STEROID HORMONES IN RELATION TO TERRITORIALITY, BREEDING DENSITY, AND PARENTAL BEHAVIOR IN MALE YELLOW-HEADED BLACKBIRDS

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ABSTRACT.—We examined relationships of circulating plasma levels of testosterone (T) and corticosterone (B) to territory ownership, breeding density, parental care, and reproductive success in polygynously breeding male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*). Testosterone levels of territory owners remained relatively high during the first 8 weeks of the breeding season. This period corresponded to the time when most males established territories, and most females initiated clutches. The temporal pattern of testosterone levels for adult floaters was very similar to that of territory owners because floaters competed for territories during the major portion of the breeding season. Plasma levels of corticosterone in adult males were low during the early part of the breeding season, but they rose sharply when females arrived in the study area and started to breed. Circulating testosterone in breeding males declined significantly by the time they fed nestlings. Males with territories in a very high-density breeding site had significantly higher testosterone levels during the main territory establishment period than males at low-density sites. There was no clear relationship between circulating levels of hormones and breeding success. *Received 28 February 1989, accepted 17 July 1989.*

THE ROLE played by steroid sex hormones, such as testosterone (T), in the regulation of breeding and territorial behavior of animals is currently under intense scrutiny (for reviews, see Balthazart 1983, Crews and Moore 1986, Wingfield et al. 1987). Circulating levels of T are directly related to short-term fluctuations in the intensity of aggressive behavior in birds (Searcy and Wingfield 1980, Moore 1984, Wingfield et al. 1987), and levels can change dramatically during the course of a breeding season and also on a daily or even hourly basis. Complex interactions of environmental stimuli, behavior, and hormone levels are suspected to be the source of this variation.

Monogamous territorial male birds in temperate areas typically have briefly high testosterone levels during periods of territory establishment and mate-guarding, when male-male aggressive interactions usually peak, but levels decline rapidly thereafter (Wingfield 1984, Wingfield and Moore 1986, Wingfield et al. 1987). Among bigamous, polygynous, and brood parasitic species that interact over territories or mates for longer periods, high levels of testosterone are maintained considerably longer (Silverin and Wingfield 1982, Dufty and Wingfield 1986, Beletsky et al. 1989). For example, in the strongly polygynous Red-winged Blackbird (*Agelaius phoeniceus*), we found that territory owners had high T levels over the entire 5-week period when most nests on their territories were initiated and males guarded their mates (Beletsky et al. 1989). Also, territory owners, who repeatedly defended their territories and guarded multiple mates, had significantly higher T levels than did adult nonterritorial floaters. However, the Red-winged Blackbird population we studied was ill-suited in some respects for comparison with other temperate breeders. The males were nonmigratory and lacked a well-defined period of territory establishment before breeding. Further, most of them did not feed offspring.

The *challenge hypothesis* (Wingfield 1985, Wingfield et al. 1987) proposes that testosterone secretion is strongly stimulated when conspecific males challenge each other for territory ownership or access to mates. Plasma T levels rise rapidly during sustained agonistic interactions (Wingfield 1984, Wingfield et al. 1987), perhaps facilitating expression of aggressive behavior at high frequency and intensity (Wingfield et al. 1987). Although it is apparently advantageous for territory owners to have high T levels during portions of the breeding season, at other times it is not. For example, several studies have revealed that high plasma T levels

dramatically reduce expression of parental behavior, at least in some species (Silverin 1980, Hegner and Wingfield 1987).

We examined the relationships between breeding behavior and plasma testosterone levels in the strongly polygynous Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). This species offered several salient contrasts with monogamous species and the polygynous Red-winged Blackbird. Yellow-heads in our study area are migratory, breed in the same marshes, and are interspecifically territorial with Red-wings (Orians and Willson 1964, Willson 1966). We predicted that male Yellow-heads would have high T levels when they first arrived and fought to establish their territories. The resident male Red-wings had relatively low T levels early in the breeding season and did not reach high T levels until females arrived. Also, male Yellow-heads assist their mates in feeding nestlings, usually at the first nest on their territories (Willson 1966, Gori 1984). We predicted that T levels would decline by the time males fed offspring, both because territorial interactions diminish later in the breeding season and because T levels in territorial birds are lower when males are engaged in parental care. We also tested the challenge hypothesis of testosterone secretion by evaluating the prediction that testosterone levels should be high only during periods of intense male-male interactions.

