REPRODUCTIVE BIOLOGY OF THE WHITE-CROWNED SPARROW (*ZONOTRICHIA LEUCOPHRYS PUGETENSIS* GRINNELL). I. TEMPORAL ORGANIZATION OF REPRODUCTIVE AND ASSOCIATED CYCLES

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Because of their wide latitudinal distribution, the races of the White-crowned Sparrow (*Zonotrichia leucophrys*) offer significant opportunities for comparative studies of the adaptive aspects of annual reproductive cycles and the mechanisms by which they are controlled. Of substantial interest among these races is *Z. l. pugetensis*, a short-distance migrant whose breeding area (ca. 40–50°N) lies on the Pacific seaboard of North America between that of the highly migratory *Z. l. gambelii* (ca. 50–70°N) and that of the sedentary *Z. l. nuttalli* (ca. 35–40°N). The shortest migratory route of *pugetensis* may be considerably less than 500 km; the longest may approach 1900 km. Both the annual photoperiodic environment of *pugetensis* and its photoperiodic responses differ from those of the two related taxa (see Farner and Lewis 1973; Lewis 1971, 1975). Furthermore, *pugetensis* and *nuttalli*, which form a cline (Banks 1964; Cortopassi and Mewaldt 1965), typically rear two or more broods per season (Banks 1959; Blanchard 1941), whereas *gambelii* appears to be obligately single-brooded (King et al. 1966). The present paper is the first of two that deal with the temporal organization of reproduction and its control in *Z. l. pugetensis*. In this paper, the breeding-season phenology and associated physiological and behavioral cycles are described and analyzed as a basis for experimental investigations of the mechanisms that control these functions.

STUDY AREAS AND METHODS

STUDY AREAS

Camano Island (Island County, Washington), the principal study area, is a well-defined physiographic unit of 12,000 ha that lies in the Puget Sound lowland of western Washington, immediately west of the mainland between 48°3′ and 48°16′ N. It is about 24 km long and 1.5–11 km wide. *Z. l. pugetensis* breeds on the island wherever suitable habitat occurs, from sea

level to the highest elevations (177 m) in the northern uplands. The island is Pleistocene in age and its upland soils are entirely derived from glacial tills formed subsequent to the meltback of the Vashon stade of the Fraser glaciation which terminated about 12,500–13,000 years ago (Easterbrook 1968, 1969; Easterbrook and Rahm 1970; Ness and Richins 1958).

There is no weather station on Camano, but the island probably has a climate that is somewhat drier than the mainland (Wolcott 1961) yet wetter than Whidbey Island which lies nearby to the west; here, the average annual precipitation ranges from about 51 cm on the central and northern portions of the island to 107 cm near the southern end (Anderson 1968). During spring and summer, prevailing winds on Camano Island are southwesterly. Ground-water levels have been rising during the past several years, apparently because of greater than average annual precipitation since 1948 (Anderson 1968). Prior to European settlement, Camano Island was entirely forested, but it is now ecologically diverse, consisting of agricultural lands, landscaped and residential areas, and old fields grading from grasses through shrubs and thickets of red alder (*Alnus rubra*), salal (*Gaultheria shallon*), salmonberry (*Rubus spectabilis*), and other brushy plants to more mature mixed or coniferous forests of less than 20 years to about 100 years of age. The last logging was completed in 1952 (Osmundson 1964) and some of the more recently logged areas now provide excellent breeding habitat, remaining in an early successional stage largely because of grazing and the resistance of the thick grass carpet to invasion by woody plants. Because of rather rapid residential land development during recent years, suitable breeding habitat for *pugetensis* has been increasing. My observations (1968–73) over the entire island indicate that wherever new habitat develops, it is soon occupied by breeding *pugetensis*. Such observations and the known history of the island suggest that the local breeding population of this finch is steadily growing. My investigations of the adjacent mainland have invariably revealed much lower breeding densities than occur on Camano Island.

METHODS

Samples from the population of *pugetensis* on Camano Island were collected by shooting at approximately weekly intervals during the breeding seasons of 1968 and 1969. Supplemental collections were made on both Camano (1970–72) and Whidbey (1967–71) islands and near Bandon, Oregon (December 1968). Collections on Camano were distributed over most of the island except where nests or marked individuals were under investigation. On Whidbey, however,

work was restricted largely to the northwestern margin of the island. With rare exception, collections were made only once per season at any given site and, when possible, both members of a pair were collected together. In addition to collections, 50 nesting pairs, most of them color-banded, were observed at frequent intervals through part or all of a breeding season during 1967 to 1969. Ten pairs were studied almost daily on the University of Washington main campus in 1967 and 1968, and 15 pairs were observed at least twice weekly on Camano Island in 1968 and 1969.

