RELATIONSHIPS OF STEROID HORMONES AND POLYGYNY TO TERRITORIAL STATUS, BREEDING EXPERIENCE, AND REPRODUCTIVE SUCCESS IN MALE RED-WINGED BLACKBIRDS

LES D. BELETSKY, GORDON H. ORIANS, AND JOHN C. WINGFIELD
Department of Zoology, NJ-15, University of Washington, Seattle, Washington 98195 USA

ABSTRACT.—We collected 354 blood samples from territorial and nonterritorial male Red-winged Blackbirds (*Agelaius phoeniceus*) to determine plasma levels of testosterone (T) and corticosterone (B) of a polygynously breeding bird, and to determine the potential influences of steroid hormone levels on obtaining breeding territories. In contrast to monogamous species, we found no peak in average T levels early in the breeding season and a five-week-long high plateau in T levels during the period when most nests were initiated. These endocrinologic characteristics may result from the long breeding season and resource defense polygyny of Red-wings. Territory owners had higher T levels during the breeding season than adult floaters. Subadult floaters had the lowest levels. Also, territory owners generally had the highest circulating levels of corticosterone during most of the breeding season. This implies greater energetic demands and stress on owners than on floaters. During early April the T levels of males for which we had complete breeding and territorial history information correlated significantly with their annual fledging success, and males with more breeding experience tended to have higher peak T levels. There was also a positive correlation between B levels in early April and eventual fledging success. Circulating levels of steroid hormones may affect territory ownership and reproductive success in this species. *Received 17 February 1988, accepted 24 August 1988.*

STEROID hormones influence the reproductive behavior of birds and other animals (for reviews see Sossinka et al. 1980, Balthazart 1983, Wingfield et al. 1987). The interrelationships among environmental stimuli, hormone levels, and behavior, however, are poorly understood. Free-ranging birds have only recently been monitored for circulating levels of steroid hormones and associated reproductive behavior (e.g. Wingfield and Farner 1978, Silverin 1983, Wingfield 1985a, Dufty and Wingfield 1986, Hegner and Wingfield 1986a, b). Most of these studies have focused on monogamous species.

Testosterone (T) levels stimulate certain behaviors such as singing (Nottebohm 1981) and are directly related to the intensity of short-term aggressive behavior. Testosterone may not trigger aggression, but may facilitate expression of the behaviors involved at high frequency and intensity (Wingfield et al. 1987). When territorial males are "challenged" by conspecific males, T levels rise as they defend their territories or mates (the "challenge hypothesis"; Wingfield 1985a, in press; Wingfield et al. 1987). In the monogamous songbird species that have been examined, this process characteristically results in circulating T levels that peak during territory establishment, peak again during a period of mate-guarding, and then decline sharply (Wingfield and Moore 1986, Wingfield et al. 1987).

The seasonal profiles of testosterone in males of bigamous Pied Flycatchers (*Ficedula hypoleuca;* Silverin and Wingfield 1982) and brood parasitic Brown-headed Cowbirds (*Molothrus ater;* Dufty and Wingfield 1986) departed significantly from those typical of monogamous breeders. In these species, T levels were elevated for prolonged periods, associated in time with sequential or continuous male mate-guarding behavior.

The Red-winged Blackbird (*Agelaius phoeniceus*) is strongly polygynous. Males maintain territories, guard multiple mates, and defend nests from predators for two to four months in the spring. Individual males acquire females over long time periods and harems differ strikingly in size. Because of high nest-predation rates and renesting by females, males often have nests in several different stages of the breeding cycle at the same time and over many weeks. Therefore, the seasonal profiles of steroid hormones for this species should be valuable for testing hypotheses about relationships among hormone levels, behavior, and mating systems, particularly those that bear on testosterone and aggression (Harding 1981; Wingfield 1984, in press; Wingfield et al. 1987).

Male Red-wings usually do not obtain territories until they are two or more years old. Therefore, in any given year, there is a sizeable floating population of nonbreeders whose hormone levels can be compared with those that hold territories. Within-season reproductive success of males is strongly correlated with harem size (Beletsky and Orians 1987, Orians and Beletsky 1989), offering the possibility of relating hormone levels to determinants of reproductive success.

We studied hormone levels in a population of Red-wings that had been monitored intensively for breeding behavior and breeding success for over a decade. Our purposes were to establish the basic seasonal patterns of steroid hormone levels in territorial and nonterritorial males, to test whether these patterns conformed to predictions from the "challenge hypothesis" of T secretion (Wingfield et al. 1987, Wingfield in press), and to examine relationships between hormone levels and reproductive success. We have now elucidated the relationships among plasma testosterone and corticosterone (B) levels and territorial status, documented average circulating levels of T and B for a broad range of individuals over the course of a breeding season, and related steroid hormone levels to reproductive success of breeding males. Corticosterone levels were measured as an indicator of stress (e.g. Harvey et al. 1984; Wingfield 1984, 1985b).