Energetic requirements of breeding are usually high, and plasma levels of corticosterone (B), a glucocorticoid secreted by adrenocortical tissue, increase during the reproductive season in several species (Wingfield 1988). Corticosterone, which is thought to regulate adaptive changes in behavior and increase available energy stores, is particularly important when individuals are stressed (Harvey et al. 1984, Wingfield and Silverin 1986, Wingfield 1988). We determined Yellow-head plasma B levels in relation to age and reproductive status, as a potential indicator of stress.

A surprising result of our study of Red-wing males was a positive correlation between annual breeding success and an individual's T and B levels during the period when average T levels peaked for the population (Beletsky et al. 1989). Because these correlations suggested a potentially important relationship between plasma steroid concentrations at certain critical times and reproductive success, we examined such relationships in Yellow-heads.

METHODS

Study area and Yellow-head breeding biology.—We studied male Yellow-heads at the Columbia National Wildlife Refuge, in eastern Washington state, from late March through early June 1988. Yellow-heads establish breeding territories in cattail (*Typha*) and bulrush (*Scirpus*) marshes that border many of the lakes on the refuge. All males were banded with unique combinations of colored leg bands.

The study area and the breeding biology of Yellow-heads are described in detail by Willson (1966), Orians and Christman (1968), and Orians (1980). Briefly, nesting begins in late April or early May and continues until late June or early July. Males arrive before females and establish territories. Most males return to the same breeding marshes in subsequent years (Gori 1984). Females construct nests over 1–3 days and incubate alone, typically for 12 days (Willson 1966, Gori 1984). Modal clutch size in the area is four eggs. Harem sizes range from 1 to 15 females, but average 3–4 (Gori 1984, this study).

Reproductive monitoring and blood sampling.—We monitored nesting on ca. 130 male territories located on Morgan, McMannamon, and Juvenile lakes (for map, see Beletsky and Orians 1987) to determine relationships between hormone levels and breeding activity. Yellow-heads settled densely on Morgan Lake (predominantly bulrush or mixed bulrush and cattail marshes) and more sparsely on McMannamon and Juvenile lakes (all cattail marshes), where many areas were unused by Yellow-heads. Approximately three times as many males ($n = 97$) established territories on Morgan Lake marshes than on McMannamon and Juvenile marshes ($n = 37$), although the combined area of the latter marshes exceeded the combined areas of the four Morgan Lake marshes.

All nests built on each male's territory were located before the start of incubation and checked at 3-day intervals. Thus, for many of the males contributing blood samples, we knew the precise dates for onset and duration of various breeding phases. Males were observed daily at Morgan Lake during the second half of the breeding season to determine when they began to feed offspring. Most males in the study area feed nestlings and fledglings (Gori 1984), but only those we witnessed feeding were used in our analysis of hormone levels and parental care activities.

Because few females were banded, and because some females renest rapidly following nest failures that occur before or during incubation (D. Gori pers. comm.), we estimated harem sizes using a method similar to that described by Searcy (1979). The nests built on each male's territory were assigned to the smallest possible number of females that could account for them, based on known nest initiation and failure dates. We assumed that a female could renest 5 days after destruction of her previous nest.

Most blood samples from territory owners came from males that resided on the three lakes we mon-

itored for breeding success. We conducted a comprehensive survey of banded territorial Yellow-heads up to 3,500 m in all directions from the center of the study area to determine if males we trapped and bled held territories elsewhere. Adult males observed not to hold a territory in the central study area or in peripheral areas were designated *floaters*. Very few banded males holding territories farther than 1,500 m from our traps were captured, and it is unlikely that males we assigned to floater status actually held territories beyond the areas we searched. Fifteen blood samples taken from a total of 11 males before they established their territories were treated as floater samples. Subadult floaters were easily identified by their distinctive plumage.