As part of a parallel study (Lewis, unpubl. data), the adenohypophysis of every bird was removed in the field immediately following collection and the fresh carcass was then weighed to the nearest 0.1 g on a triple-beam balance. To correct for the pituitary dissection, 0.1 g was added to the recorded body weight. Depot fat was assessed after the method of McCabe (1943). The condition of the ventral apterium was then assessed and the gonads and oviduct were removed and placed in a fixative composed of 10 parts glacial acetic acid, 10 parts formalin, 30 parts 95% ethanol, and 50 parts distilled water. After five days in fixative, the gonads and oviducts were transferred to 70% ethanol, and after five additional days they were carefully debrided of extraneous tissue (the mesovarium being retained intact), blotted, and weighed on a precision balance. Tissue specimens weighing 10.0 mg or less were weighed to the nearest 0.01 mg and larger specimens were weighed to the nearest 0.1 mg. The greatest diameters of all preovulatory follicles larger than 2.5 mm (or at least the four largest, regardless of size) were measured to the nearest 0.1 mm under a dissecting microscope, using fine dividers.

Damage to tissues by shooting accounts for differences in the size of samples of various tissues of specimens collected on the same date. Damaged tissues were not weighed. If only one testis of an individual sustained damage, however, the combined weight of the testes was taken to be twice that of the undamaged testis. Estimates of central tendency and statistical variance are given in terms of the sample mean and 95% confidence intervals ($X \pm t_{0.95} s_{\bar{x}}$; Snedecor 1956).

IDENTIFICATION OF RACE

From mid-April to mid-May and again from about mid-September to mid-October, Z. l. pugetensis and Z. l. gambelii are temporarily sympatric in the areas of this investigation. However, individuals of these two races are easily separable on the basis of morphological characters (Cortopassi and Mewaldt 1965; Banks 1964; Blanchard and Erickson 1949). Adult gambelii, in particular, show a very low degree of variation both in mensural and color characteristics and individuals that are intermediate between the two races seldom occur (Banks 1964). Of the more than 2000 White-crowned Sparrows that I have examined in the Puget Sound region in the hand, including both adults and birds of the year, all could be confidently assigned to one of these two races, usually on the basis of chromatic differences alone. These differences were detailed by Lewis (1971). The song of pugetensis is distinctive and the gonads in April–May are substantially larger than those of gambelii (figs. 2, 3). Furthermore, late summer and fall birds undergoing intense postnuptial and postjuvenal molt can be considered to be local pugetensis (King et al. 1966; Morton et al. 1969; Lewis, present investigation).

RESULTS AND DISCUSSION

THE BREEDING CALENDAR

The annual breeding calendar (1968, 1969) of Z. l. pugetensis on Camano Island is summarized in table 1.

The calendar of events in 1971 differed substantially from that of 1968–69. In 1971, the first females arrived on Camano Island by 11 April, and first ovulations occurred by 21 April. By the end of June, a high proportion of the population had apparently initiated a third nesting cycle. On 6 July, of 12 females collected at various sites on the island, one was preovulatory, two were ovulating, one had just completed a clutch, and at least two were incubating eggs. Of the remaining six females, all but one apparently had chicks less than 10 days old.

The calendar of the Camano Island population (table 1 and above) differs in certain respects from that of the 1938 San Juan Island, Washington, population studied by Blanchard (1941). A review of her communications on pugetensis (Blanchard 1941, 1942; DeWolfe 1968b) will provide a useful background.

ARRIVAL

Infrequent, intensive searches of Camano and Whidbey islands during three winters (October 1968–March 1971) revealed no wintering Z. leucophrys, although Golden-crowned Sparrows (Zonotrichia atricapilla) were present in modest numbers. Male pugetensis usually first appear on Camano and Whidbey islands and on the campus of the University of Washington in the early days of April; females arrive two to three weeks later (table 2). Z. l. gambelii is a fairly common migrant through all three of these stations. My observations and collections, however, reveal no migrants of this race earlier than 14 April (Seattle) or 17 April (Camano Island); they are seldom present in large numbers before the third week in April. These observations conform closely with observed dates of spring departure from California (earliest = 4 April; Blanchard and Erickson 1949) and appearance at stations in British Columbia (earliest = 20 April; DeWolfe et al. 1973). The locally wintering Z. atricapilla complete the prenuptial molt in late April. I have collected specimens of this species as late as 22 May, and my latest sight record is 30 May (1968, Camano Island).

In 1968, territorial male pugetensis were present on my first visit to Camano and Whidbey islands on 6 April; flocks of (presumably migrant) male pugetensis were also present at

TABLE 1. The breeding calendar of Z. *l. pugetensis*, Camano Island, Washington.

