monitored their survival through subsequent years in the study area. Maximum-likelihood estimation and model fitting (with program MARK) revealed that birds sampled for corticosterone in colonies of all sizes late in the season had curvilinear survival; individuals with very low and very high levels of corticosterone had lower survival than those with intermediate levels. Annual survival of birds sampled earlier in the season, however, generally declined with increasing corticosterone level. More birds than expected, given the survival functions, had the very low corticosterone levels in nonfumigated colonies later in the year, suggesting perhaps a compensatory benefit unrelated to survival for very low corticosterone levels. In a more limited analysis, testosterone appeared to have little effect on annual survival, although some evidence suggested that females with endogenous testosterone levels below the mean for a given date might have survived better.

Key words: Cliff Swallow; coloniality; corticosterone; endogenous steroid hormones; life history; mark–recapture; Petrochelidon pyrrhonota; *social behavior; survival; testosterone.*

INTRODUCTION

The steroid hormones corticosterone and testosterone play critical roles in the breeding biology of wild birds. Circulating levels of corticosterone increase when birds are faced with physiologically challenging conditions such as food scarcity, the energetic demands of offspring, parasitism by blood-feeding arthropods, or increased rates of social interaction brought about by crowding (e.g., Astheimer et al. 1994, Wingfield 1994*b*, Marra and Holberton 1998, O'Reilly and Wingfield 2001, Rogovin et al. 2003; S. Raouf, L. C. Smith, M. B. Brown, J. C. Wingfield, and C. R. Brown, *unpublished manuscript*). Temporary rises in corticosterone are believed to be beneficial, serving to redirect individuals' behavior and physiology to foraging or self-maintenance and to enhance assimilation of energy during the stressful period (Wingfield et al. 1983, 1994, 1995). Testosterone modulates the expression of sexual

and aggressive behavior, parental care, and the development of some secondary sexual characteristics in both males and females, and most species show a seasonal rise in circulating testosterone concentrations that tends to be directly correlated with the intensity of intrasexual competition and extent of parental care (Wingfield et al. 1990, 2000, Wingfield 1994*a*). Higher testosterone levels among birds competing for mates appear to be advantageous because they promote aggression and/or mate-guarding.

Chronically high levels of either steroid hormone, however, can be deleterious. High levels of corticosterone over an extended period are known to reduce or impair reproductive function among captive individuals in various taxa (e.g., Moore and Miller 1984, Sapolsky 1985, Orr and Mann 1992, DeNardo and Licht 1993, Knapp and Moore 1995, Cameron 1997, Fox et al. 1997), may impair cognitive abilities (Kitaysky et al. 2003), and are thought to suppress immune function in some cases (Grossman 1990, Fowles et al. 1993, Boonstra et al. 2001, Saino et al. 2003). High concentrations of testosterone may also have a suppressive effect on the immune system, making individuals more susceptible to deleterious pathogens and parasites (e.g.,

PLATE. 1. Adult Cliff Swallow (*Petrochelidon pyrrhonota*) at its nest in a colony in southwestern Nebraska. Photo credit: C. R. Brown.

Folstad and Karter 1992, Slater and Schreck 1993, Zuk et al. 1995, Hillgarth and Wingfield 1997, Verhulst et al. 1999, Peters 2000). Less is known about the consequences of very low levels of steroid hormones in wild birds, but without the change in behavior and energy uptake during stressful events modulated by corticosterone, it seems likely that individuals with very low levels of that hormone would be disadvantaged.

Despite the potential trade-offs associated with different steroid hormone levels, almost nothing is known about how endogenous concentrations of these hormones influence the likelihood of survival in free-living animals. Some studies have assessed annual return rates of individuals whose testosterone levels were artificially increased (Dufty 1989, Nolan et al. 1992) or whose endogenous levels of corticosterone were known (Rogovin et al. 2003), but this work was based on a relatively few number of animals and did not employ formal survival analyses. Other studies have measured nestling survival in relation to corticosterone levels over a 5-day period before young birds fledged (Suorsa et al. 2003), and correlated corticosterone levels measured in response to handling stress with survival during periods of food scarcity (in iguanas; Romero and Wikelski 2001).

Knowing how annual survival varies with hormone level is important in evaluating the costs and benefits associated with evolved hormonal responses; for example, reduced survival with very high testosterone levels might constrain the magnitude or duration of the seasonal rise in testosterone seen in many birds, and

any survival costs associated with both high and low levels of corticosterone could select for an intermediate baseline level of that hormone. In this study, we measured annual survival probability over a four-year period as a function of endogenous levels of corticosterone and testosterone in colonially nesting Cliff Swallows (*Petrochelidon pyrrhonota*). Using a sample of over 1000 birds for which baseline corticosterone levels were measured (S. Raouf, L. C. Smith, M. B. Brown, J. C. Wingfield, and C. R. Brown, *unpublished manuscript*), and a similar sample of over 800 birds for which testosterone was measured (Smith et al. 2005), we had enough data to apply mark–recapture statistical models (e.g., Lebreton et al. 1992). By fitting different survival models with and without hormone levels as covariates, we evaluated whether differing levels of corticosterone and testosterone were associated with increased or decreased annual survivorship. Because levels of each hormone varied among birds in colonies of different sizes, we also analyzed whether any effect of hormones on survival depended on colony size. Our results provide one of the few formal tests of how endogenous (baseline) corticosterone and testosterone levels potentially affect annual survival in free-living animals.

METHODS

Study animal and study site

Cliff Swallows are highly colonial passerines that breed throughout most of western North America (Brown and Brown 1995; see Plate 1). 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 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. 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. There are ~160 Cliff Swallow colony sites in our 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 two to 3700 nests, with some birds nesting solitarily. Over a 20-year period, colony size (n = 1363) was 363 ± 16 nests (mean ± 1 SE). 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).

