CHANGES IN BLOOD LEVELS OF THYROID HORMONES IN TWO SPECIES OF PASSERINE BIRDS

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ABSTRACT.—Annual changes in plasma levels of thyroxine (T_4) and triiodothyronine (T_3) were compared in White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) and House Sparrows (*Passer domesticus*) using serial blood samples from birds maintained in outdoor aviaries and from feral birds. Gonadal size was monitored by monthly laparotomy, and plumage was examined for molt at frequent intervals. Hormone levels were examined in relation to cycles of reproduction and molt, and to changes in ambient temperature. Thyroxine levels increased during postnuptial molt in both species, although in White-crowned Sparrows the increase was similar to that noted in late April and early May, which may have been associated with premigratory activity. However, in House Sparrows, thyroxine levels were highest throughout the three-month period of molt (mid-August to mid-November). They did not increase immediately after gonadal regression, giving no support for the hypothesis of a thyroid-gonad antagonism. Cold winter temperatures and changes in day length appeared to have little effect on T_3 and T_4 levels. In both species T_3 levels showed little seasonal variation, and changes in T_4 levels were independent of those in T_3.

Beginning more than half a century ago, with the experiments in which thyroid tissue was fed to birds (Carlson et al. 1912), a voluminous literature has accumulated that implicates thyroid hormones as the cause for molt (for reviews see Assenmacher 1958, Voitkevich 1966, Payne 1972). Although thyroidectomy appears to inhibit molt and thyroid-inhibiting drugs often alter feather morphology (Voitkevich 1966), histological studies in several species, using epithelial cell height as a measure of thyroid activity, do not support the hypothesis that an increase in thyroid gland function is the primary mechanism responsible for molt and feather replacement (reviews by Wilson and Farner 1960, Payne 1972). Progesterone and prolactin also induce molt, but in experiments with such hormones feathers are usually dropped in an abnormal sequence (Assenmacher 1958, Tanabe and Katsuragi 1962).

Using radioimmunoassay, I measured changes in plasma levels of thyroid hormones in order to determine if there were increases in thyroid activity associated with molt or with seasonal cycles in ambient temperature, and if there was a hormonal basis for the temporal separation of reproduction and molt. I compared the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*), a migratory species having two molts per year, with the House Sparrow (*Passer domesticus*), a sedentary species which has a single extended molt per year.

METHODS

I captured the birds for the laboratory study with mist-nets in January 1976, on the Sunnyside Game Refuge, Mabton, Yakima Co., Washington, and transported them within 24 h to outdoor aviaries in Seattle (48°N, 122°W). At approximately biweekly intervals I collected serial blood samples in heparinized capillary tubes from the brachial vein in the left wing of 40 birds, 10 adults of each sex and of each species. I collected the samples between 10:00 and 12:00 and, following centrifugation, froze the plasma at −20°C until analysis. I checked body weight and molt status at each sampling and estimated gonadal weight at monthly intervals by laparotomizing the birds and visually comparing their gonads with a preserved set of standards.

I collected additional blood samples from free-living birds, also at the Sunnyside Game Refuge, during the fall, winter, and spring (1976–1977). I sampled birds between 10:00 and 14:00 PST, marked them with numbered aluminum bands (U.S. Fish and Wildlife Service), and released them. A few were recaptured and resampled. Their blood samples were centrifuged in the field, and the plasma removed and frozen immediately on dry ice (for details, see Wingfield and Farner 1976). John C. Wingfield provided me with blood samples from breeding White-crowned Sparrows (*Z. l. gambelii*) collected near Fairbanks, Alaska, 65°N, 148°W (Wingfield and Farner 1978).