Event	1968	1969
Arrival period		
Arrival of males	ca. 3 Apr–1 May	2–30 Apr
Arrival of females	ca. 20–30 Apr	17–30 Apr
Territorial encounters	16 Apr–2 May	19 Apr–7 May
Unmated territorial males present in substantial numbers (at least 20–35% of the population)	6–22 Apr	2–24 Apr
First clearly established pairs	23 Apr	22 Apr
Unpaired females present	none observed	17–24 Apr
Nonterritorial males present	7 Apr–1 May	2–30 Apr
Flocks of nonterritorial birds present	7 Apr–1 May	12–30 Apr
Foraging flocks of established residents observed	1–13 May	30 Apr–13 May
Courtship (copulation, sexual chases, trilling)	20 Apr–9 May	22–24 Apr
First completely developed brood patch	before 9 May	6 May
First nesting cycle		
Completed nests	ca. 1–20 May	ca. 5–20 May
First eggs of a clutch	6–20 May	4–21 May
Incubation	11 May–11 June	7 May–11 June
First nestlings observed	21 May	17 May
Last eggs to hatch	30 May (or later)	12 June
First ("stub-tailed") young out of nest	4 June	5 June
First flying young	11 June	7 June
First fully independent young	20 June	25 June
Second nesting cycle		
Territorial encounters	none observed	3 June only
Completed nests	uncertain	ca. 5–20 June
Courtship	none observed	one observation, 17 June only
First eggs of a clutch	ca. 7–21 June	5–20 June
Incubation	ca. 9–24 June	ca. 11 June–7 July
First nestlings	22 (± 1) June	23 (± 2) June
First ("stub-tailed") young out of nest	2 July	ca. 10 July
First fully independent young	uncertain	27 (± 3) July
Latest partially dependent young	uncertain	at least as late as 1 Aug
Third nesting cycle (may include late renestings)		no distinct third nesting cycle observed but a few females were incubating during the last week of July
First eggs of a clutch	ca. 4–16 July	
Incubation	11–24 July	
First nestlings	25 July	
First ("stub-tailed") young out of nest	6 Aug	
Postbreeding period		
Onset of postnuptial molt first observed—male	17 July	17 July
Onset of postnuptial molt first observed—female	25 (± 3) July	24 July
Small flocks of adults (3–4 birds) first observed	9 July	24 July
Family-size flocks (i.e., mixed flocks of young & adults; up to 7 birds)	as late as 25 July	as late as 1 Aug
Flocks of more than 7 birds	from 17 July	from ca. 1 Aug
Last flocks observed	29 Aug	27 Aug
Completion of postnuptial molt	incomplete	incomplete
First year birds in plumage with first winter aspect first observed	none on Camano; 2 Sep, Whidbey Isl.	none on Camano; 28 Aug, Whidbey Isl.

TABLE 2. Dates of first arrivals.

First arrivals		Camano Island	Whidbey Island	University of Washington
Males:	1968	present by 6 Apr	present by 6 Apr[a]	3 Apr
	1969	2 Apr	2 Apr[a]	2 Apr[a]
	1970	present by 3 Apr[a]	———	3 Apr[a]
	1971	3 Apr	3 Apr[a]	3 Apr
	1972	31 Mar	———	after 4 Apr[b]
	1973	———	———	6 Apr[a, b]
Females:	1968	20 Apr	———	20 Apr
	1969	17 Apr	———	———
	1970	———	———	———
	1971	ca. 11 Apr	———	first observed on 20 Apr

[a] No females were present at this time nor during the following 7–10 days.
[b] Present in Seattle in very small numbers during the last week of March; the total breeding habitat on the main campus of the University is now more restricted; consequently, the later arrival dates may simply be a function of the reduced breeding population.

this time. The behavior of the territorial males (patrolling and singing) suggested that they had been present for at least two to three days. Males had first appeared on the main campus of the University of Washington on 3 April, and by 8 April, five territories were occupied by singing males; six were occupied by 9 April, and a total of ten by 22 April. A few females may have been present on Camano Island on 18 April, though none were collected on that date. On 22 April, of 17 closely watched territories, nine of the resident males were definitely solitary and each of six territories was occupied by a brace of birds, the sex of one or both being unknown. The first female was collected on Camano Island on 23 April, and on the main campus of the University of Washington the first female was seen and banded on 20 April. By 22 April, of the ten territories on the main campus, only three (possibly four) were occupied by both a male and a female. In 1969, the first substantial influx of females was during the night of 21–22 April, and the first definitely established pairs were observed very early on 22 April.

Census. In April 1969, I made a thorough roadside census of territorial males whose territories bordered the margins of an 11.5 km stretch of road near the northern end of Camano Island. The results are presented in figure 1. The course was traversed by automobile twice weekly from 05:00 to 07:00. Each male was observed closely to establish the presence or absence of conspecifics on the territory. When necessary, short excursions on foot were made to locate individuals that might not be evident from the road. The route followed was selected primarily because of (1) the relatively high breeding densities known from 1968; (2) the proximity of good habitat and conspicuous singing posts at or very near

the road; (3) the limited screening effect of vegetation (i.e., these roads are predominantly bordered by pastures, lawns, relatively open fields, and occasional orchards); (4) traffic and other disturbances are very light during the hours that the census was conducted.

This count represents, I believe, a total census of the resident population of males along the route. The efficiency of counting nonsinging associates is probably also high since they strongly orient their activities about the territory holder and are seldom outside his field of vision. Some associates are only temporarily present and most, probably all, of those observed prior to 22 April were also males. Collections were, of course, not made in the census area at this time, but the census data conform quite well with the data of collections and observations made elsewhere on the island throughout April. While this census does not distinguish between purely male associations and those of actual pairs, the data
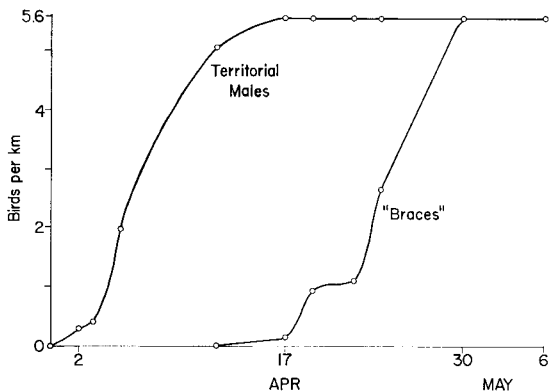

FIGURE 1. Temporal dispersion of resident males and "braces" during the arrival period. "Braces" represent associations of two birds, one of which was a territorial male, the other unsexed. See text for complete details of census.