Males were trapped either in a large walk-in grain trap located between Morgan and McMannamon lakes or in smaller walk-in traps near their territories. No male was bled more than once per week. Many were bled only once or twice, but a few entered our traps almost daily, providing up to nine weekly samples. Birds were left in traps only a few minutes, where they fed quietly until we approached to remove them. Blood samples (300–400 μl) were collected from a wing vein into heparinized microhematocrit capillary tubes within 10 min of removal from traps (see Wingfield and Farner 1976, 1978). Circulating sex steroid hormone levels in songbirds remain stable for at least 10 min after capture (Wingfield et al. 1982b). Territorial males returned directly to their territories after release.

Assays.—Plasma levels of testosterone and corticosterone were measured by radioimmunoassay after extraction and partial purification on diatomaceous earth/glycol columns. Purification and assay procedures are given by Wingfield and Farner (1975) and Ball and Wingfield (1987). Samples were selected randomly for each of the six arrays required to complete the analysis. Intra- and inter-array variation were within the limits presented by Wingfield and Farner (1975) and Wingfield et al. (1982a). Least detectable concentrations were 1.9 pg for testosterone and 7.8 pg for corticosterone.

Statistical analysis.—We divided the breeding season into 10 ca. 1-week-long periods. Each month was divided into four periods of 7, 8, 7(8), and 8 days. Because nesting began earlier on some territories than on others, data are presented both chronologically and by breeding stage. Breeding sequences of territory owners were divided into six periods: (1) before the first female settled, (2) after the first female settled but before nest completion, (3) between completion of the first nest and initiation of incubation by the first female, (4) during incubation of the first nest, (5) while the first nestlings were on the territory, (6) after the first nestlings fledged.

Differences in T and B levels among samples and among groups were tested for significance by Mann-Whitney U-tests and Kruskal-Wallis one-way ANO-VA. We chose nonparametric tests because of large differences in sample sizes and because of uncertainty about the homogeneity of variances among tested groups (Sokal and Rohlf 1969). Samples of <8 were not tested. Significance was accepted at the 0.05 level. Average hormone levels are $\bar{x} \pm$ SE; all other averages are $\bar{x} \pm$ SD.

RESULTS

A few males settled on Morgan Lake by the end of March, but large numbers of males did not arrive in the area until mid-April. Only 11% of ca. 100 males that bred on the four Morgan Lake marshes possessed territories by 1 April, and 30% more had settled by 15 April (occupying for the first time all available breeding habitat). Another 37% established territories by 1 May, 13% more by 15 May, and the final 9% by 1 June. Between 15 April and 1 May, 81.0% of eventual territory owners settled on Mc-Mannamon Lake (total $n = 21$) and 93.8% settled on Juvenile Lake ($n = 16$). Few new males gained territories during May and early June. On Morgan Lake particularly, males contested for territories and inserted themselves between established residents throughout the major part of the breeding season. Females began to arrive and settle on territories during the third week of April. First nests were built during the last week of April and first week of May (Fig. 1a). Hatching began on most territories during the third week of May, and males were first observed to feed nestlings during the last week of May, usually when young were 5–6 days old.