We divided male Red-wings in the population into three territorial classes. *Adult territory owners* were males at least two years old that successfully held territories. *Adult nonterritorial floaters* were males at least two years old that did not have territories. Floaters remained in particular areas over prolonged periods, attempting to acquire territories. Adult floaters often intruded on occupied territories. Sometimes they persistently challenged established males for ownership; they quickly filled territory vacancies when they occurred; and they attempted to copulate with unguarded females. *Subadult floaters* were one-year-old, nonterritorial males. They weighed, on average, about 10% less than adults and had a distinctive plumage (brown primaries and orange epaulet feathers as opposed to the jet black and red-epauleted adults). They had functional testes (Payne 1969, Wiley and Hartnett 1976). Each year a few subadults at the study site succeeded in establishing territories and attracted at least one mate, but they rarely produced offspring. Most remained in small groups feeding and roosting together. Due to their roving nature, the behavior of floaters is not well understood in this and other species.

We predicted that territory owners would have the highest plasma T levels during the breeding season, and that adult floaters, the most aggressive territorial challengers, would have higher levels than subadult males. The predictions were based on the observation that circulating levels of T are positively correlated with intensity of aggressive behavior in Red-wings and other birds (Searcy and Wingfield 1980, Harding 1981, Balthazart 1983, Wingfield 1983, Moore 1984) and that territorial dominance is clearly linked with aggressive behavior.

Corticosterone is thought to regulate adaptive changes in behavior when individuals are exposed to stressful environmental conditions (Wingfield and Silverin 1986, Wingfield in press). During a breeding season without major storms or nutritional stresses, only one of the three classes of male Red-wings (territory owners) are likely to be regularly stressed. Floaters probe for territorial opportunities but they typically withdraw when the owner approaches. Floaters forage primarily in communal, undefended areas where there are few agonistic interactions. Territory owners, on the other hand, patrol and defend their territories many times per day. Owners continually advertise to attract mates; they court, chase, and guard their multiple mates; and they defend their nests from a variety of predators. There is a temporal tradeoff between territorial activities and foraging off territory (Ydenberg and Krebs 1987). In fact, body mass of most territorial males declines as breeding progresses (Orians and Beletsky unpubl. data). Therefore, we predicted that corticosterone levels of territorial males would be consistently higher than those of nonterritorial males.

METHODS

This study was conducted at the Columbia National Wildlife Refuge in eastern Washington State, from late February to mid-June 1987. All males were marked with U.S. Fish & Wildlife Service and colored leg bands.

TABLE 1. The number of blood samples obtained from male Red-wings each week and subjected to hormonal assay.

	Feb	Mar				Apr				May				June	
	4	1	2	3	4	1	2	3	4	1	2	3	4	1	Total
Territory owners	2	0	40	24	16	16	32	15	10	6	17	13	8	5	204
Adult floaters	2	0	32	5	9	1	7	5	5	0	2	2	3	0	73
Subadult floaters	1	0	23	10	6	5	13	1	6	0	5	3	3	1	77
Total	5	0	95	39	31	22	52	21	21	6	24	18	14	6	354

The breeding biology of the Red-wing is described in detail by Orians and Christman (1968) and Orians (1980). In the population we studied, males occupy their territories in late February. Competition for territories in the study area is common and frequently intense (Beletsky and Orians 1987). The migratory females arrive in late March and April. Nesting usually begins in early April, peaks in May, and continues through June. Females build nests and incubate unassisted by their mates, and they feed young entirely or predominantly by themselves.

We monitored nesting on about 80 territories in a core study area (for a map and a more detailed account of reproductive monitoring, see Beletsky and Orians 1987). We located all nests built on each male's territory and checked them periodically until fledging or nest failure. We therefore knew the precise dates for onset and duration of the various breeding phases for some males from which blood samples were taken. Quality of territories was judged on the basis of past histories of reproductive success on the marshes in which they were located. "Low" quality territories were usually in grassy areas along streams, easily accessible to predators. "Moderate" quality territories were located on narrow marshes that bordered lakes. "High" quality territories were located in large marshes that had broad expanses of vegetation and historically supported territories that produced the most fledglings in the study area. For example, from 1978 through 1986, males with territories on "moderate" quality marshes produced an average of 3.9 ± 5.0 (SD) fledged young/year ($n = 351$ male breeding-years), whereas those breeding on "high" quality marshes produced an average of 7.3 ± 7.5 fledged young/year ($n = 209$).