TABLE 3. Time budget of male *Z. l. pugetensis* prior to the arrival of females (4–20 April 1968).[a]

	05:00–07:00	11:00–15:00	17:00–19:00	Daily Mean
Territorial males:	(Observations were approximately equally distributed over the three time periods)			
Singing	75.7%	41.7%	28.1%	49.4%
	(56.3–95.2)	(8.7–96.9)	(0–64.4)	
Foraging	17.4%	14.0%	29.9%	20.3%
	(0–25.0)	(0–52.1)	(0–100.0)	
Other maintenance activities	0.9%	3.6%	15.3%	6.4%
	(0–3.8)	(0–11.5)	(0–35.0)	
Flight	0.7%	0.7%	0.4%	0.6%
	(0–2.1)	(0–1.9)	(0–1.0)	
Out of view	5.3%	40.0%	26.3%	23.3%
	(0–16.7)	(0–91.3)	(0–100.0)	
Nonterritorial males:	(Observations were made whenever such males were encountered and, because of the smaller sampling, all data for the period were pooled; most observations were made before noon.)			
Singing	trace (curtailed song only)			
Foraging	71.1%			
	(62.7–95.3)			
Other maintenance activities	2.8%			
	(0.9–3.5)			
Flight	4.7%			
	(0–6.4)			
Out of view	21.4%			
	(0–30.5)			

[a] The data are based on a total of 21.0 hr of observation of at least 15 territorial males and 6.6 hr of observation of a probably larger number of nonterritorial males. Data are given as percent and range of total observed time occupied in each activity.

unambiguously demonstrate that females appear on territories only after most of the males have arrived and established territories. The census data probably also fairly delimit the arrival period in the census area.

Conclusion. *Z. l. pugetensis* arrives in the southern part of its breeding range in late March and in the northern part by mid-April (Blanchard 1941, 1942; Cortopassi and Mewaldt 1965; Schultz 1958; Lewis, present investigation). Arrival patterns of males and females show considerable local and latitudinal variation. Nevertheless, Blanchard's (1941) report that both sexes arrive on the same day on San Juan Island, Washington, is exceptional. Both males and females arrive in Island and King counties over a period of many days, the first resident males arriving well before the first females and about two to three weeks prior to effective pair formation. Some birds arrive and establish territories in late April. Transients usually do not remain more than two or three days. Males arrive before the females not only in Island and King counties but also on the Olympic Peninsula and the lower Puget Sound region generally (Lewis, unpubl. data). From 4 through 8 April 1972, between Cape Foulweather and Otter Rock, Oregon, I closely observed 12 definitely territorial male *pugetensis*, all of which were soli-

tary at this time. Only once during this period was a brace of birds observed; these were foraging together and their sex was not established.

THE ESTABLISHMENT AND MAINTENANCE OF TERRITORY

Territorial and nonterritorial males compared. Arrival of male *pugetensis* on Camano and Whidbey islands and at the University of Washington is marked by the appearance of solitary, fully territorial males singing full vigorous song and occupying fixed stations. At this time and sporadically throughout April, flocks of two to five males that exhibit no territorial behavior are common. The behavior of territorial and known resident males in April is distinctive and contrasts sharply with that of males that occur in flocks. Known residents, usually from their first appearance on the territory, exhibit typical territorial behavior; they sing vigorously and frequently from conspicuous, exposed perches situated at or very near the top of nearby vegetation or on telephone wires above fence rows. The mean singing height of 15 resident males during 26 bouts of singing before the arrival of females (3–20 April) was 7.6 ($\pm$ 7.2) m above ground. More significantly, the mean height of the singing perch in relation to foliage height was 88.6

(± 4.0) %. The height of the foliage was taken to be the height of the tallest tree or shrub in the neighborhood of the singing perch, including not only the perch itself but also the trees and shrubs that were its nearest neighbors. The activities of these territorial males are localized; the birds will sometimes pursue conspecifics that enter their territory. They are not at all shy at this time and are conspicuous in nearly all of their activities. Initially, a territorial male sings from one or a few stations. Within a few days following arrival, the boundaries of his territory are fully established and the periphery is frequently patrolled throughout the day. Solitary males that appear not to be territorial occur occasionally and associate temporarily with territory holders. I collected some of these birds in order to ascertain their sex and physiological state.

Birds in flocks, on the contrary, fail to exhibit most of the above characteristics. Song is very infrequent (table 3), is usually curtailed, and may be delivered from the ground or from low, inconspicuous perches. Some flocks in late April, however, contain males that sing full song. Birds in flocks are often shy and do not venture far from thick cover, whereas the territorial males may feed at considerable distances from such cover. With rare exception, nonterritorial birds are seldom seen at any given site for more than a few days. While present, nonterritorial males commonly have a tree, shrub, or small area about which much of their activity is centered and to which they retreat when "disturbed." Males in flocks often show a high degree of affinity for territorial males, and foraging associations between them and single territorial males are common.