Testosterone levels of territory owners.—Average plasma T concentrations were high when male Yellow-heads first arrived in the study area and established their territories (Fig. 1a). Male testosterone levels differed significantly among months (April, May, June; Kruskal-Wallis test, $\chi^2 = 81.59$, $P < 0.001$). Testosterone levels rose significantly between the second and third weeks of April, which coincided with the first arrival in the area of large numbers of adult males (personal observations). Testosterone levels then declined significantly between the third and fourth weeks of April (Fig. 1a). Levels remained high and stable through the second week of May, and then declined steadily until the end of May, when males began feeding their nestlings. The long plateau of relatively high T levels lasted into the third week of May, which encompassed the period when 73% (total $n = 432$) of nests we monitored were initiated (Fig.
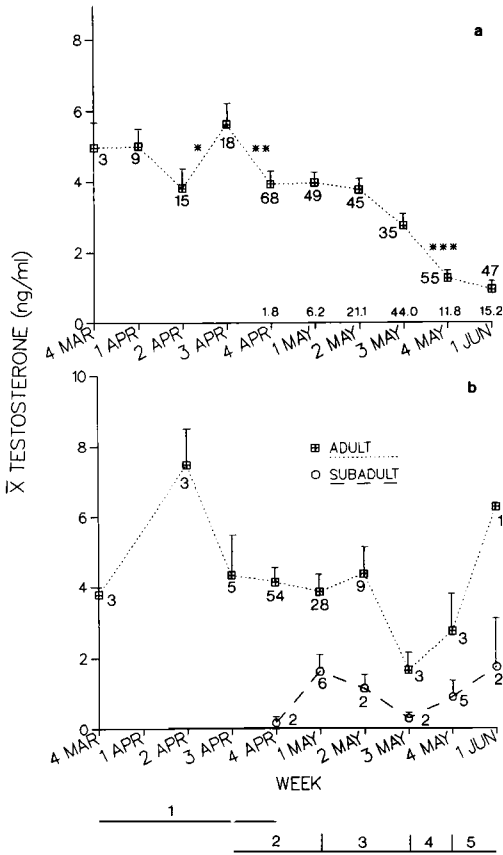
Fig. 1.   Weekly average plasma levels of testosterone in (a) adult territory owners and (b) adult and subadult floaters. Data are pooled from all marshes. Vertical bars show SE. Numbers next to weekly averages are sample sizes. Significant differences between weeks (Mann-Whitney U-tests) are indicated (* = two-tailed $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). Numbers along the horizontal axis in (a) are the weekly percentages of the total number of nests built ($n = 432$). Lines below the horizontal axis in (b) represent approximate reproductive stages on male territories: (1) before first females arrived on territories, (2) first females settled on territories, (3) first nests built and clutches laid and incubated, (4) first nestlings, and (5) first young fledged.

1a). Weekly plasma T levels of nine individuals, each of whom provided 6–9 samples (Fig. 2), showed seasonal T patterns similar to the weekly averages (Fig. 1a).

There was a significant decline in average testosterone levels of males shortly after the first females settled on their territories, but T remained relatively high until the first nest-
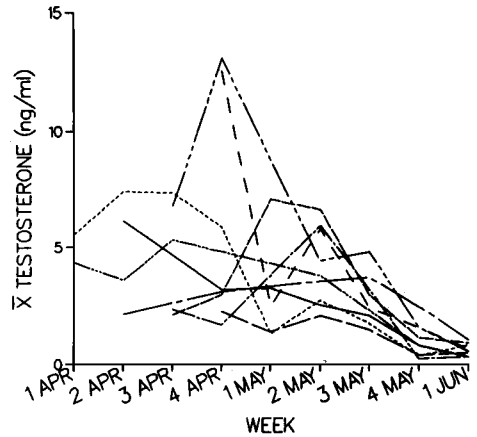

Fig. 2.   Weekly plasma testosterone levels of 9 individual territory owners.