Subadult floaters were distinguished by their plumage. All males with territories in the core area were known to us, as were those that bred on adjacent marshes. Most blood samples from territorial males came from these groups. We conducted a comprehensive census of banded territorial Red-wings in peripheral breeding areas, to a distance of 4,000 m or more in all directions from the center of the study area, to determine which other males we trapped and bled were territorial elsewhere. We were confident that we correctly identified all territory owners in our sample because males in this population rarely venture more than 1,500 m from their territories during breeding (Beletsky and Orians 1987). Adult floaters were either known floaters (observed repeatedly in the area) or probable floaters (never observed on territory in the core or peripheral areas).

We operated grain traps in several parts of the study area for several hours at a time, usually 0800 to 1130. Blood samples were taken from all males, but none was bled more than once in any 10-day period. Many males were bled only once or twice. A few males, especially those with territories adjacent to the main trapping areas, provided up to seven samples each during the breeding season.

Traps were of the "funnel" variety, into which birds walk to obtain seeds but cannot escape. Birds were removed from traps within minutes of entering, during which time they fed quietly. They were not stressed until we approached to remove them. Blood samples (200–400 μl) were collected from a wing vein into heparinized microhematocrit capillary tubes within 10 min of removal from traps (Wingfield and Farner 1976, 1978). Steroid hormone levels in songbirds remain stable for at least 10 min after capture (Wingfield et al. 1982a). Most territorial males flew back to their territories immediately after release. None of the males we bled lost territories during the breeding season (see also Wingfield and Farner 1976).

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 randomly selected for each of the five arrays required to complete the analysis. Intra- and inter-array variations were within the limits presented by Wingfield and Farner (1975) and Wingfield et al. (1982b). Least detectable concentrations were 1.9 pg for T and 7.8 pg for B.

We present our data chronologically and by breeding stage. We divided the breeding season into 14 approximately week-long periods; each month was divided into 4 periods of 7, 8, 7(8), and 8 days, respectively (Table 1). Nesting began earlier on some territories than on others, so that males reached different stages of breeding at different times. Also, because of extensive nest predation, young first fledged from territories over a period of 5–6 weeks. We divided breeding sequences into 5 stages: 1) the period during female arrival but before first nests were ini-

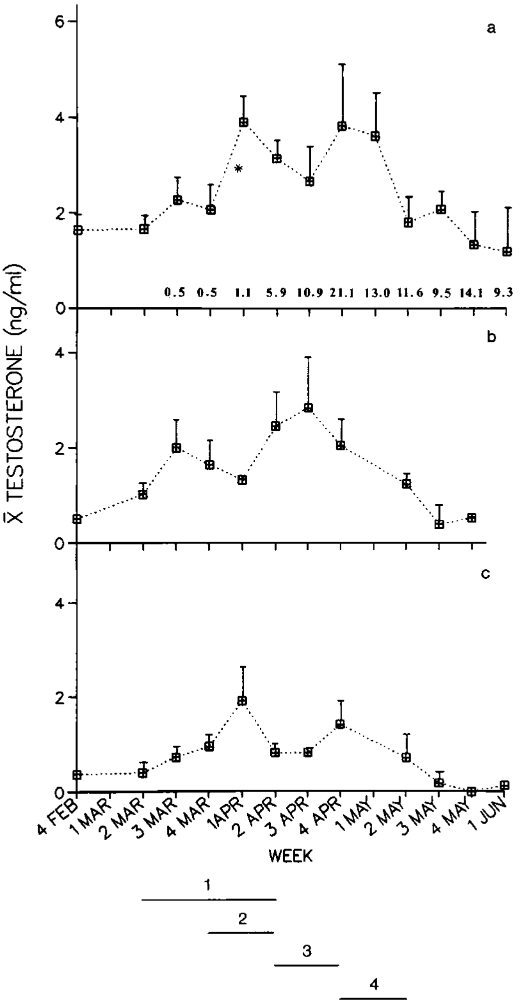

Fig. 1. Comparison of weekly average plasma levels of testosterone in (a) adult territory owners, (b) adult floaters, and (c) subadult floaters. Sample sizes are in Table 1 (samples of <8 were not tested). Vertical bars represent SEs. Between-week differences in T concentrations were not significant, except between 4 March and 1 April (* $U = 72.0$, $P < 0.01$). Numbers along the horizontal axis in (a) are the weekly percentages of the total number of nests built in 1987 that reached the egg-laying stage ($n = 441$). Lines below the horizontal axis in (c) represent approximate reproductive stages on male territories: (1) female arrival, (2) first nests built, (3) first nestlings, and (4) first young fledged.

tiated; 2) the period from construction of the first nest through completion of the first clutch on the territory; 3) the period of incubation of the first clutch; 4) the period of the first nestlings on the territory; and 5) the period after the first nest successfully fledged young.

We tested differences in hormone levels among samples and among groups for significance with Mann-Whitney *U* tests and Kruskal-Wallis one-way ANOVA tests. Significance was accepted at the 0.05 level. The Mann-Whitney tests, which require sample sizes of at least eight, were one-tailed.