The time budget of resident males during the arrival period differs from that of birds in flocks (table 3). Foraging by territorial males at this time (4–20 April) is most intense during the last few hours of the day. Only about 20% of the day is spent in foraging and many of the territorial males are in a state of negative caloric balance at this time (Fig. 5 and Lewis, unpubl. data).

Territorial behavior is not closely related to gonadal size. Nevertheless, males that associate in flocks and fail to exhibit territorial behavior have generally lower testis weights than those exhibiting territorial behavior (fig. 2). Whereas the territorial males are local residents, the samples of nonterritorial males appear largely to represent a succession of transient populations. Differences in gonadal weight thus may be a function of sampling
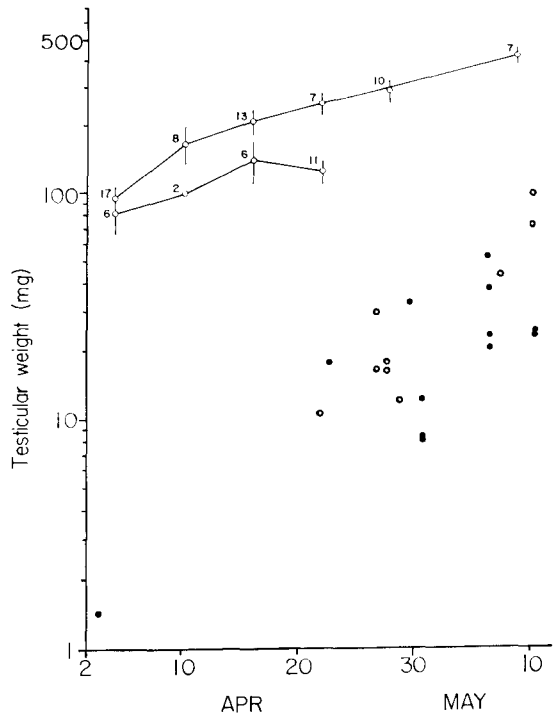

FIGURE 2. Testicular weights of *Z. l. pugetensis* (Camano and Whidbey islands) that exhibited territorial behavior (upper curve) and of flocking, nonterritorial males (lower curve). These data are grouped data for 1968 and 1969 (class interval: 5 days). Open circles below the curves represent individual *Z. l. gambelii* and the shaded circles represent individual *Z. atricapilla* that were collected in the same study areas during the same period.

populations that differ with respect to genetic constitution and/or environmental history. This inference is strengthened by the observations of Blanchard (1942), who found a diversity of behavioral and physiological states among *pugetensis* present in Humboldt County, Oregon, in the latter half of March 1939. It also supports the observations of Mewaldt et al. (1968), that the rate of vernal testicular growth of captive *pugetensis* and *nuttalli* that were held in the natural environment of San Jose, California, was (with minor exception) an inverse function of the latitude of the breeding population from which the birds had been drawn.

Establishment of territory. Territory establishment is rapid and is accomplished with few hostile encounters. The first resident males to arrive disperse and establish territory largely through loud singing from a single perch or a very few conspicuous perches. Beginning usually on the second or third day following arrival, this "sentinel" singing is succeeded by a routine of patrolling and singing on more and more perches about a definite periphery which
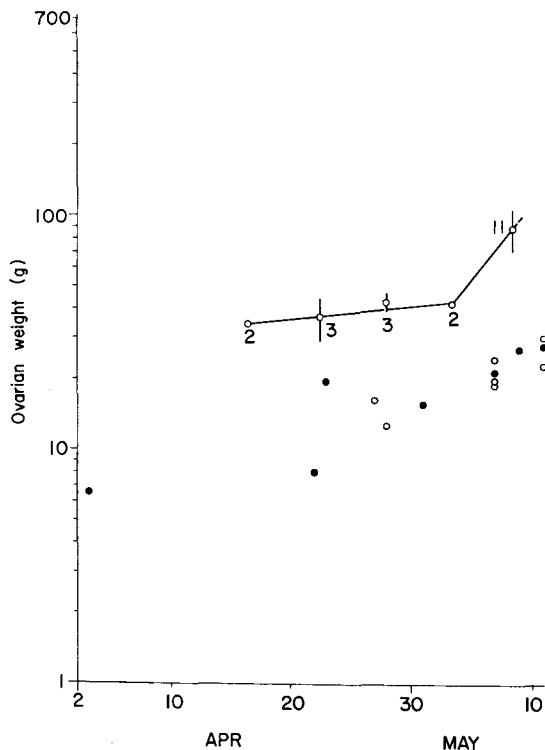
FIGURE 3. Ovarian weights of Camano Island Z. l. pugetensis (curve). The data are grouped for 1968 and 1969 (class interval: 5 days). Open circles below the curve represent individual Z. l. gambelii and the shaded circles represent individual Z. atricapilla that were collected on Camano and Whidbey islands during the same period.

soon form a boundary within which a male restricts his activity in most cases. This space is generally stable until the arrival of females. In the last third of April, small flocks of males that sing full song, but which do not show full territorial behavior, appear. A few new territories are established at this time. In 1968 and 1969, 70–80% of territories that I observed throughout the breeding season were established by males that arrived during the first ten days of April; those remaining were established during the last third of April.