lings hatched (Fig. 3). We took blood samples from 22 males during the 2 weeks before, and then within 1–3 days after, they were first observed feeding offspring. Testosterone levels of individuals declined significantly between the two sampling times (mean T level before feeding = 1.7 ± 0.5 ng/ml plasma vs. 1.0 ± 0.4 ng/ml during feeding; Wilcoxon matched-pairs test, $z = -1.74$, one-tailed, $P = 0.04$). The 13 prefeeding samples taken within 1 week of the onset of feeding had a similar significant decline (mean T level before feeding = 1.3 ± 0.5 ng/ml plasma vs. 0.5 ± 0.1 ng/ml during feeding; Wilcoxon, $z = -1.85$, $P = 0.03$).
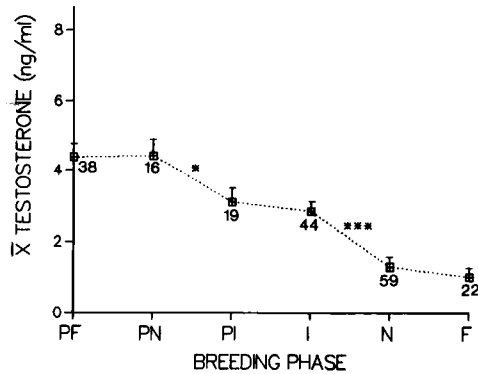

Fig. 3.   Average testosterone levels for territorial males, by breeding phase. PF = prefemale; PN = prenest; PI = preincubation; I = first incubation; N = first nestlings; F = first fledglings. Numbers below averages are sample sizes. Significant differences between stages are indicated by asterisks (see Fig. 1).
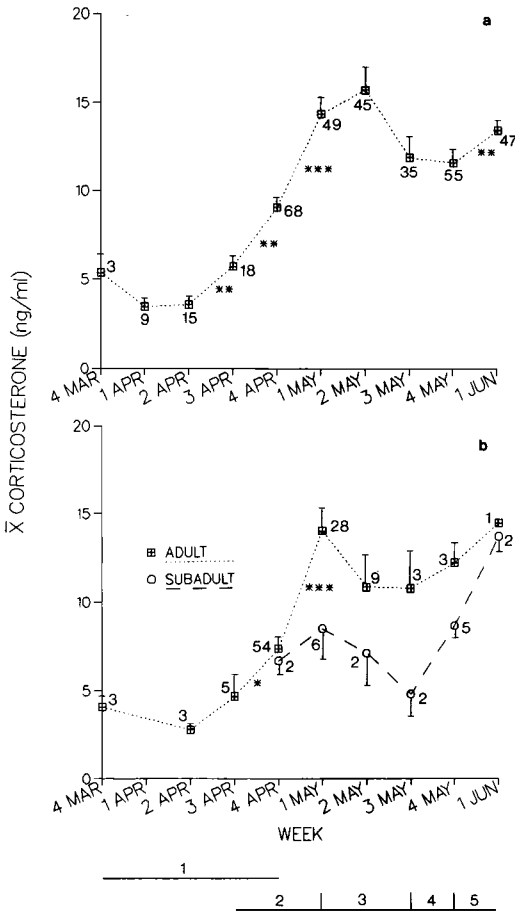
Fig. 4. Weekly average plasma levels of cortico-sterone in (a) adult territory owners and (b) adult and subadult floaters. Vertical bars show SE. Significant differences between weeks are indicated by asterisks (see Fig. 1). Lines below the horizontal axis represent approximate breeding stages (see Fig. 1).
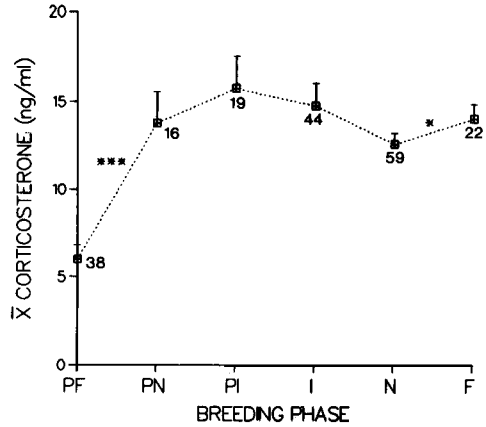

Fig. 5. Average corticosterone levels of territorial males, by breeding phase. Numbers next to averages are sample sizes. Significant differences between stages are indicated by asterisks (see Fig. 1 legend). For definitions of axis labels, see Figure 3.