RESULTS

TESTOSTERONE LEVELS OF TERRITORY OWNERS

Seasonal pattern.—Plasma T levels started to rise during the third week of March. This rise coincided with the period when significant numbers of females arrived and settled on the territories (pers. observ.). There were significant differences in plasma T levels from week to week (second week in March through the last week of May; Kruskal-Wallis test, $\chi^2 = 37.61$, $P < 0.001$), as well as from month to month (March-May; $\chi^2 = 20.63$, $P < 0.001$). Average T levels rose sharply and significantly (Fig. 1a) in these males during the first week of April and remained at relatively elevated levels until the second week of May. During this five-week period, 52% of nests in the study area that progressed at least to the stage of containing eggs were built (Fig. 1a). Because copulation, fertilization, and associated mate-guarding behavior by males occur during and directly following nest building (Nero 1956; Davies and Orians MS, pers. observ.), elevated plasma T levels were associated in time with increased aggression by males during these activities. Plasma T levels declined significantly between the first and third weeks of April ($U = 77.0$, $P < 0.05$), but average concentrations in mid-April remained generally higher than those in early March. By mid-May to early June, plasma T concentrations returned to the levels characteristic of the period before female arrival, despite the fact that ca. 45% of nests were initiated during that period (Fig. 1a).

Individual levels.—Because average values can mask significant individual differences, we present plasma T concentrations for territorial individuals for which we obtained at least 4 blood samples (Table 2). These data show a pattern of seasonal T levels generally similar to the population mean (Fig. 1a), but not all individuals followed this pattern rigidly. Several males had plasma T levels at various points much higher or lower than average (Fig. 1a, Table 2). Individual differences in territory quality and

TABLE 2. Weekly plasma T concentrations (ng/ml plasma) and breeding success of individual male territory owners.

Male	March			April				May				Harem size	No. of nests	No. of young fledged	Estimated territory quality	No. of years breeding
	2	3	4	1	2	3	4	1	2	3	4					
1	0.27	—	0.73	—	—	0.95	—	—	—	—	0.63	1	1	3	low	1
2	0.29	—	1.02	—	3.67	—	1.50	—	2.08	—	2.01	na	na	na	low	1
3	0.77	—	1.71	—	—	3.05	—	1.11	—	—	—	1	2	0	low	1
4	—	—	2.84	6.60	—	—	1.23	—	1.63	2.45	—	15	19	20	high	5
5	—	1.76	—	2.30	—	0.18	—	—	0.24	—	—	5	7	9	high	5
6	—	6.15	—	1.35	1.96	0.91	—	—	—	—	0.00	3	3	7	high	1
7	7.09	5.45	—	4.65	—	—	—	—	6.05	—	—	7	12	19	high	3
8	—	—	—	5.86	—	0.86	—	—	1.37	—	0.18	4	5	10	high	2
9	1.13	—	—	2.90	3.89	—	2.57	—	—	1.29	—	4	7	13	high	1
10	0.59	—	—	—	—	—	2.15	—	6.64	2.35	—	na	na	na	low	1
11	0.40	0.36	—	1.85	1.38	—	2.41	—	1.21	—	—	3	6	7	low	1
12	0.25	—	0.89	—	—	2.65	—	—	1.12	—	0.32	na	na	na	moderate	1
13	9.04	—	4.78	—	—	10.32	—	4.09	3.16	—	0.56	6	12	8	moderate	2

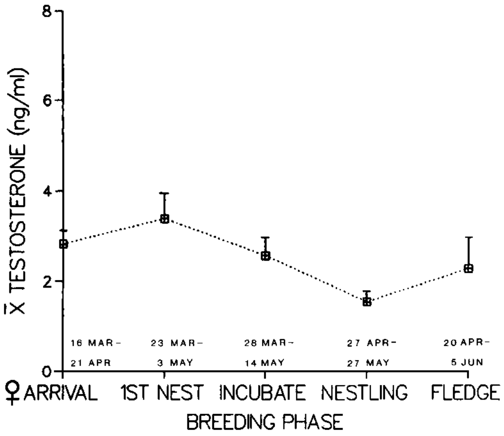

Fig. 2. Seasonal changes, by breeding stage, in average testosterone levels for territorial males for which we had complete breeding histories. Dates indicate the range over which the various males initiated each period. Sample size for female arrival period was 39; first nest, 8; incubation, 16; first nestlings, 7; and first fledglings, 17.

social behavior may account for these variations (see below).

Variation among breeding phases.—The testosterone curve for those males for which we knew precise breeding dates (Fig. 2) was generally similar to the population curve (Fig. 1a; note that the first period in Fig. 2 corresponds in time to the third and fourth weeks of March). Male T levels were high when females arrived, slightly greater during construction of the first nest on their territories (i.e. when the first female was sexually receptive), and then declined somewhat during the incubation of the first clutch and feeding of the first brood. However, plasma T levels neither increased significantly between the males' prenesting phase and the period of first nest construction nor decreased significantly between nest construction and the first incubation period ($U = 208.5$, $P = 0.28$ and $U = 44.0$, $P = 0.11$, respectively). The dates on which males entered into the various breeding phases did vary over 30–45 days (Fig. 2).