The first aggressive encounters among residents that are not precipitated by human or other disturbances generally occur with the arrival of transients. During certain phases of the nesting cycle (especially late incubation through fledging), both members of a pair are easily excited by the presence of a person on their territory. They may even fly "excitedly" onto an adjacent territory, in which case the territory holders may respond aggressively. Occasional aggressive encounters occur during the last week of April, when some of the late-arriving males establish territories.

Such contests are short-lived and boundary disputes are usually settled within seconds or minutes. Males unable to secure territories probably leave within a matter of days. Transients are sometimes chased by resident males.

Foraging flocks of established pairs. Resident pugetensis recognize certain categories of conspecifics other than mates and progeny. Members of a breeding pair often exhibit little or no aggression toward their nearest neighbors, allowing certain of them to forage undisturbed *anywhere* on the territory. Furthermore, as many as four pairs may forage together within the combined area occupied by their territories or, in some instances, in selected areas at least as much as 400 m distant. When such a flock is disturbed, each pair tends to return directly to its own nesting territory. My collections and observations of banded females reveal that such flocks may include preovulatory, ovulating, and postovulatory females (see fig. 3). Females in the terminal stages of incubation are sometimes included. Males with combined testicular weights ranging as high as 507 mg (this is near maximal; fig. 6) are included.

PAIR FORMATION

Segregation of females onto territories is so rapid that I never observed initial encounters between prospective mates; such encounters undoubtedly occur very early on the morning of arrival. Courtship, consisting mostly of trilling and sexual chases, is most frequent during the first two days following arrival of the females and is most intense during the two to three hours before sunset.

All banded pairs remained paired throughout the breeding season. Maintenance of the pair bond is favored by several circumstances: (1) both parents attend the young from one nesting cycle until about the time that incubation of the next clutch begins; (2) the female usually builds second nests well within the original territorial boundaries, and both male and female show site tenacity until after the nesting activities are over for the season; and (3) there appears to be no significant surplus of unmated birds that would be free to court the attention of mated birds during the internesting period.

SCHEDULE OF OVIPOSITION AND CLUTCH SIZE

Eggs of Camano Island *pugetensis* are generally laid one per day until the clutch of two to five eggs is complete. Occasionally, a day is

skipped, usually between the laying of the penultimate and ultimate eggs of the clutch. The eggs are invariably laid approximately at sunrise and the next ovulation occurs about three hours later. This topic will be treated in a separate paper. The mean size of 23 clutches on Camano Island was 3.84 (± 0.83).

INCUBATION

Only females incubate the eggs and brood the young. This was confirmed by repeated observations of marked birds at the nest and by the failure of most males to develop incubation patches. In only three males did I record nearly complete defeatherization, slight edema, and slight to moderate vascularization of the ventral apterium. These were breeding males with large testes. In all other male specimens, including the more than 130 that might be expected to have had eggs or young in the nest at the time of examination, the ventral apterium was completely down-covered and without edema or visible vascularity on gross inspection. Females rarely sit closely or frequently before laying the ultimate or penultimate egg of a clutch, and the eggs are never warm to the touch before this time.

CARE OF THE YOUNG

The young usually remain in the nest until they are nine or ten days old, but leave permanently in response to disturbance near the nest any time after about eight days. These young "stub-tailed" birds generally remain well hidden in cover near the nest. Fledglings are able to fly when 11–12 days old and are strong fliers by day 15.

While females are building the second nest, and during the second ovulatory cycle, the birds spend much time foraging in family groups. The birds generally remain together when disturbed, showing that these family flocks are cohesive units. It is difficult to determine the precise age at which the young become fully independent because the male alone attends the young of the first nesting while the female incubates the second clutch of eggs. Both the male and the young may feed at considerable distances from the territory at this time, and the young are especially shy and often difficult to locate. Nevertheless, in the case of first broods, the young are independent of the female parent at about 17 days of age and of the male parent at about 30 days. The young of late broods may leave Camano Island when 40–60 days old. I have seen strong-flying juveniles still attended by one parent as late as 22 August.
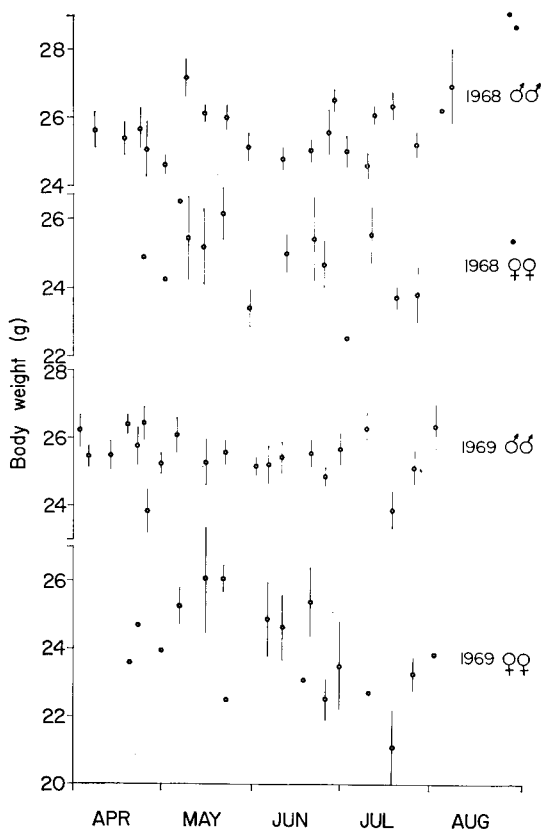

FIGURE 4. Body weights of adult Camano Island Z. l. pugetensis. A few Whidbey Island specimens are included (late August only).