Testosterone levels of floaters.—Average T levels of adult floaters matched those of territory owners during most of the breeding season (Fig. 1b). Floaters sampled in early April ($n = 3$) and early June ($n = 1$) had unusually high T levels, but the sample sizes were too small to conclude that these were typical levels. Testosterone levels of floaters did not differ significantly between April ($n = 62$) and May ($n = 43$; Mann-Whitney test, $z = -1.09$, two-tailed, $P = 0.28$). The seasonal pattern of T levels among those floaters that provided at least 2 blood samples at least 1 week apart ($n = 24$ samples from 10 individuals) was the same as that of the floater population as a whole.

Owners and floaters had statistically indistinguishable T levels in April (Mann-Whitney test, $z = -0.16$, two-tailed, $P = 0.87$) and during the first 3 weeks of May ($z = -0.21$, $P = 0.84$). The average circulating T level among 4 floaters sampled during the last week of May and first week of June (3.6 ± 1.2 ng/ml plasma) was three times greater than the average for territory owners during that period ($n = 102$; 1.1 ± 0.1 ng/ml).

Fifteen blood samples from 11 eventual territory owners (taken before they gained territories) provided no evidence that these males had higher T levels than other floaters. About half the samples ($n = 8$) contained T concentrations lower than average for floaters during the week sampled, and the others ($n = 7$) had higher than average T levels.

We trapped few subadult floaters, although many were present in the study area. Their circulating T levels were well below those of adult owners and floaters (Fig. 1b) and levels did not change significantly between the first three weeks for which we had samples ($n = 10$, last week in April to second week in May) and the last three weeks ($n = 9$, last two weeks in May and first week in June; Mann-Whitney test, $z = -0.37$, two-tailed, $P = 0.71$). Subadults had significantly lower T levels than adult floaters during the last week of April and first two weeks of May (data pooled to increase sample size for subadults; Mann-Whitney test, $z = -3.78$, one-

TABLE 1.   Testosterone and corticosterone levels ($\bar{x} \pm$ SE) of male Yellow-heads holding territories in high-density (Morgan Lake) and low-density (McMannamon and Juvenile lakes) breeding areas. Sample sizes are in parentheses.

| Week | Breeding areas | | z^a | One-tailed P |
	High-density	Low-density		
	Testosterone levels			
4 April	4.0 ± 0.6 (24)	2.4 ± 0.5 (13)	−2.07	0.02
1 May	3.8 ± 0.3 (27)	3.8 ± 0.7 (9)	−0.16	0.43
3 May	2.5 ± 0.4 (24)	3.4 ± 0.8 (10)	−1.17	0.12
	Corticosterone levels			
4 April	9.8 ± 1.1 (24)	8.5 ± 1.2 (13)	−0.49	0.31
1 May	14.6 ± 1.3 (27)	12.2 ± 2.2 (9)	−1.19	0.12
3 May	11.9 ± 1.5 (24)	11.7 ± 2.3 (10)	−0.08	0.47

[a] Mann-Whitney U-tests.

tailed, $P < 0.001$) and during the last two weeks of May and early June ($z = -2.17$, $P = 0.03$).

Corticosterone levels of owners and floaters.—Average B levels of territory owners were low at the beginning of the breeding season, rose sharply and significantly between mid-April and mid-May, and then declined slightly but remained high as males fed their young (Fig. 4a). Kruskal-Wallis tests revealed significant differences among weeks (first week in April through first week in June; $\chi^2 = 104.74$, $P < 0.001$) and among months (April, May, June; $\chi^2 = 75.29$, $P < 0.001$). Among those territory owners for which we had breeding dates, average B levels rose rapidly and significantly as females arrived in the area and settled on their territories and then plateaued at a high level during the incubation, hatching, and fledging of their first nests (Fig. 5).