I used radioimmunoassay to measure plasma thyroxine (T_4) and triiodothyronine (T_3). In this assay system (see Chopra 1972), a known quantity of radioactively-labeled hormone competes with the unknown quantity of the same hormone in the plasma sample for a few specific binding sites on an antibody. The binding sites on the antibody are filled in proportion to the ratio of labeled-to-unlabeled hormone in the mixture. After equilibrium is reached, the excess, unbound hormone is removed, and the amount of radioactivity bound to the antibody is measured; from this, the level of the hormone in the plasma sample is calculated. I used the procedure developed by Dickhoff et al. (1978). I used two or three 25-μl aliquots of a plasma sample for assay, to each of which I added a mixture containing antiserum and I^{125}-labeled hormone. Following incubation, I precipitated the antibody by the addition of polyethylene glycol, and, after centrifugation, discarded the supernatant and measured the radioactivity of the pellet using a scintillation counter. Antiserum for T_4 came from Wien Laboratories (Succasunna, NJ) and for T_3 from Endocrine Sciences (Tarzana, CA). The cross reaction of each antibody with related tyrosine-based compounds was less than 5%.

Dilution of plasma from both species showed parallel cross-reactivity with a series of dilutions of hormone standards. Addition of these hormone standards to plasma previously treated with an equal volume of dextran-coated charcoal (to remove endogenous thyroid hormones) resulted in recoveries between 89 and 114%. Interassay variation, estimated from measurements on plasma pooled from White-crowned Sparrows, was 13.6% for T_4 ($n = 17$) and 18.3% for T_3 ($n = 11$).

I determined the statistical significance of changes in the hormone levels of feral birds with the Newman-Keuls multiple range test (Zar 1974) and used a Wiener-Levy time series analysis (Bell et al. 1979), which corrects for a lack of independence of serial samples, to
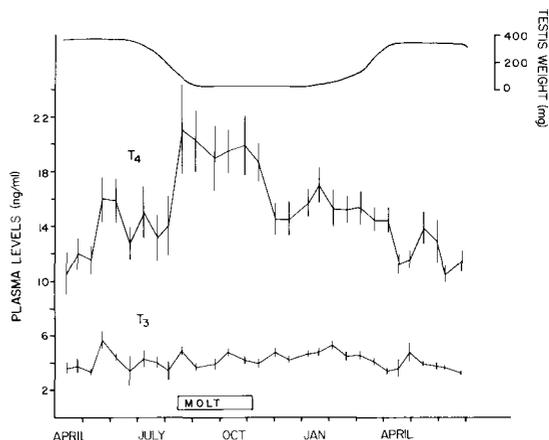

FIGURE 1. Plasma levels of thyroxine (T_4) and triiodothyronine (T_3) of captive male and female House Sparrows (10 of each sex), together with estimated testicular weights and molt periods. In this and other figures, hormone levels are expressed as means ± SE.

analyze the data from the caged birds. I used the Student's t-test to examine differences in hormone levels related to sex; and correlation coefficients first to determine if hormone levels changed as a function of temperature (weekly means of daily means and daily minimums) in Seattle, Fairbanks, and Sunnyside (climatological data obtained from the National Oceanic and Atmospheric Administration, National Climatic Center, Asheville, NC), day length in Seattle, or body weight, and second for correlations between plasma levels of T_3 and T_4.

RESULTS

Prebasic molt in House Sparrows began in mid-August, after the breeding season, and was heaviest during the first four weeks. Replacement of the last few primaries and completion of feather growth continued through early November. The pattern of molt was similar to that reported by Davis (1955) and Zeidler (1966).

Prebasic molt in White-crowned Sparrows

TABLE 1. Correlations between plasma titers of T_4 and other selected seasonal variables in *Zonotrichia leucophrys gambelii* and *Passer domesticus*.[a]

Variable	Zonotrichia leucophrys		Passer domesticus	
	Captive ($n = 20$)	Free-living ($n = 16$)	Captive ($n = 20$)	Free-living ($n = 10$)
Day length	0.21	—[b]	−0.46	−0.05
Ambient temperature	0.26 (0.61)[c]	0.28	0.16 (−0.002)[c]	−0.34
Body weight	−0.40	0.10	0.50	0.04
T_3	0.30	−0.035	0.43	—[b]