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 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 reported here were from birds bled within 3 minutes of initial contact with a net, to avoid the effects of handling stress on gluco-

corticoid 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).

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 transported back 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). 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.

In 2001, some adult Cliff Swallows were held for 60-minute periods in order to measure the stress 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, then more slowly to reach a maximum by 60 minutes (S. Raouf, L. C. Smith, M. B. Brown, J. C. Wingfield, and C. R. Brown, *unpublished manuscript*).

At the time when hormone samples were taken at each colony, 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 was when over half of the colony was incubating, and late was when over 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 of the breeding season. The exact nesting stage was not known for any of the adult birds sampled, as 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. Survival analyses involving corticosterone were done by stage because we found significantly higher corticosterone levels among birds during the late stage than during the early and mid stages (S. Raouf, L. C. Smith, M. B. Brown, J. C. Wingfield, and C. R. Brown, *unpublished manuscript*). However, we combined birds from the early and mid stages because there was no difference in corticosterone levels between those two periods. In no case did we use data for the

same individual in more than one stage in the same year.

We continued mark–recapture at colonies in the study area in 2002 and 2003, but without sampling for hormones. During the 2000–2003 period, we mist-netted adult Cliff Swallows at 20–35 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 numbers of captures during the four years of this study were 18 717, 16 401, 19 087, and 20 309 birds. This enabled us to determine whether individuals sampled for hormones in 2000–2001 were recaught in the study area in a subsequent year, and an encounter history over the four years (indicating whether a bird was caught in a given season) was created for each individual for which corticosterone or testosterone was measured. Some birds were caught in subsequent years at colony sites different from that where they were initially sampled for hormones.

Each year, two to four colonies were fumigated to remove ectoparasites as part of other work (e.g., Brown and Brown 2004a). Nests within these colonies were sprayed with a dilute solution of an insecticide, Dibrom, that was highly effective in killing swallow bugs (Brown and 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 cholinasterase inhibitor. We diluted the insecticide 1:150 parts water 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.

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, 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). The number of birds sampled per colony (usually 5–30) was not sufficient for estimating annual survival on a per site basis. Thus, we established (for corticosterone analyses) colony size categories to which all birds sampled for corticosterone were assigned. These were small colonies, 15–130 nests; medium colonies, 210–550 nests; and large colonies, 700–3400 nests. These categories were based, in part, on the actual distribution of colonies sampled, using obvious gaps in the distribution for designating category boundaries. The categories also reflected our own experience with the species over many years and the extent of social interaction and behavioral differences that we have observed in groups of different sizes. Only nonfumigated colonies were categorized by size; we did not have enough fumigated colonies sampled to divide into size categories.

Statistical analysis of survival

We estimated annual survival 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 and recapture probabilities. We identified a priori a set of survival and recapture models that were fit to the data for each colony size category (or for each sex in the case of testosterone). Some of these models incorporated time dependence (different parameters for different years, denoted $_{(t)}$) in the survival (ϕ) and recapture (p) probabilities, whereas others modeled survival as constant across years. Some models had the birds initially sampled at the two different stages (early-mid and late) as separate groups (denoted $_{(e, l)}$); comparison of these models with equivalent ones without a group effect (stages considered equal) allowed us to test whether survival varied with when in the season a bird was initially sampled.

To examine the effect of corticosterone hormone level on survival, we used the actual value obtained for each individual as a continuously distributed covariate. Some models incorporated corticosterone as a linear function of survival (denoted $_{(c)}$); others tested for a curvilinear survival function using corticosterone and its square $_{(csq)}$ as covariates (denoted $_{(c-csq)}$). By comparing the fit of survival models with and without corticosterone as a covariate, we assessed whether survival varied as a function of a bird's corticosterone level and whether it varied in a linear or curvilinear way. Models with corticosterone as a covariate used the log-link function in MARK in generating the survival function, and ϕ was back-transformed from the logit scale using the expression,

$$\phi = e^{\mathrm{logit}(\phi)}/1 + e^{\mathrm{logit}(\phi)}.$$

MARK automatically standardized all covariates by subtracting the mean from each and dividing by the standard deviation.

For testosterone, actual values were meaningless as a covariate because of a strong date-related effect on testosterone level across the season (Smith et al. 2005). Testosterone concentrations in Cliff Swallows peaked relatively early in the breeding season and then gradually declined as the season progressed. Sample sizes were not sufficient to estimate survival separately by date. Thus, for analysis we first calculated the mean value for testosterone level on each date for each year per sex, and classified each individual as either above or below the mean on the day that it was sampled (birds matching the mean were excluded). This yielded two groups for each sex, and we tested for an effect of testosterone on survival by comparing the fit of models

with the groups separate (denoted $_{(g)}$) to those with the groups considered the same. This approach meant that we did not need to include an effect of nesting stage or colony size for testosterone.

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 recatching birds (due to sampling effort or number of sites netted) were accounted for in estimating annual survival 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). The total χ^2 value allows estimation of a variance inflation factor, $\hat{c}$, as χ^2/df. The $\hat{c}$ value is used in MARK to adjust the AIC$_c$ through quasi-likelihood, resulting in a QAIC$_c$ whenever $\hat{c}$ departs from 1.0. Whenever QAIC$_c$ was used, model selection and parameter estimation was based on models with the lowest QAIC$_c$ values as just described for AIC$_c$. This variance inflation adjustment allowed use of data sets that departed from the assumptions of the binomial distribution (Wedderburn 1974, Burnham and Anderson 2002). We based our goodness of fit on the CJS model because as yet there are no tractable goodness-of-fit methods available for models with individual covariates. The approach generally recommended is to perform goodness-of-fit tests based on the more general CJS model and to use the same $\hat{c}$ value for the models that contain covariates (Cooch and White 2002).