Testosterone levels and breeding success, experience, and territory quality.—Annual reproductive success of males in this population was directly related to harem size (Orians and Beletsky 1989). To test whether the most aggressive males (perhaps those with the highest plasma T concentrations) maintained the highest quality territories and attracted large numbers of mates, we correlated the breeding success of 12 males for

TABLE 3. Mann-Whitney U tests, weekly and monthly comparisons of T and B levels, between territory owners and floaters (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

	Weekly comparisons					Monthly comparisons		
	2 Mar	3 Mar	4 Mar	1 Apr	2 Apr	Mar	Apr	May
Testosterone								
Territory owners vs. adult floaters	*	—	NS	—	—	*	NS	*
Territory owners vs. subadult floaters	***	**	—	—	***	***	***	***
Adult floaters vs. subadult floaters	**	—	—	—	—	***	***	*
Corticosterone								
Territory owners vs. adult floaters	NS	—	*	—	—	*	*	NS
Territory owners vs. subadult floaters	NS	*	—	—	NS	***	**	***
Adult floaters vs. subadult floaters	NS	—	—	—	—	NS	NS	NS

which we had complete breeding information with their T levels during the first week of April (the period of peak T levels). We included seven males listed in Table 2 and five others. There were nonsignificant trends for peak T levels to be positively related to harem size (Spearman $r = 0.33$, $P = 0.15$) and the number of nests built on the males' territories ($r = 0.38$, $P = 0.11$), and a significant positive correlation with fledging success (number of young fledged/male territory; $r = 0.55$, $P = 0.03$).

There was a positive but not quite significant relationship between T levels during the first week of April and the number of years of breeding experience of the males (Spearman $r = 0.48$, $P = 0.06$, $n = 12$). These males had bred between 1 yr (1987 was their first) and 5 yr ($\bar{x} = 2.6 \pm 1.7$ yr). This correlation suggests a direct relationship between age and peak T levels for breeding males, because the great majority of males in this population obtain territories when they are two or three years old (Orians and Beletsky 1989).

Four of the 24 males with known breeding histories for which we had blood samples in April held low quality territories (T concentration $\bar{x} = 1.84 \pm 0.89$ ng/ml plasma), 11 had moderate quality territories (T $\bar{x} = 4.25 \pm 2.81$ ng/ml plasma), and 9 had high quality territories (T $\bar{x} = 3.24 \pm 2.22$ ng/ml plasma). The sample size for males with low quality territories was too small for statistical comparisons. The low average T level among males with low quality territories suggests either that these males obtained poor territories because of their lower T levels, or that they were under less pressure than other males to defend their territories. They may have had fewer aggressive interactions.

Testosterone Levels of Floating Males

The seasonal pattern of T levels among adult floaters was similar to that of territory owners, but absolute values and the amplitudes of the peaks were lower (Fig. 1b). There were significant differences in T levels among the three territorial classes of males in March (Kruskal-Wallis test, $\chi^2 = 34.20$, $P < 0.001$), April ($\chi^2 = 26.49$, $P = 0.02$), and May ($\chi^2 = 18.10$, $P < 0.001$). Statistical testing of the differences in T levels between owners and adult floaters was precluded because of small weekly sample sizes for floaters, except for the second and fourth weeks of March (Table 3). Territory owners had significantly higher T levels in March and May, and there was a nonsignificant trend for higher T levels for territory owners in April.

The seasonal pattern of T levels among subadult floaters was similar to those of territory owners and adult floaters, but base and peak levels were much lower (Fig. 1c). Subadult T concentrations were significantly lower than those of territory owners and adult floaters during March, April, and May (Table 3).

Corticosterone

Average weekly plasma concentrations of corticosterone (B) in territorial males did not fluctuate widely or rapidly during the breeding season (Fig. 3a). However, there were significant differences in B levels among weeks (second week in March through the last week of May; Kruskal-Wallis test, $\chi^2 = 20.25$, $P = 0.04$) and among months (March-May, $\chi^2 = 10.39$, $P = 0.006$). B levels dropped significantly between the third and fourth weeks of May.