[a] Values in the table are correlation coefficients. None is statistically significant.
[b] Correlation coefficient was not calculated because hormone levels did not vary significantly.
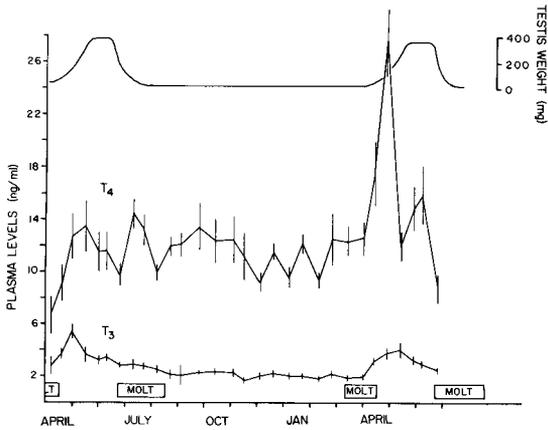[c] Winter months only (November to March).

FIGURE 2. Plasma levels of T_4 and T_3 in captive male and female White-crowned Sparrows (10 of each sex), together with estimated testicular weights and molt periods.

began in late June in captive birds and in mid-July in feral individuals. This molt was completed in five weeks, i.e., before the fall migration, which occurs in late August (as described by Morton et al. 1969). The prealternate molt of the body feathers and often the two central rectrices occurred during late March before the spring migration (as described by Michener and Michener 1943).

In captive male House Sparrows, the testes were largest from early April through early July (as found earlier by Davis and Davis 1954) and smallest from September to early January (Fig. 1). In captive and feral White-crowned Sparrows, the testes were largest from mid-May through mid-June and smallest from
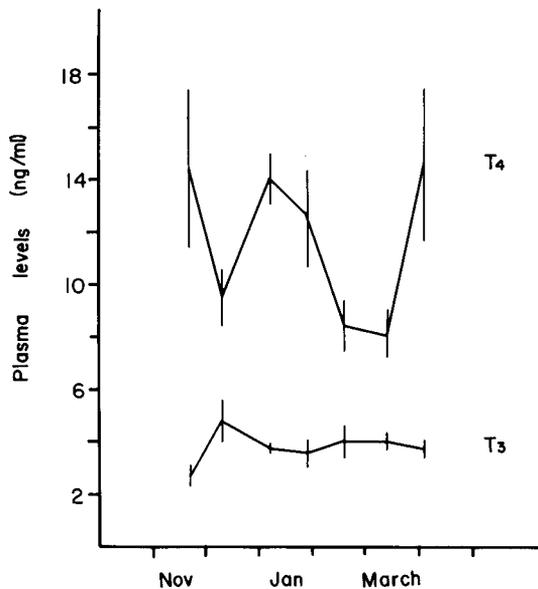

FIGURE 3. Plasma levels of T_4 and T_3 in feral House Sparrows (five of each sex).
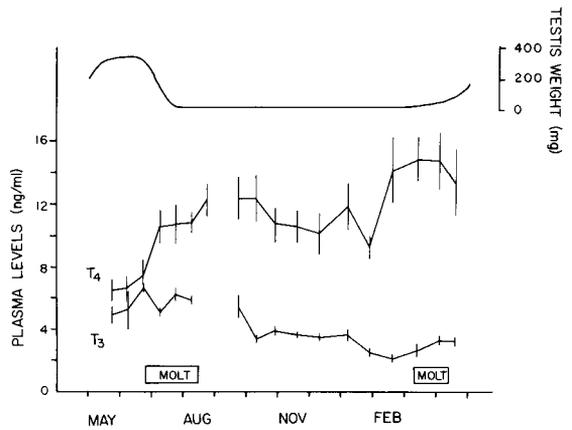

FIGURE 4. Plasma levels of T_4 and T_3 in feral White-crowned Sparrows (eight of each sex).

mid-July through late March (Fig. 2). This is consistent with the findings of Blanchard and Erickson (1949) and King et al. (1966). The reproductive system of captive females did not mature completely. For example, the diameter of ovarian follicles did not exceed 2 mm in either species. Consequently, I have not included information about the female reproductive system in the figures and have ignored it in the discussion. However, T_3 and T_4 levels in all figures are means for both sexes since the sexes did not differ significantly at any time in either species ($P > 0.05$).