RESULTS

An earlier study of the same birds showed that baseline corticosterone levels in Cliff Swallows were unaffected by sex, age, body mass, or extent of colony disturbance prior to sampling (S. Raouf, L. C. Smith, M. B. Brown, J. C. Wingfield, and C. R. Brown, *unpublished manuscript*), and thus these variables were not considered in our survival analyses. Baseline corticosterone levels did vary significantly with colony size, nesting stage, and whether a colony was fumigated.

For nonfumigated colonies of each size class, models with survival constrained as a function of baseline corticosterone were the better fits, and for each size class, the better-fitting models included an effect of nesting stage (Table 1). A model with a separate curvilinear effect of corticosterone on survival for each nesting stage was the best fit for both the small and medium colony size classes, as judged from QAIC$_c$ weights (Table 1). For the large colony size class, the best-fitting model was one with survival constrained as a linear function of corticosterone in the early-mid stage and as a curvilinear function in the late stage (Table 1). However, for both small and large colonies, there was at least one additional model that was relatively well supported (Table 1). For the small colonies, the second-best model had a curvilinear effect of corticosterone during the late stage, but a linear effect during the early stage; for large colonies, the second-best model was one with a curvilinear effect of corticosterone during both stages (Table 1). There was little evidence for time dependence in any of the colony size categories, suggesting no detectable annual variation in survival.

The estimated survival function derived from the best-fitting model for both small and large nonfumigated colonies (Table 1) showed a general decrease in survival with increasing corticosterone level for birds sampled during the early and mid stages (Figs. 1A, 3A). During the late stage for colonies of each size class, the best-fitting model indicated a peak in survival at intermediate levels of corticosterone (Figs. 1B, 2B, 3B). An inverse curvilinear relationship was found for birds sampled during the early and mid stages at medium-sized colonies (Fig. 2A).

For fumigated colonies, a model with survival as a curvilinear function of corticosterone during both nesting stages was the best fit, although one with survival as a linear function of corticosterone during the late stage was almost as well supported (Table 1). None of the other candidate models were close. During both nesting stages, the estimated survival function showed a peak at intermediate corticosterone levels (Fig. 4). This analysis combined birds from the seven fumigated colonies studied, as sample sizes were insufficient to analyze survival separately by colony size or class; the colony sizes of the fumigated sites were 72, 110, 290, 825, 955, 1500, and 1600 nests.

To determine whether there might be a threshold effect of corticosterone on survival, perhaps with birds with very high baseline levels of corticosterone for a given colony size class having a markedly different survival probability than all others, we categorized in-

TABLE 1. Models to estimate annual survival (ϕ) and recapture probabilities (p) in relation to endogenous corticosterone levels in Cliff Swallows, and the models' degree of fit to the data.

Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	No. parameters
Nonfumigated, small colonies ($N = 177$)				
$\phi_{(e-c-csq,\ l-c-csq)}\ p_{(t)}$	1520.257	0.00	0.41489	9
$\phi_{(e-c,\ l-c-csq)}\ p_{(t)}$	1521.725	1.47	0.19917	8
$\phi_{(e-c,\ l-c)}\ p_{(t)}$	1522.071	1.81	0.16755	7
$\phi_{(e,l)}\ p_{(t)}$	1523.036	2.78	0.10338	5
$\phi_{(e-c-csq,\ l-c)}\ p_{(t)}$	1523.528	3.27	0.08084	8
$\phi_{(e-t,\ l-t)}\ p_{(t)}$	1525.703	5.45	0.02726	8
$\phi_{(t)}\ p_{(t)}$	1529.866	9.61	0.00340	5
$\phi\ p_{(t)}$	1531.247	10.99	0.00170	4
$\phi_{(c)}\ p_{(t)}$	1532.120	11.86	0.00110	5
$\phi_{(c-csq)}\ p_{(t)}$	1533.000	12.74	0.00071	6
Nonfumigated, medium colonies ($N = 340$)				
$\phi_{(e-c-csq,\ l-c-csq)}\ p_{(t)}$	2766.131	0.00	0.63461	9
$\phi_{(e-t,\ l-t)}\ p_{(t)}$	2768.562	2.43	0.18819	9
$\phi_{(t)}\ p_{(t)}$	2769.792	3.66	0.10173	5
$\phi_{(e-c-csq,\ l-c)}\ p_{(t)}$	2770.468	4.34	0.07257	8
$\phi_{(e-c,\ l-c-csq)}\ p_{(t)}$	2777.428	11.30	0.00224	8
$\phi_{(e-c,\ l-c)}\ p_{(t)}$	2781.715	15.58	0.00026	7
$\phi_{(e,l)}\ p_{(t)}$	2782.144	16.01	0.00021	5
$\phi_{(c-csq)}\ p_{(t)}$	2782.452	16.32	0.00018	6
$\phi_{(c)}\ p_{(t)}$	2791.142	25.01	0.00000	5
$\phi\ p_{(t)}$	2793.412	27.28	0.00255	4
Nonfumigated, large colonies ($N = 267$)				
$\phi_{(e-c,\ l-c-csq)}\ p_{(t)}$	264.637	0.00	0.36802	8
$\phi_{(e-c-csq,\ l-c-csq)}\ p_{(t)}$	264.769	0.13	0.34445	9
$\phi_{(e-c-csq,\ l-c)}\ p_{(t)}$	267.247	2.61	0.09977	8
$\phi_{(t)}\ p_{(t)}$	267.612	2.98	0.08314	5
$\phi_{(e-c,\ l-c)}\ p_{(t)}$	267.712	3.08	0.07907	7
$\phi\ p_{(t)}$	272.101	7.46	0.00881	4
$\phi_{(e-t,\ l-t)}\ p_{(t)}$	272.164	7.53	0.00854	8
$\phi_{(c)}\ p_{(t)}$	273.850	9.21	0.00368	5
$\phi_{(e,l)}\ p_{(t)}$	274.116	9.48	0.00322	5
$\phi_{(c-csq)}\ p_{(t)}$	275.917	11.28	0.00131	6
Fumigated, all colonies ($N = 261$)				
$\phi_{(e-c-csq,\ l-c-csq)}\ p_{(t)}$	2609.853	0.00	0.50769	9
$\phi_{(e-c-csq,\ l-c)}\ p_{(t)}$	2610.041	0.19	0.46225	8
$\phi_{(e-c,\ l-c-csq)}\ p_{(t)}$	2617.765	7.91	0.00972	8
$\phi_{(e-c,\ l-c)}\ p_{(t)}$	2617.962	8.11	0.00881	7
$\phi_{(c)}\ p_{(t)}$	2618.613	8.76	0.00636	5
$\phi_{(c-csq)}\ p_{(t)}$	2619.264	9.41	0.00459	6
$\phi_{(e-t,\ l-t)}\ p_{(t)}$	2624.428	14.57	0.00035	8
$\phi\ p_{(t)}$	2626.181	16.33	0.00014	4
$\phi_{(e,l)}\ p_{(t)}$	2627.789	17.94	0.00006	5
$\phi_{(t)}\ p_{(t)}$	2630.063	20.21	0.00002	6
Birds held 60 minutes ($N = 218$)				
$\phi\ p_{(t)}$	399.591	0.00	0.45826	3
$\phi_{(c-csq)}\ p_{(t)}$	401.265	1.67	0.19849	5
$\phi_{(c)}\ p_{(t)}$	401.462	1.87	0.17989	4
$\phi_{(t)}\ p_{(t)}$	401.654	2.06	0.16336	4