NUMBERS OF BROODS

There were three distinct nesting cycles on Camano Island in 1968, and two plus the suggestion of a third in 1969 (fig. 7). Males generally assume all care of the young of the first brood after the second clutch of eggs is complete, behavior that favors earlier laying of the next clutch. Several ovulating females and a few recently postovulatory females in late May to late June were attending two to four fully fledged young, some of which were capable of sustained flight at the time. Furthermore, nine banded pairs that successfully fledged broods in late May to early June initiated a second nesting cycle. No individuals were actually known to rear three broods successfully.

About three days after the first brood is out of the nest, the female begins constructing the new nest and the second clutch is complete about 7–11 days later. Approximately 30 days intervene between the first ovulation of the first cycle and the first one of the second cycle. The observed breeding season phenology and the female gonadal cycles (table 1, fig. 7), together with the above information, strongly
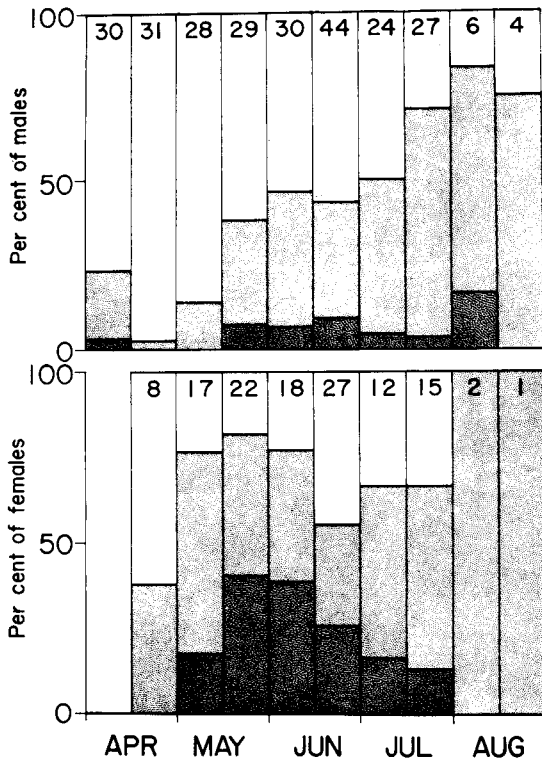
FIGURE 5. Semi-monthly changes in visible depot fat of Camano Island *Z. l. pugetensis*. The data are grouped for 1968 and 1969. Unshaded portions of the graph represent birds with little fat; lightly shaded portions represent moderately fat birds; heavily shaded portions represent fat birds. Sample size is indicated at the top of each column. Depot fat determinations were made by the method of McCabe (1943).

imply that many breeding birds reared three broods in 1968, but that most did not do so in 1969.

BODY WEIGHT AND DEPOT FAT

Body weight (fig. 4) and depot fat (fig. 5) change during the breeding season. Females generally had greater fat reserves on arrival at Camano Island than did the males, and they became progressively fatter until early to mid-May. The body weight cycle of females is strongly bimodal, closely paralleling the ovulatory cycle. Variations among females reflect largely the great increase in size of the reproductive organs and liver (Lewis, unpubl. data) as ovulation and egg-laying approach, followed by an abrupt decrease with each oviposition. Females also continue to fatten during the rapid growth phase of the ovary. The weight of the maximally developed reproductive tract of six females in which ovulation was judged to be imminent was 4–9% of the total body weight. In 11 ovulating females, the total weight of the reproductive tract including an

egg in the oviduct was 10–14% of the total body weight. The body weight of females declines during incubation and even more during the period of dependence of the young. This decline is accompanied by, and is partly the result of, a gross involution of the reproductive tract and a decline in liver weight and in depot fat.

The large variations in female body weight in association with the nesting cycle mask somewhat a decline in body weight, particularly pronounced in 1969, that begins by about mid-May. The minimum seasonal weight of both sexes is reached at about the time when postnuptial molt begins. Thereafter, weight increases steadily until departure from Island County.

TESTICULAR CYCLES (fig. 6)

The combined weight of the testes of first arrivals is less than 100 mg. The testes grow to a mean maximum combined weight of 520 mg by about 15–20 May, six weeks after arrival and about three weeks following pair-formation. Testicular weights generally remain high until about 10 July and then rapidly regress. The onset of this regression anticipates the onset of postnuptial molt by about a week. Combined weights of the testes of adult *pugetensis* collected near Bandon, Oregon, in December average 0.7 (± 0.4) mg.