Pronounced seasonal variations occurred in the plasma T_4 of captive House Sparrows (Fig. 1). Levels were significantly higher ($P < 0.05$) throughout the period of molt than at other times of the year. They rose after gonadal regression, but before any feather loss. They then declined during November, and showed no significant changes during winter months. In contrast, concentrations of T_3 in the plasma were one quarter to one third those of T_4 and showed no statistically significant seasonal variations. Seasonal changes in T_3 and T_4 did not parallel one another. Thyroxine levels did not correlate significantly with day length, body weight, or environmental temperature, even when analysis was restricted to the winter months (Table 1).

No significant changes occurred in either T_3 or T_4 levels of House Sparrows sampled in the field between late fall and early spring (Fig. 3). Plasma concentrations did not differ from those found in captive birds. Although T_4 rose during the cold weather of January, the increase was not significant. Correlation coefficients indicated no significant relationship between T_4 and several other seasonal variables (Table 1).

White-crowned Sparrows exhibited a different pattern of changes in plasma levels of thy-

roid hormones. In the aviary population there was no clear relationship between T_4 levels and molt (Fig. 2): no rise accompanied prenuptial molt and the elevation during postnuptial molt was not significantly higher than the significant increases in late April. Levels during the winter were significantly lower than at all other times of the year ($P < 0.05$). Except for the brief increase in late April, plasma T_3 levels did not vary significantly throughout the year. The large and significant increase in T_4 in late April and early May of 1977 (and which was not quite as pronounced in 1976) may have been associated with premigratory activities (hyperphagia, fat deposition, Zugunruhe). Hormone titers, however, did not correlate significantly with body weight during either of these periods, and T_4 did not correlate significantly with any of the other variables (Table 1).

Breeding birds in Alaska had lowest T_4 levels during the reproductive phase (Fig. 4). A significant increase occurred at the onset of postnuptial molt ($P < 0.05$). However, no significant changes occurred during the winter in a distinct free-living population of Z. l. gambelii in eastern Washington (Fig. 4). Plasma T_3 showed no significant variations. T_4 levels did not correlate with important seasonal variables (Table 1).

House Sparrows showed only small fluctuations in body weight, except for a 2-g increase during the period of heaviest molt (late August through mid-September). White-crowned Sparrows gained weight during the vernal and autumnal migratory periods and lost weight at the onset of molt and during winter months. Similar data have been reported previously for both species (Kendeigh 1949, Davis 1955, King and Farner 1965).

DISCUSSION

Investigating specific roles of thyroid hormones is not simple since they may be simultaneously regulating numerous metabolic processes. Thyroidectomy and induced hypothyroidism may have profound and pathological effects on metabolic activities, consequently yielding information on specific thyroid functions that must be interpreted cautiously (Thapliyal et al. 1973). For example, thyroid hormones have often been implicated in the initiation and control of molt (for reviews, see Voitkevich 1966, Payne 1972). In many cases, however, it is difficult to evaluate the role of the thyroid gland in the molt process because the experiments employed domestic fowl whose molt, due to domestication and artificial selection, no longer always occurs at discrete times of the year. Furthermore, in experiments involving the injection of T_4, the doses used were often poorly quantified or were so large that their molt-producing effect may be pharmacological (Takewaki and Mori 1944).

Histological studies (e.g., Oakeson and Lilley [1960] for the White-crowned Sparrow) that attempt to correlate thyroid activity with postnuptial molt, migration, reproduction, and low ambient temperature contain conflicting results (Wilson and Farner 1960, Voitkevich 1966). This may be due to differences among investigators in selection of histological criteria and high individual variability among the birds. Since it is not yet clear how histologically defined activity relates to plasma levels of thyroid hormones in birds, it is difficult, perhaps impossible, to assess the functions of thyroid hormones in such processes as postnuptial molt solely on the basis of histological observations.