Notes: Time dependence is indicated with $_{(t)}$; models without this subscript were time constant. In some models, corticosterone $_{(c)}$ alone or combined with its square $_{(c-csq)}$ were linear or curvilinear covariates, respectively; those without these subscripts had no effect of corticosterone. Those with $_{(e,\ l)}$ considered the two nesting stages (early-mid and late) as separate groups; models without this subscript treated the two stages as the same. N is the number of birds for whom corticosterone was measured.

dividuals into two arbitrary groups: those with corticosterone levels <10 ng/mL ("low" group) vs. ≥10 ng/mL ("high" group) for each colony size. This grouping was chosen based on the observed distribution of corticosterone values (Figs. 1–4). In no case did a model with these groups, separated by nesting stage, provide a better fit than those shown in Table 1. The best model with birds categorized into high and low groups had QAIC$_c$ values that were 12.5, 16.6, 8.8, and 10.5 higher than the best-fitting overall model for small, medium, and large nonfumigated colonies and for fumigated colonies, respectively.
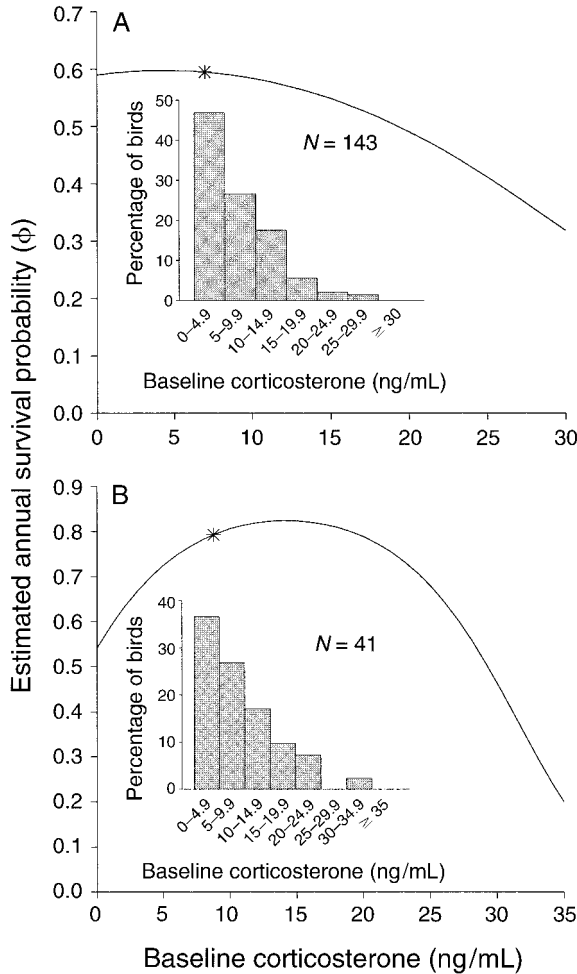
FIG. 1. Estimated annual survival function for the observed values of endogeneous corticosterone in Cliff Swallows for birds sampled (A) during the early and mid stages and (B) during the late stage of the nesting season in small, nonfumigated colonies (15–130 nests). The inset shows the frequency distribution of observed corticosterone values, and the star denotes mean corticosterone level. The survival function in (A) was $logit(\phi) = 0.323 + 0.0893(x - 7.114/5.873) - 0.237(x^2 - 84.893/134.934)$, and in (B), $logit(\phi) = 0.967 + 1.134(x - 7.114/5.873) - 0.917(x^2 - 84.893/134.934)$. Note the different x- and y-axis scales in panels (A) and (B).

For birds whose corticosterone levels were measured after 60 minutes (the stress response), a model without an effect of 60-minute corticosterone level was 2.3 times more likely than the next best one with corticosterone as a covariate (Table 1). However, the two models with corticosterone as a covariate were within 2.0 in $QAIC_c$, suggesting some limited support for them (Table 1). The survival function estimated from the better-fitting covariate model, $\phi_{(c-csq)} p_{(t)}$, showed a peak in survival at intermediate (60-minute) corticosterone levels. In analyzing the effect of corticosterone after 60 minutes, we combined colony sizes and colony fumigation status, as these had no significant effects on levels of corticosterone measured at 60 minutes (S.