Weekly average B levels for owners and adult floaters are very similar (Fig. 4a, b). Corticosterone levels of owners and floaters did not differ significantly during April (Mann-Whitney test, $z = -0.16$, two-tailed, $P = 0.87$) or May ($z = -0.53$, $P = 0.60$). Subadult floaters had B levels similar to adult floaters during the last week of April and first two weeks of May (Fig. 4b; data pooled to increase sample size for subadults; Mann-Whitney test, $z = -0.18$, one-tailed, $P = 0.43$) and during the final two weeks of May and early June ($z = -1.32$, $P = 0.09$).

Steroid hormones and breeding density.—Because the number of samples from McMannamon and Juvenile lakes was small, we had sufficient numbers for statistical comparisons with Morgan Lake males only during the last week of April and the first and third weeks of May (Table 1). Males breeding at high densities on Mor-

gan Lake had significantly higher T levels only during the last week of April. There were no significant differences in B levels between the two groups during these weeks (Table 1).

Steroid hormone levels and breeding success.—Harem sizes on 134 male territories averaged 3.0 ± 1.7 females/male. An average of 3.3 ± 1.9 nests were built and an average of 3.1 ± 2.7 offspring were fledged on each territory. There were no significant correlations between male harem size or fledging success and individual testosterone levels during the third week in April, when average T levels peaked in the population (Spearman $r = -0.21$, $P = 0.26$, $n = 12$ and $r = -0.39$, $P = 0.11$, respectively), during the first two weeks of May, when the first nests were built on each territory and clutches were laid ($r = -0.01$, $P = 0.47$, $n = 52$ and $r = -0.17$, $P = 0.11$, respectively), or during the last week of May and first week of June, when males fed nestlings ($r = 0.13$, $P = 0.18$, $n = 53$ and $r = -0.14$, $P = 0.16$, respectively).

There was a significant positive correlation between the corticosterone levels of individual males during the first two weeks of May, when B levels peaked, and harem size (Spearman $r = 0.27$, $P = 0.03$, $n = 52$), but not with eventual fledging success ($r = -0.06$, $P = 0.33$). The correlations between B levels during the period males fed nestlings and breeding success were not significant (harem size, $r = -0.01$, $P = 0.47$, $n = 53$; fledging success, $r = -0.08$, $P = 0.29$).

DISCUSSION

Testosterone.—Circulating T levels were high in male Yellow-heads when they arrived in the study area. Levels remained high as birds con-

tested for territories and, in individuals that obtained territories and attracted mates, declined sharply only toward the end of the breeding effort when males fed nestlings. The 2-month period of high T levels included the time when essentially all territories were established, all females settled, almost all clutches were initiated, and males guarded mates.

Our finding that T levels of territory owners remained high through most of the breeding season is therefore consistent with the predictions of the challenge hypothesis. Males guarded their mates from other males during the weeks of elevated T, but we made no specific effort to quantify this behavior. Sexually receptive females may also cause elevated T levels in male birds (Wingfield and Moore 1986, Wingfield et al. 1987). However, the fact that testosterone levels were high before females arrived in the study area, and breeding males and nonbreeding floaters had very similar seasonal T patterns, strongly implies that male-male interactions are the more powerful determinant of circulating T levels among Yellow-heads during the breeding season.

Testosterone levels of territory owners declined toward the end of the breeding season. Presumably, the high T levels that facilitate aggressive behavior must decline before male parental behavior is expressed (Silverin 1980, Hegner and Wingfield 1987). Male Pied Flycatchers (*Ficedula hypoleuca*) with exogenous, implanted testosterone maintained territorial and aggressive behavior beyond normal limits and provided less parental care than control males (Silverin 1980). Artificially elevated T levels inhibited male parental care in monogamous House Sparrows (*Passer domesticus*; Hegner and Wingfield 1987). Conversely, parental care was prolonged by administration of an androgen blocker. Gori (in prep.) showed that T-implanted male Yellow-heads have a lower probability of feeding young than control males. He suggested a trade-off between high T levels that facilitate male advertisement for additional mates and parental care activities. The natural decline in T levels that apparently permits the expression of male parental care in Yellow-heads may be adaptive because control males, which fed their nestlings at a higher rate, fledged more young than T-implanted experimentals (Gori in prep.).