Few investigators have measured plasma levels of thyroid hormones in birds, even though this could provide important information about thyroid activity relative to metabolic requirements. Although I present here only correlations between thyroid hormone levels and events in the annual cycle, these can be used at least in a preliminary way to expose possible relationships. Since birds appear to lack a thyroid-binding globulin (Tata and Shellabarger 1959, Refetoff et al. 1970), plasma hormone levels may indicate thyroid activity more accurately in birds than in mammals. Nonetheless, additional information about the kinetics of less specific binding proteins, the relative importance of T_3 and T_4 and interconversion rates, changes in secretion and clearance rates, and responsiveness of target tissues is needed for a complete assessment. This is especially important since T_3 may be the metabolically active form of the hormone in birds, as has been suggested for mammals (Klandorf et al. 1978). Since plasma levels of T_4 always exceeded those of T_3 in my study, and particularly because I found almost no significant variation in T_3 levels, my discussion centers on the relationship between T_4 levels and events in the annual cycle.

THYROID ACTIVITY AND MOLT

A comparison of the available data from the few species studied so far does not present a clear picture of the role of thyroid hormones in the normal molting process. In House Sparrows, plasma concentrations of T_4 were highest during the three-month period of molt (Fig. 1), and increased just before the onset of feather loss. Similar relationships between T_4 and molt have been found in male Pekin ducks (Anas platyrhynchos) and male teal (A. crecca;

Jallageas, Tamisier, and Assenmacher 1978). In White-crowned Sparrows, however, T_4 levels were not specifically related to molt, since significant increases occurred at the time of postnuptial molt (Figs. 2 and 4). Increases of similar magnitude not related to molt were noted on other sampling dates. Seasonal fluctuations in plasma T_4 similar to those found in White-crowned Sparrows were reported for Turkeys (*Meleagris gallopavo*) by Burke et al. (1977). Blood levels of the hormone are also elevated during the postnuptial molt of the Canada Goose (*Branta canadensis*; John and George 1978), although they decrease during molt in the Ruffed Grouse (*Bonasa umbellus*; Garbutt et al. 1979).

Metabolic rates increase during postnuptial molt (Payne 1972, Thompson and Boag 1976, Dolnik and Gavrilov 1979), presumably because feather growth and thermoregulation are energetically costly in molting birds, and increases in plasma titers of thyroid hormones at such times may be related to changes in metabolism. The energetic cost of completing a postnuptial molt in five weeks in the White-crowned Sparrow may be high, as it is in several European passerines (Gavrilov and Dolnik 1974, Dolnik and Gavrilov 1979), and may require increased metabolic activity. However, most temperate zone passerines, including White-crowned Sparrows, undergo postnuptial molt in late summer when the energetic cost should be at its lowest because food is abundant and ambient temperatures are high. Gavrilov and Dolnik (1974) found that the body weights and stored fats of Chaffinches (*Fringilla coelebs*) were at their lowest point of the year when postnuptial molt began; they suggested that this would be maladaptive if heat loss due to decreased insulation were an important factor during molt. Low body weights are also characteristic of White-crowned Sparrows at the onset of postnuptial molt (this study; King and Farner 1965, Chilgren 1977, Wingfield and Farner 1978).

Gavrilov and Dolnik (1974) stated that the physiological condition required by birds at the onset of molt is so specific that it cannot coincide with other phases in the annual cycle. They suggested that T_4 establishes the rate, but not the onset of molt. Their scheme is clearly intended to describe the situation in *migratory* species for which periods of molt and reproduction do not overlap. It may also apply, however, to *sedentary* forms such as the House Sparrow, which do not schedule molt and reproduction around migration (although these two activities occur at separate times). My data (Fig. 1), for example, suggest that the postnuptial molt of House Sparrows is the most active period in their annual cycle for thyroid-dependent metabolism. This suggestion is consistent with the finding that they gain weight during the period of molt. However, because the molt is extended, the *daily* energy expenditure at this time must be less than it is in a migratory species, such as the White-crowned Sparrow, which completes molt in a few weeks.