Raouf, L. C. Smith, M. B. Brown, J. C. Wingfield, and C. R. Brown, *unpublished manuscript*), and combined the nesting stages due to small sample sizes within each stage.

For baseline corticosterone in nonfumigated colonies, the mean corticosterone level measured for each nesting stage and colony size class tended not to match the corticosterone level associated with the highest sur-
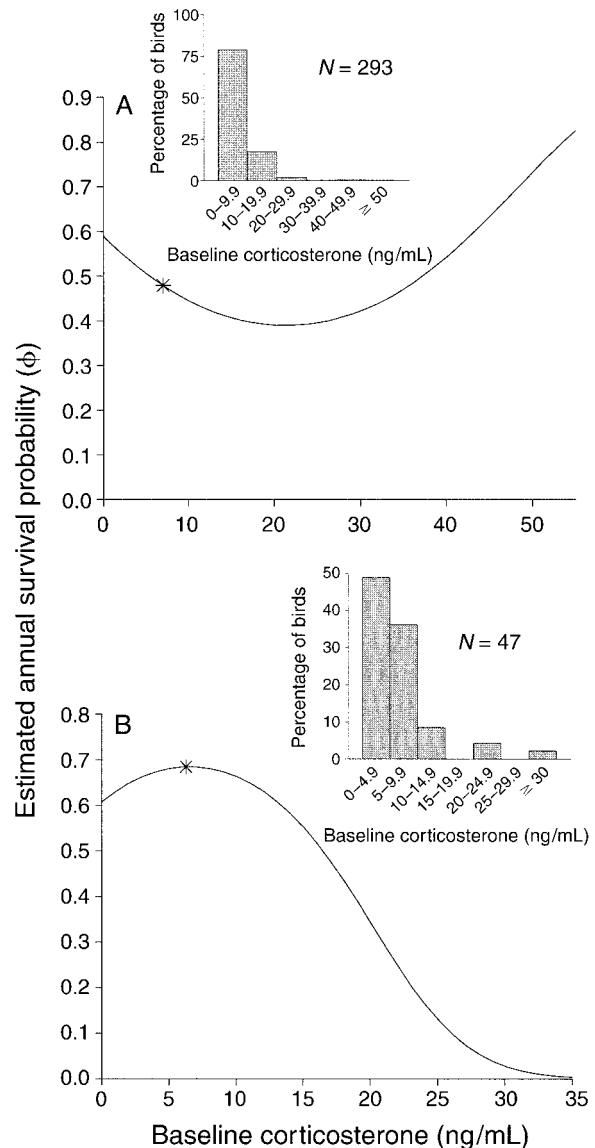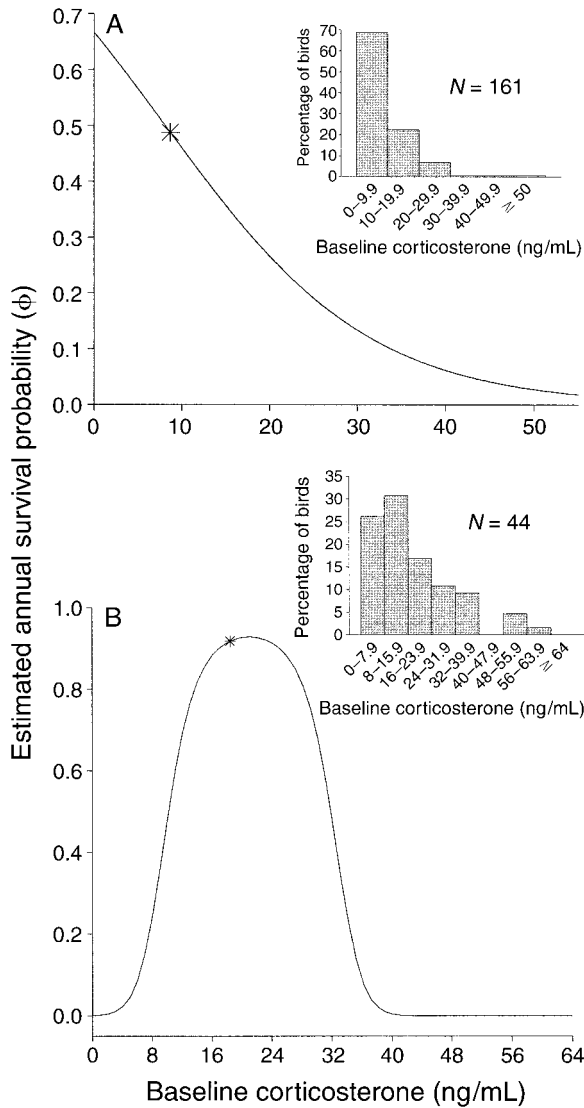

FIG. 2. Estimated annual survival function for the observed values of endogeneous corticosterone in Cliff Swallows for birds sampled (A) during the early and mid stages and (B) during the late stage of the nesting season in medium-sized, nonfumigated colonies (210–550 nests). The inset shows the frequency distribution of observed corticosterone values, and the star denotes mean corticosterone level. The survival function in (A) was $logit(\phi) = 0.0011 - 0.510(x - 6.924/6.740) + 0.449(x^2 - 93.230/253.469)$, and in (B), $logit(\phi) = 0.418 + 0.694(x - 6.924/6.740) - 1.985(x^2 - 93.230/253.469)$. Note the different x- and y-axis scales in panels (A) and (B).