Territory owners and adult floaters had sim-

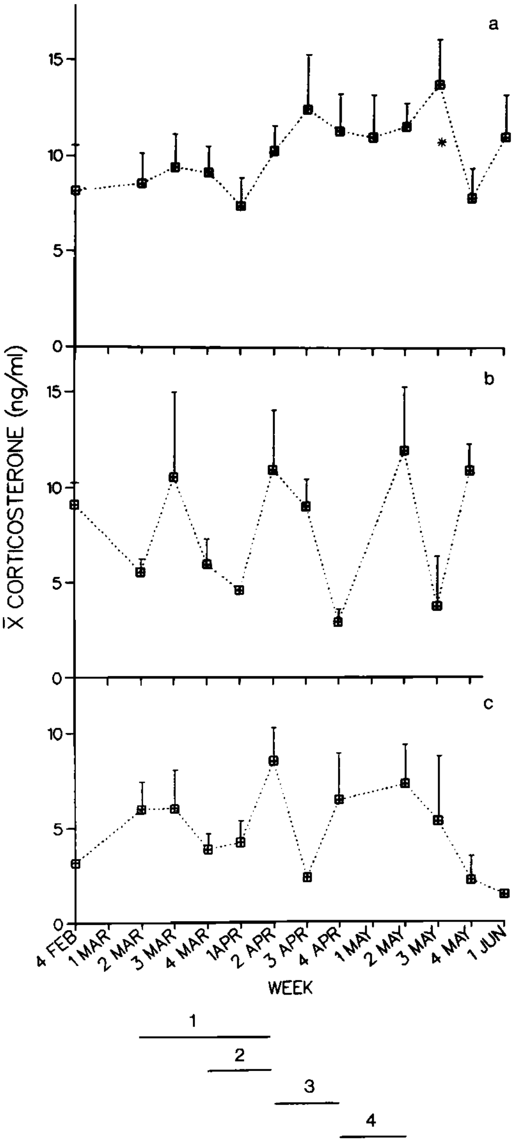

Fig. 3. Comparison of weekly average corticosterone plasma levels in (a) adult territory owners, (b) adult floaters, and (c) subadult floaters. Vertical bars represent SEs. Between-week differences in B concentrations were not significant, except between 3 May and 4 May (* $U = 29.0$, $P < 0.05$). Lines below horizontal axis in (c) represent approximate reproductive stages on male territories: (1) female arrival, (2) first nests built, (3) first nestlings, and (4) first young fledged.

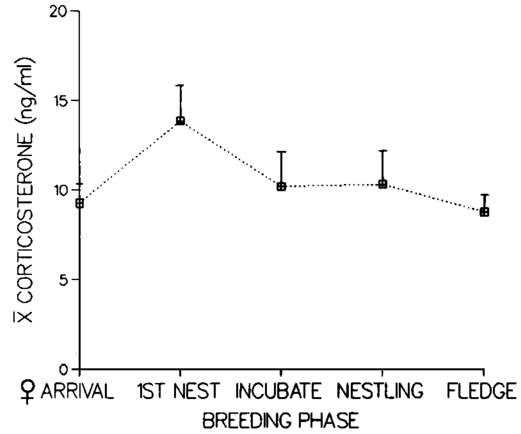

Fig. 4. Seasonal changes, by breeding stage, in average corticosterone levels for territorial males for which we had complete breeding histories. Sample sizes are given in Fig. 2.

ilar average B levels during many weekly periods (Fig. 3a, b). Subadult B levels were consistently below those of territory owners (Fig. 3c). There were significant differences among territory owners, floaters, and subadults throughout the breeding season (Kruskal-Wallis tests: March, $\chi^2 = 9.50$, $P = 0.009$; April, $\chi^2 = 7.96$, $P = 0.02$; May, $\chi^2 = 10.29$, $P = 0.006$). Territory owners had significantly higher B blood concentrations than adult and subadult floaters, at least during one week in each case for which we had sufficient sample sizes to test (Table 3). Corticosterone levels of territory owners were significantly higher than those of floaters during March and April (Table 3).

Plasma B levels rose significantly between the prenesting periods and the first nest-building periods ($U = 79.5$, $P = 0.02$), and declined significantly between the nest-building and the first incubation period ($U = 35.0$, $P = 0.04$; Fig. 4). These changes suggest increased energetic demands on males during their first mating period.

We tested for relationships between early April circulating corticosterone levels and eventual breeding success, because the peak T levels during the first week of April suggest heightened aggression and thus increased energetic demands at that time. Males with high plasma B levels in early April tended to have large harems (Spearman $r = 0.38$, $P = 0.11$). There were significant positive correlations between B levels and the number of nests eventually built on each male's territory ($r = 0.57$, $P = 0.03$) and the number of fledglings produced ($r = 0.50$, $P = 0.049$). There was a nonsignificant trend for males with higher plasma B levels to have lower body mass ($r = -0.33$, P

= 0.07, n = 12). These individuals may have been subject to greater energetic stresses than others, but our information on body mass is at present insufficient to test whether the rate of loss was correlated with plasma B levels.