THYROID ACTIVITY AND REPRODUCTION

Since sex hormones, as well as thyroid hormones, appear to influence the onset of postnuptial molt (reviewed by Payne 1972; but see McCreery and Farner 1979), several investigators have suggested that thyroid-gonad interactions are responsible for both the termination of the reproductive period and the induction of molt. For example, in European Starlings (*Sturnus vulgaris*) thyroidectomy three months prior to the normal molt or before photostimulation did not affect gonadal growth, but did prevent gonadal regression and molt (Voitkevich 1966, Wieselthier and van Tienhoven 1972). Similarly, the inverse relationship between the annual cycles of the thyroid gland and the gonad in several species of subtropical Indian finches (see Payne 1972) has led to the proposal that T_4 inhibits gonadotropin secretion at the level of the hypothalamo-hypophyseal complex, perhaps by affecting the response to changes in day length (Chandola et al. 1973). However, the influence of day length on cycles in gonad weight, body weight, molt, and thyroid activity of these Indian finches has not yet been characterized. Silverin (1979) has also reported that T_4 inhibits the testicular activity of the Pied Flycatcher (*Ficedula hypoleuca*).

The thyroid-gonad interaction has been studied most thoroughly by Assenmacher and his colleagues on the Pekin duck and the Common Teal. In these species, thyroid activity, as measured by plasma T_4 levels, is maximal during gonadal regression and at the onset of postnuptial molt (Assenmacher et al. 1975, 1977, Jallageas, Astier, and Assenmacher 1978, Jallageas and Assenmacher 1979). These workers proposed that thyroid hormones reduce the sensitivity of the testis to luteinizing hormone and accelerate, although not necessarily initiate, gonadal regression, perhaps by increasing the ratio of circulating T_4 levels to testosterone (Jallageas and Assenmacher 1974, Assenmacher et al. 1975). A sharp decrease in plasma testosterone levels at the time of gonadal regression was associated with an increased metabolic clearance rate of this hormone, and this also occurred after T_4 injections (Jallageas et al. 1974). Jallageas and Assenmacher (1979) have also demonstrated that

thyroidectomized Pekin ducks show unseasonal increases in luteinizing hormone and testosterone and that castration increases plasma levels of luteinizing hormone and T_4. Hence, in these two species, thyroid hormones apparently inhibit testicular activity, which in turn permits the postnuptial molt to occur. However, the stimulus for the seasonal increase in T_4 remains unknown (Jallageas and Assenmacher 1979).

I found no significant increases in plasma T_4 in either House Sparrows or White-crowned Sparrows during gonadal regression (Figs. 1, 3, and 4), and my data provide no support for any significant thyroid-gonad antagonism. Such an antagonism may be an important factor controlling the onset of molt in subtropical Indian finches (Estrildidae and Ploceidae), ducks (Anatidae), and the Pied Flycatcher (Muscicapidae), but this does not seem to be the case for House Sparrows (Ploceidae), White-crowned Sparrows (Fringillidae), and Turkeys and Ruffed Grouse (Phasianidae). Perhaps there is no *single* endocrine control mechanism that is responsible for molt, but many different ones that have evolved independently in various groups of birds.

THYROID ACTIVITY AND PREPARATIONS FOR MIGRATION

Increases in plasma concentrations of thyroid hormones in White-crowned Sparrows during late April (Fig. 2) may be associated with the physiological preparations for migration reported by deGraw et al. (1979). However, the birds underwent vernal fattening before titers of these hormones increased. In fact, body weight and T_4 levels are negatively correlated at this time. It is also possible that the increase in T_4 during April was associated with migratory behavior, as suggested by Merkel (1938) and more recently by Robinzon and Rogers (1979). This possibility requires further investigation.

THYROID ACTIVITY AND ENVIRONMENTAL CUES

The effects of changes in day length on the activity of the thyroid gland have been difficult to distinguish from the interacting effects of sex hormones (Follett and Riley 1967, Jallageas and Assenmacher 1972), although long days appear to increase the plasma T_4 levels of some species (Péczely et al. 1979). Stetson and Erickson (1971) reported an increase in thyroid gland weight in intact, but not in castrated, White-crowned Sparrows beginning on day 45 of photostimulation. My data neither support a simple role of day length in the control of thyroid function nor constitute strong

evidence against the possibility that long daily photoperiods stimulate thyroid activity during molt in species that breed at mid- and high latitudes.