FIG. 3. Estimated annual survival function for the observed values of endogeneous corticosterone in Cliff Swallows for birds sampled (A) during the early and mid stages and (B) during the late stage of the nesting season in large, nonfumigated colonies ($\geq$700 nests). The inset shows the frequency distribution of observed corticosterone values, and the star denotes mean corticosterone level. The survival function in (A) was logit(ϕ) = 0.702 − 3.896(x − 10.999/10.511) + 6.305(x^2 − 231.035/499.019), and in (B), logit(ϕ) = −2.032 + 9.635(x − 10.999/10.511) − 10.877(x^2 − 231.035/499.019). Note the different x- and y-axis scales in panels (A) and (B).

stage (Figs. 1–3). For fumigated colonies, there was closer agreement between both the observed mean and the frequency distribution of corticosterone levels and the values at which survival was estimated to be greatest (Fig. 4).

Models with birds separated into those with testosterone values above and below the mean for a given date were not the best fit for either males or females (Table 2). For each sex, the best-fitting model was one that considered birds above and below the mean as a single group, implying no difference in survival between them. For females, however, a model with a
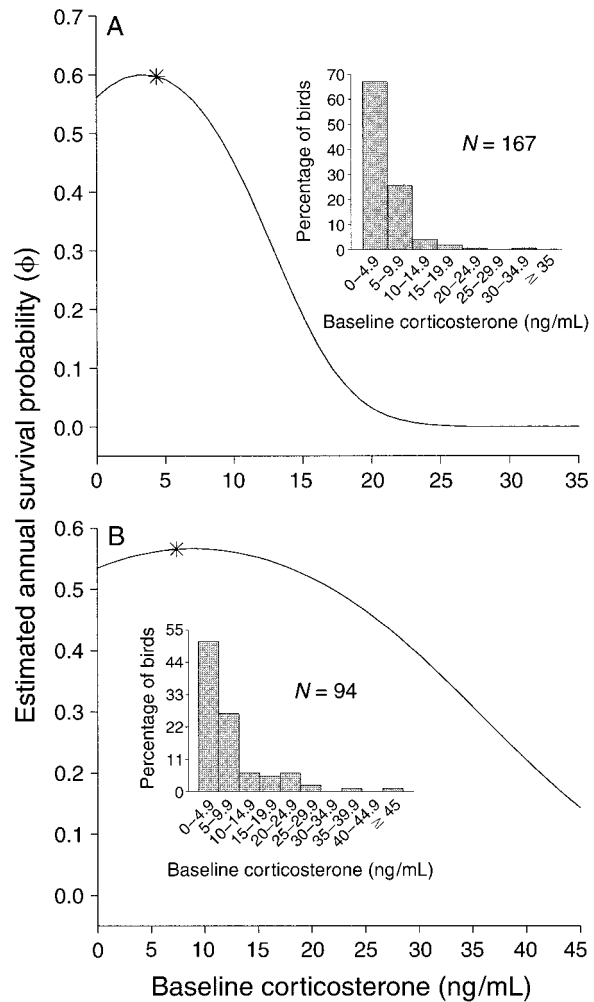

FIG. 4. Estimated annual survival function for the observed values of endogeneous corticosterone in Cliff Swallows for birds sampled (A) during the early and mid stages and (B) during the late stage of the nesting season in fumigated colonies of all sizes combined. The inset shows the frequency distribution of observed corticosterone values, and the star denotes the mean corticosterone level. The survival function in (A) was logit(ϕ) = −0.211 + 0.600(x − 5.474/6.356) − 2.762(x^2 − 70.215/199.197), and in (B), logit(ϕ) = 0.185 + 0.181(x − 5.474/6.356) − 0.316(x^2 − 70.215/199.197). Note the different x- and y-axis scales in panels (A) and (B).

vival (Figs. 1–3). During the late stage in all three colony size categories, the observed mean corticosterone level was less than the value yielding maximal survival, and during the early and mid stages, the mean was greater than that yielding maximal survival. The distributions of observed corticosterone values also tended to be skewed toward smaller values than those yielding the highest survival, especially during the late

TABLE 2. Models to estimate annual survival (ϕ) and recapture probabilities (p) in relation to endogenous testosterone levels in Cliff Swallows, and the models' degree of fit to the data.

Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	No. parameters
Males ($N = 436$)				
$\phi\ p$	526.687	0.00	0.28138	2
$\phi_{(t)}\ p$	527.285	0.60	0.20862	4
$\phi\ p_{(t)}$	527.324	0.64	0.20462	4
$\phi_{(g)}\ p$	528.531	1.84	0.11190	3
$\phi_{(t)}\ p_{(t)}$	529.033	2.35	0.08706	5
$\phi_{(g)}\ p_{(t)}$	529.142	2.45	0.08246	5
$\phi_{(t-g)}\ p$	532.303	5.62	0.01697	7
$\phi_{(t-g)}\ p_{(t)}$	534.073	7.39	0.00701	8
Females ($N = 428$)				
$\phi\ p$	953.849	0.00	0.27104	2
$\phi_{(g)}\ p$	954.303	0.45	0.21603	3
$\phi\ p_{(t)}$	955.247	1.40	0.13474	4
$\phi_{(t)}\ p$	955.401	1.55	0.12476	4
$\phi_{(g)}\ p_{(t)}$	955.756	1.91	0.10444	5
$\phi_{(t-g)}\ p$	956.525	2.68	0.07112	7
$\phi_{(t)}\ p_{(t)}$	957.248	3.40	0.04956	5
$\phi_{(t-g)}\ p_{(t)}$	958.367	4.52	0.02831	8

Notes: Time dependence is indicated with $_{(t)}$; models without this subscript were time constant. Those models with $_{(g)}$ considered birds with testosterone above and below the mean for a given date as two separate groups; models without this subscript treated the two groups as the same. N is the number of birds for whom testosterone was measured.

group effect was very close in both QAIC$_c$ and QAIC$_c$ weight (Table 2). This model estimated annual survival as 0.618 ± 0.062 (mean $\pm$ SE) for females with testosterone levels above the mean and 0.692 ± 0.053 for females with testosterone levels below the mean; the best-fitting model without a group effect estimated survival as 0.668 ± 0.049 for both classes combined. For males, the model with a group (testosterone) effect was less well supported but still within 2.0 in QAIC$_c$. This model estimated annual survival as 0.563 ± 0.067 for males with testosterone levels above the mean, and 0.592 ± 0.057 for males with testosterone levels below the mean; the best-fitting model without a group effect estimated survival as 0.581 ± 0.051 for both classes combined.