DISCUSSION

The seasonal plasma T pattern of Red-wings differed from a typical monogamous pattern. There was no early peak associated with territory establishment, and once T concentrations rose in early April, they tended to remain at high levels for about five weeks. The lack of elevated levels in early spring, when many temperate species normally establish territories, may be due to the fact that Red-wings winter in the study area and visit their territories regularly. Time spent on territories gradually increases in late winter until by early March males are on or near their territories most of the day. Migratory Red-wings that must reestablish territories in early spring may exhibit early T peaks.

Average plasma T levels peaked in early April. The peak coincided with the initiation of nesting by females. Levels remained elevated for several weeks and then declined. This T profile closely resembles that found in the Brown-headed Cowbird, a brood parasite in which males lack territorial and parental behavior, but guard females from other males during the entire breeding season (Dufty and Wingfield 1986). The prolonged peak in male Red-wings may be explained by the multiple, sequential nest initiations on male territories. Females settled on male territories and began to breed over a 10-week period. Up to 20 nests were built on some male territories. Because nesting is dispersed in time, males must guard mates during their fertile periods over many weeks. In fact, Davies and Orians (MS) have shown that male Red-wings in this population guard their mates throughout April and May. This interpretation is supported by data from Pied Flycatchers. Monogamous males exhibited seasonal plasma T patterns similar to those found in other monogamous breeders; but bigamous males, mating sequentially with two females, maintained high T levels until the second female was incubating, i.e. no longer fertile (Silverin and Wingfield 1982).

Challenges by floaters for territories also continued throughout April. Vocal and visual advertisement displays by territory owners also continued at relatively high rates. For example, territorial males in this population—monitored during 500 15-min periods during 1983, 1984, and 1985—gave song spread displays at average rates of 38.5 ± 20.5 per 15-min period during March (n = 161 periods), 22.2 ± 17.8 per 15 min during April (n = 200 periods), and 13.7 ± 10.7 per 15 min during May (n = 139). Thus, the relatively long period of high plasma T concentrations in these males was correlated with prolonged territorial aggression, advertisement, and sexual behavior.

Recent research suggests that elevated T concentrations are physiologically incompatible with parental care activities such as feeding young (Silverin 1980, Hegner and Wingfield 1986a). The observation that only a few males in our study fed nestlings or fledglings, and then only during the last few weeks of the breeding season, supports this idea. Males feeding young were first observed on 13 May. By 20 June, only 19% of territorial males had been observed feeding young, usually fledglings. Three males that were bled when they were feeding young had very low plasma T concentrations (<0.10, <0.10, and <0.18 ng/ml plasma), in two cases too low to be measured by our assay. Most nests of the season were either built or were under construction by mid-May, and few new females were added to harems after that. Competition for territories apparently declined at this time. Some males, whose nests had already terminated, left their territories by early June. Thus, our observations indicate that feeding young occurred only when T levels were low, even in this highly polygynous species.

If high T levels are associated with mate-guarding behavior among Red-wings, then it is perhaps surprising that average T levels did not remain elevated during the final three weeks of May. About 35% of all nests were initiated during this time. One certain contributing factor is that no new nests were built on the territories of some of the males providing blood samples during this period. Also, the number of floaters that trespassed on male territories declined during this period (pers. observ.). Lower average T levels would be expected if the frequency of male-male encounters declined. Similarly, European Starling (*Sturnus vulgaris*) males at a high-density breeding site had higher T levels than males at a low-density site (Ball and Wingfield 1987).

It is difficult to compare average T levels associated with breeding phases between monogamous and polygynous breeders because well-defined breeding phases are absent among males of strongly polygynous species. Once secondary (second-breeding) and perhaps tertiary females have initiated breeding, a male's breeding status is not clearly "prefemale" or "sexual" or "parental," for example. At times, and for many weeks, it may be all three. Thus, even as the primary nest progresses to incubation and feeding stages, the male remains exposed to sexually receptive females and challenging males, both of which can elevate T level (Wingfield and Moore 1986, Wingfield et al. 1987). This may explain the flattened plot of testosterone vs. breeding stage (Fig. 2).

Individual territory owners sampled periodically through their breeding efforts had variable plasma T patterns (Table 2). This is consistent with the "challenge hypothesis" of T secretion (Wingfield in press). Not every male followed the average pattern of T concentrations precisely, which would be the case if endogenous controls or unchanging environmental stimuli, and not social stimuli, governed circulating T levels. The challenge hypothesis also predicts that males on relatively poor and less desirable territories, challenged less often or with fewer mates to guard, should, on average, have lower T levels than males with higher quality territories. Our limited data on territory quality vs. individual T levels support this idea.

The transitory nature of elevated T levels must have also affected individual readings. Plasma T levels can rise significantly 10 min after an aggressive encounter begins (Wingfield et al. 1987) and, because steroid hormones are catabolized rapidly, can also decline fairly rapidly. Thus, closeness of the times of bleeding to an aggressive episode may have affected individual readings.