The effects of low temperature on thyroid activity are also not clear. For example, plasma levels of T_4 were not noticeably elevated in several avian species acclimated to winter temperatures (Assenmacher et al. 1975, Burke et al. 1977), but were high in Canada Geese just after they arrived on the breeding ground in Manitoba, where mean environmental temperatures were -3 to $-12°C$ (John and George 1978; in this case, high levels could be associated with migratory behavior). In my study, neither feral nor captive populations of either species showed increases in plasma levels of thyroid hormones associated with low ambient temperature (Figs. 1–4; Table 1). Other measures of thyroid function should be examined, however, before dismissing the possibility that temperature affects thyroid activity, since Hendrich and Turner (1967) found that the biological half-life of T_4 in the plasma of the domestic fowl decreased in winter. Furthermore, Wilson and Farner (1960) made a strong, if histological, case for an increase in thyroid activity in White-crowned Sparrows during winter in eastern Washington and suggested that differences between their findings and those of Oakeson and Lilley (1960) for the same species in California were due to the mild winter temperatures in the latter area.

ACKNOWLEDGMENTS

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RECENT PUBLICATIONS

Acta XVII Congressus Internationalis Ornithologici.— Edited by Rolf Nöhrig. 1980. Deutsche Ornithologen-Gesellschaft, Berlin. 1463 p. in two volumes. These are the proceedings of the 1978 International Ornithological Congress, held in Berlin. After the opening list of members, committee reports, and other business, there follow special lectures by D. S. Farner, K. Lorenz, E. Mayr, J. Aschoff, W. T. Keeton, and C. M. Perrins. The volumes are mostly devoted to papers, grouped according to the 36 symposia in which they were given. As usual at such congresses, a wide spectrum of subjects is covered: morphology, endocrinology, temperature regulation, flight, biorhythms, migration and orientation, vocalizations and hearing, behavior, habitat use, tropical ecology, community structure, co-evolutionary systems, speciation, urbanization, and much more. Furthermore, the papers tend to be more innovative, comprehensive, and carefully written than those given at national meetings. They are variously illustrated and each furnished with a list of references. The second volume closes with abstracts of the special interest group discussions, the poster presentations, and the films. Indexes.

Colonial Waterbird Group.— 1980. Transactions of the Linnaean Society of New York, Volume IX. 158 p. Paper cover. $12.00. Source: Secretary, Linnaean Society of New York, 15 West 77th St., New York, NY 10024. As the final event marking its Centennial Year in 1978, the Linnaean Society of New York hosted the second annual meeting of the Colonial Waterbird Group. A symposium on colonial species of waterbirds was arranged, and ten of the invited papers are presented here; the volunteered papers have been published separately by the C.W.G. The papers variously consider distribution, populations, census methods, feeding ecology, and nesting ecology, chiefly in seabirds, herons, and larids. They are each illustrated and furnished with a list of references. In addition, each paper is followed by a transcript of the ensuing discussion, often valuable comments and questions.

First Technical Meeting on Western Palearctic Migratory Bird Management: *Branta bernicla bernicla*/Proceedings.— Edited by M. Smart. 1979. International Waterfowl Research Bureau, Slimbridge (Glos.), England. 228 p. Paper cover. The dark-bellied race of the Brant breeds in the Russian Arctic and winters on estuarine and offshore mudflats in northwestern Europe, principally Britain and France. The population was at an alarmingly low level in the 1950's but has since increased to over 100,000. In order to obtain guidance on an international scale for sound management of the geese, a technical meeting was held in Paris in 1977, convening not only biologists but also hunting organizations, government agencies, and international conservation bodies. The reports (in French or English) are published in this volume, grouped by topic: status on the breeding, migration and wintering areas; migratory routes; feeding and breeding biology; and impact of human activities (conflicts with agriculture, hunting, and management). Two papers on the management of North American subspecies of Brant in Canada and the U.S. are given. Included with each report is the ensuing discussion, and the volume closes with the conferees' list of recommendations. Illustrations, references, list of participants.