DISCUSSION

This study indicates that variation in endogenous levels of corticosterone is associated with annual survival differences in Cliff Swallows. Across all analyses, the most common pattern was one in which survival was greatest at intermediate levels of corticosterone, and there was no evidence for a threshold (stepwise) effect on survival. The curvilinear survival functions suggest a form of stabilizing selection in which individuals with very high and very low baseline levels of corticosterone are at a disadvantage. Confidence in these patterns (and thus our subsequent interpretations) is determined by how well the curvilinear model in each case fit the data. In most cases there was

at least one other plausible alternative model, but all included an effect of baseline corticosterone during both stages, either as a curvilinear function or as one with survival declining more or less linearly over the range of observed corticosterone concentrations (Table 1). For testosterone, however, we found no strong evidence for an effect on annual survival.

Inherent limitations of mark–recapture studies

As with most mark–recapture studies, two general caveats are in order. One is that we estimated apparent (or local) survival only. Cliff Swallows that permanently dispersed out of the study area between years would be counted as dead in our analyses (those temporarily leaving but returning in a later year are accounted for in estimating recapture probability). This is a general problem for open populations, 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 will be unaffected by undetected permanent emigration, as long as emigration does not covary with endogenous corticosterone or testosterone levels. Relative survival probabilities among different classes of birds still allow one to test legitimately for differences among individuals. Although Silverin (1997) found that juvenile Willow Tits (*Parus montanus*) with higher corticosterone levels were more likely to disperse in the fall, this was not the case with breeding adults, and we are not aware of any other studies in free-living birds showing that permanent, long-distance emigration of adults is associated with levels of corticosterone or testosterone.

The other caveat is that hormone level is not a fixed covariate, that is, it can presumably change for an individual between days or years. Our survival analyses implicitly assume that hormone level is a fixed, single-state variable. The ideal way to analyze survival in relation to hormone level would be to sample the same individuals repeatedly and use a multistate approach (Nichols and Kendall 1995, Lebreton and Pradel 2002), in which hormone level represents a covariate that can change among capture occasions and colony sites that a bird uses. Unfortunately, neither is this practical in the field, given the laborious nature of taking hormone samples, nor do tractable statistical methods exist at present for handling varying covariates in multistate models (Bonner and Schwarz 2003). 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 2004*c*).

Endogenous corticosterone and survival

The survival patterns reported here are generally consistent with the known or suspected benefits and

costs of glucocorticoid hormones such as corticosterone. In Cliff Swallows, corticosterone levels are higher when birds are exposed to large numbers of ectoparasitic swallow bugs, especially in larger colonies, or when bad weather restricts food availability early in the season (S. Raouf, L. C. Smith, M. B. Brown, J. C. Wingfield, and C. R. Brown, *unpublished manuscript*). The increased corticosterone levels in such situations probably modulate a reallocation of effort to foraging and energy uptake, which would clearly be advantageous when the birds are nutritionally or energetically stressed. Too little endogenous corticosterone production may hinder the Cliff Swallows' ability to deal with ectoparasitism, the principal source of environmental stress that these birds encounter (Brown and Brown 1986, 1996, 2002, Brown et al. 1995, 2001; S. Raouf, L. C. Smith, M. B. Brown, J. C. Wingfield, and C. R. Brown, *unpublished manuscript*). Too much corticosterone may cause deleterious physiological effects that impact survival; the most likely is suppression of the immune system (Grossman 1990, Fowles et al. 1993, Dunlap and Schall 1995, Boonstra et al. 2001, Saino et al. 2003). Interestingly, even though corticosterone levels varied in magnitude among nonfumigated colonies of different sizes and there were differences in absolute survival probabilities among different colony size classes, the same survival patterns with respect to corticosterone generally applied across all colony sizes in Cliff Swallows. The only obvious outlier was the survival curve for birds sampled in the early-mid stage in medium-sized colonies (Fig. 2A), although only the unexplained rise in survival at high corticosterone levels was inconsistent with the results from the other colony sizes at that time of year. The overall congruence in results among colonies and times of year suggests that the costs and benefits of different corticosterone levels vary in the same direction regardless of social environment.

Birds from fumigated colonies generally exhibited the same survival patterns as those from nonfumigated sites. However, in the parasite-free sites, there appeared to be less disadvantage in having very low corticosterone levels during the late stage (Fig. 4B). This is consistent with the reduced parasite-related stress of the fumigated colonies. With fewer bugs there, perhaps Cliff Swallows do not reallocate as much time to energy acquisition late in the season, and thus birds with very low levels of corticosterone may pay less of a price.

Without experimental manipulation of corticosterone (which generally is not possible on a large enough scale to study annual survival), it is difficult to establish corticosterone level as a direct cause of the survival differences among birds reported here. Other factors may also be correlated with corticosterone level and may independently affect survival. For example, Cliff Swallows with the highest levels of corticosterone at the time of sampling may have been ones that were stressed by other events such as recent encounters with predators, unusually high numbers of ectoparasites in their nests, or disappearance of a mate. Their lower subsequent survival might have reflected these events and not the high corticosterone per se. However, we controlled for colony size and ectoparasitism, two factors most likely to have major independent effects on Cliff Swallow survival (Brown and Brown 1996, 2004b, Brown et al. 1995). Our results show that baseline corticosterone is a reliable predictor of the likelihood of annual survival in Cliff Swallows (see also Romero and Wikelski 2001).