Differences between Yellow-headed and Red-

winged blackbirds.—Yellow-heads and Red-wings are both strongly polygynous and breed in the same marshes at approximately the same time. There are large numbers of nonbreeding adult males in both species. However, Red-wings winter in the study area, occupy their territories sporadically during the winter, and few males lose or gain territories during the breeding season (Beletsky and Orians 1987, Beletsky et al. 1989). Perhaps because of this seasonal stability, Red-wing territory owners had relatively low T levels during the first month of the breeding season, before and during female settlement (Beletsky et al. 1989). In contrast, male Yellow-heads were migratory, arrived in waves over many weeks, and competed for territories during most of the breeding season. This pattern was associated with high T levels in territory owners throughout April and May.

The difference in territorial stability during breeding between Yellow-heads and Red-wings may also explain why Yellow-head floaters had T levels indistinguishable from those of territory owners during the period of territory establishment, whereas Red-wing floaters had T levels significantly below those of territory owners. When relative social stability prevails—whether enforced by "social inertia," individual recognition of status, or accepted territory boundaries (Ramenofsky 1984, Wingfield and Ramenofsky 1985)—the challenge hypothesis predicts low T levels. Accordingly, the lower T levels of Red-wing floaters indicate either that they seldom challenge for territories or that their challenges are too brief to stimulate strong testosterone secretion (Wingfield 1984, Wingfield et al. 1987). Conversely, Yellow-head floaters successfully challenged established males and obtained territories during much of the breeding season; an almost identical T profile in owners and floaters is expected under the challenge hypothesis. The only period during which Yellow-head owners and floaters differed in average T levels was late May and early June, when breeders fed offspring (but the sample for floaters was very small). Lower T levels in territory owners during this period suggests that the social environment (in this case, the presence of nestlings) may regulate T levels and the expression of parental behavior.

Corticosterone (B).—Corticosterone levels of territory owners were initially low and rose rapidly as females arrived on territories and

nesting began. We believe that Yellow-head males probably were not stressed nutritionally or socially early in the breeding season. When males began to defend their territories against rising numbers of floaters, and as females settled on their territories, energy requirements and social interactions increased. It is unlikely that individuals became nutritionally stressed later in the breeding season because their primary food source (insects) increased. However, restrictions of movement imposed by increased territorial intrusions could have reduced both time available for foraging and foraging efficiency. Unlike T levels, circulating B levels did not decline when males fed nestlings. Because owners and floaters had similar seasonal B patterns, involvement in parental care could not have strongly influenced B secretion.

The challenge hypothesis predicts elevated testosterone levels in high-density breeding areas, because agonistic interactions are more frequent or more intense there than in low-density areas. Ball and Wingfield (1987) found such a relationship between T levels and breeding densities in male European Starlings (*Sturnus vulgaris*). Yellow-heads that breed at high density on Morgan Lake had significantly higher T levels at the end of April than males on the low-density marshes. The second half of April was the period of peak settlement on Morgan Lake, and aggressive interactions among males probably peaked at this time. In contrast, McMannamon and Juvenile lakes remained sparsely settled throughout the breeding season. Differential T levels in Yellow-heads that bred at high and low density are consistent with the challenge hypothesis, but we have no information on the relative durations or intensities of owner/challenger interactions on Morgan vs. the other study lakes.

Unlike the situation among Red-wings (Beletsky et al. 1989), we found no significant relationships between T levels of individual Yellow-head males and their annual harem sizes or reproductive success. Although absolute T levels and variation in T levels among individuals are similar in the two species, breeding success was higher and more variable among Red-wings. Male Red-wings in 1987 fledged an average of 6.2 ± 6.2 offspring, whereas male Yellow-heads in 1988 fledged an average of 3.1 ± 2.7 offspring. Because differences in success among male Yellow-heads are usually smaller,

potentially subtle effects of testosterone on male success would be more difficult to detect.

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