The significant correlation between male fledging success and peak T levels in early April suggests either that territory owners physiologically capable of sustained high T levels do better reproductively or that males on higher quality territories, likely to fledge more young, are challenged more frequently. We are currently unable to discriminate between these alternatives, because of small sample sizes and lack of comparative behavioral data on the frequency of challenges on territories of differing qualities.

Plasma T levels of adult floaters were, as predicted, usually lower than those of territory owners, but they tended to track those of the territory owners. The fact that territory owner and floater levels covaried is not surprising because it is against floaters that males defend their mates (although females are guarded from neighboring males also). Therefore, these aggressive encounters might also increase T levels in floaters.

Subadult males consistently had relatively low average T levels. These yearlings rarely obtained territories or seriously challenged territory owners, and they were not regularly exposed to the intensely aggressive, male-male interactions that characterize the behavior of adult territory owners. Lower plasma T levels of subadults, therefore, also support the challenge hypothesis.

Corticosterone (B) levels of territorial males were usually higher than floaters'. This supports the prediction that territory owners were probably under greater energetic demands than floaters. The rise in average B levels in late April and consistently high levels through May in territory owners was notable, because this was the period when territorial challenges probably declined in frequency and obtaining food became easier. One stressful activity in which all territorial males participated regularly was nest defense. Nest predation rates were high throughout the breeding season. The relationship between plasma hormone levels and antipredator behavior is largely unknown. However, the positive correlation between early B levels in territorial males and their reproductive success suggests that relative concentrations of this hormone may influence breeding success in this species.

ACKNOWLEDGMENTS

We thank Sharon Birks, Thomas Steedle, and Krista Hanni for assistance in the field, especially with blood sampling, and Lynn Erckmann and Diane Steeck for assistance in the laboratory. Refuge Manager David Goeke provided permission to conduct this study at the Columbia National Wildlife Refuge. This work was supported by National Science Foundation grants BSR 8614620 to Gordon Orians and DCB 8616189 to John Wingfield. Les Beletsky was supported by National Science Foundation Post-doctoral Fellowship BSR 8600123.

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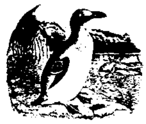
100 Years Ago in The Auk



Excerpts from "Notes and News" (1889, *Auk* 6: 79–84):

"AT THE meeting of the American Ornithologists' Union recently held in Washington the matter of revising the proposed additions to the A.O.U. Check-List of North American birds, together with sundry suggested changes of nomenclature made since the publication of the Check-List, was referred to the Committee on Publications, with authority to publish the results of their work at the earliest practicable date, as a Supplement, to the A.O.U. Code and Check-List, and uniform with it as regards matter and typography. The Committee held a six days' session, ruling upon upwards of one hundred distinct questions. The status of the newly described species and subspecies, and the claims to admission of a number of extra-limital species were duly considered, as also a number of proposed changes in generic, subgeneric, and specific names. The preparation of the manuscript was provided for, as also the early publication of the report, in the hope of issuing it early in the year 1889 . . .

"THE COUNCIL of the A.O.U. decided at its late meeting in Washingtou [sic] to issue an abridged edition of the Check-List, consisting of the scientific and common names, the serial numbering, and the 'concordance,' omitting the bibliographical references and the habitats; the abridged edition, however, to include the additions and changes of the 'Supplement,' interpolated in their proper places. It will be printed on fine paper, and on one side of the page only, in order that it may be conveniently used for labelling purposes when desired, or the blank pages, when the list is used merely for a check-list, may be utilized for additions or other notes. This abridged list is already in the hands of the printer, and its publication may be looked for during January, 1889 . . .

"THE DESIRABILITY of adopting some uniform method of measuring birds having been brought to the attention of the Council of the A.O.U., by a letter on the subject addressed to it by Col. N. S. Goss, the Council appointed a Committee, consisting of Dr. Coues, Mr. Ridgway, Mr. Cory, Dr. Merriam, and Dr. Stejneger, to prepare a report on the subject to be presented at the next meeting. The committee at its first session discussed the matter at some length, deciding some general matters, and referring special points to a subcommittee, consisting of Mr. Ridgway and Drs. Merriam and Stejneger, with instructions to prepare directions, illustrated with diagrams, for taking measurements of the bill and tail, in reference to which it is found that the systems employed by different authors widely vary. It is thus evident that a uniform method is highly desirable, and it is hoped the Committee will be able to formulate one which can be commended for general adoption . . .

"THE question of the adoption of the metric system in ornithology, mentioned above, was discussed by the Council of the A.O.U. at the meeting recently held in Washington, and the matter of its adoption in 'The Auk,' was referred to the Committee on Publications. It was here again discussed at length, but the motion to adopt was finally lost, much to the surprise of some of the members advocating it. It would seem, however, that a reform of such evident desirability, must sooner or later meet with general favor."