Endogenous corticosterone and fitness

The rather substantial differences in estimated survival probabilities across the observed range of corticosterone values translate into potentially major effects on mean life span and fitness. For example, using the formula of Brownie et al. (1985:208) for calculating mean life span from ϕ, for birds sampled late in small, nonfumigated colonies (Fig. 1B), the estimated range in survival probabilities yielded differences in mean life span of up to 4.5 years across the observed range of corticosterone levels; for birds in medium-sized, nonfumigated colonies (Fig. 2B), up to 1.3 years; and for birds in large, nonfumigated colonies (Fig. 3B), up to 13 years. The latter is near the maximum longevity known for the species (Brown and Brown 1995).

One of our more perplexing results is the displacement of the observed distribution of corticosterone values, relative to the survival function, for the late stage in the nonfumigated colonies (Figs. 1B, 2B, 3B). In these cases, there were far more birds with very low levels of corticosterone than would be predicted from the respective survival functions. The range in survival probabilities described by these survival functions, all else being equal, should lead to strong stabilizing selection for birds with the more intermediate levels of endogenous corticosterone during the late stage. Individuals with very low and very high levels should be selected against strongly, and this indeed appears to be the case for the very high concentrations, given the few birds exhibiting those. However, perhaps the survival advantages of very low corticosterone levels earlier in the season compensate for the survival costs of low levels later in the season. The observed distributions of corticosterone levels during the earlier part of the season (Figs. 1A, 2A, 3A) may reflect strong directional survival selection for the lowest values at that time of the year.

For fumigated colonies, the observed distribution of corticosterone values at all times was largely consistent with what would be expected from selection based on the survival function (Fig. 4). On balance, the different survival functions for birds under natural (nonfumigated) conditions, depending on when the covariate was measured, suggest a complex relationship between corticosterone level and survival and illustrate the chal-

lenge of studying natural selection when it apparently varies in direction at different times of the season.

Corticosterone, the stress-response, and survival

The stress-series approach, in which animals are held for up to 60 minutes and corticosterone is sampled at intervals, is commonly employed in field endocrinological investigations. In marine iguanas (*Amblyrhynchus cristatus*), corticosterone levels measured in response to handling stress predicted subsequent survival (Romero and Wikelski 2001). We found that the corticosterone levels obtained from birds after 60 minutes of handling (presumably reflecting their physiological maximum) were not a good predictor of annual survival probability in Cliff Swallows. The model without an effect of corticosterone level at 60 minutes was the best fit to the capture–recapture data for those 218 individuals. This may mean that the maximum level of corticosterone observed after a bird is subjected to handling is not the best index for studying how corticosterone potentially affects life-history traits such as survival. After all, endogenous hormone levels are what an individual continually experiences day in and day out, and thus presumably should have a major effect on longevity. However, even for Cliff Swallows subjected to the stress response, there was some limited support for a curvilinear survival function, again suggesting an advantage for an intermediate phenotype.

Testosterone and survival

Cliff Swallows of both sexes exhibit a seasonal increase in testosterone concentrations that peak during the early part of the nesting season as nests and pairs are being established and then decline as the birds switch to parental duties (Smith et al. 2005). Testosterone levels in this species are related to the intensity of competition for nesting sites and possibly to extrapair mating opportunities, and there is extensive variation in observed testosterone levels after controlling for date and colony size (Smith et al. 2005). However, we found no obvious effect of endogenous testosterone levels on annual survival in Cliff Swallows, although because of the strong date-related variation in testosterone concentrations, our analysis of survival and testosterone was necessarily less sophisticated than that for corticosterone.

The lack of a strong relationship between testosterone level and annual survival is largely consistent with results from other species (based strictly on return rate and with much smaller sample sizes; Dufty 1989, Nolan et al. 1992), showing that, even though survival was impaired when male birds were implanted with extremely high levels of testosterone over the entire year, when implants were removed before fall, return rates were similar among birds previously implanted and controls. Our results do not support the widely held view that high levels of testosterone can suppress immune function (e.g., Folstad and Karter 1992, Slater

and Schreck 1993, Zuk et al. 1995, Hillgarth and Wingfield 1997, Verhulst et al. 1999, Peters 2000) and thus make birds with high testosterone concentrations more susceptible to disease and less likely to survive for that reason. On balance, based on the survival analyses reported here, seasonal increases in testosterone concentration do not appear to represent an important cost for either male or female Cliff Swallows, although the second-best model for females, suggesting reduced survival for females with testosterone above the average for a given date, was relatively well supported and should not be discounted.

To our knowledge, this study is the first to estimate annual survival probability in relation to endogenous corticosterone and testosterone levels in a free-living bird using mark–recapture statistical methods. Most previous studies on survival and hormone levels measured only the return rates of individuals to a study area and did not account for potential differences among classes of animals in recapture probabilities (Dufty 1989, Nolan et al. 1992, Rogovin et al. 2003; cf. Romero and Wikelski 2001). We were able to apply maximum likelihood estimation to our data and to account for both survival and recapture probabilities because our sample size was greater by an order of magnitude (or more) than in most field endocrinological studies of birds or mammals. Such large sample sizes are critical in avoiding the problem of low statistical power that afflicts so many avian hormone studies (Ketterson et al. 1996). This is especially important in inferring fitness effects associated with hormones.

Our results indicate that steroid hormone levels, particularly of corticosterone, can be related to variation in annual survival in natural populations. This study emphasizes that natural phenotypic variation in hormone levels can be instructive and that manipulating hormones to levels near the upper extreme of the observed distribution, via either implants or handling stress (e.g., Ketterson et al. 1996), may not always be the most insightful way to assess the fitness associated with hormonal mechanisms.

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