OVARIAN AND OVIDUCAL
CYCLES (fig. 7)

These cycles can be described in terms of four stages of development: (1) a period of slow follicular growth; (2) a period of vitellogenesis and rapid follicular growth; (3) culmination and ovulation; and (4) regression. Cycles in ovarian and oviducal weight closely parallel the follicular cycle throughout the season, but are not fully descriptive of functional state. Females are nearing the terminus of stage (1) when they first appear on Camano Island and enter stage (2) soon thereafter; culmination of the initial cycle of growth and development occurs at a median date of about 15 May. Following ovulation, the ovary and oviduct undergo a gross involution that persists until initiation of the second nesting. The cycle is then repeated.

MOLT AND REPRODUCTION

I have never observed prenuptial molt in the Camano and Whidbey island or Seattle populations of *pugetensis* (but see Blanchard 1942).
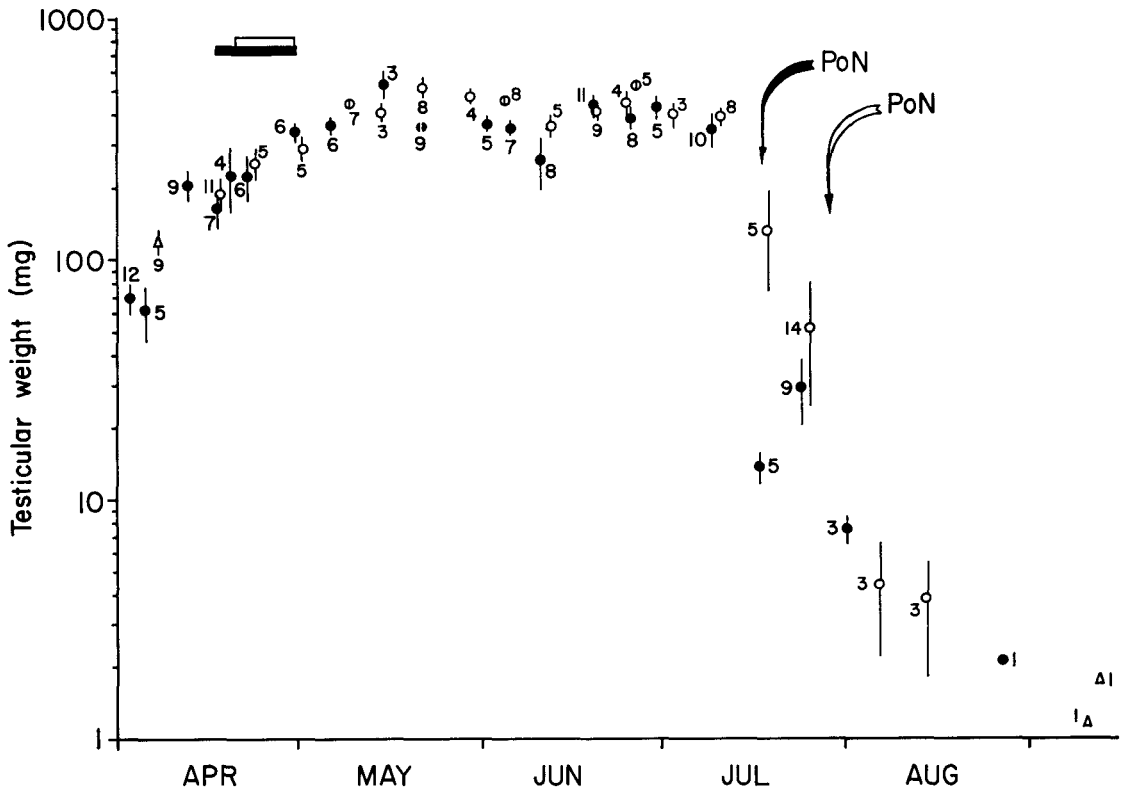
FIGURE 6. The natural testicular cycle of Camano Island *Z. l. pugetensis* in 1968 (open circles) and 1969 (closed circles). A few Whidbey Island specimens (1968; open triangles) are included. Horizontal bars (open, 1968; closed, 1969) indicate the period of arrival of females each year. Onset of postnuptial molt (PoN) is also indicated (open arrow, 1968; closed arrow, 1969). Numbers indicate sample size.

At all of these locations, newly arrived birds are typically in fresh plumage. The gonads of nearly all adult *pugetensis* undergoing postnuptial molt are grossly involuted.

DISCUSSION

INITIATION OF BREEDING

The culminative stages of ovarian growth and maturation in birds usually occur during the few days (ca. 4–11) immediately before egg-laying (see Farner and Lewis 1971). The specific environmental factors that induce the final stages of ovarian maturation and egg-laying in wild birds are regarded as mostly psychic and associated with the nesting situation (see Lewis and Orcutt 1971). Furthermore, the precise time of breeding in a wide variety of species is determined effectively by females through mate selection and sensitivity to the local microenvironment during the terminal stages of ovarian maturation and ovulation (see Farner and Lewis 1971; Lewis and Orcutt 1971; Orians 1969). Males of many species stimulate sexual behavior in females and may induce the final stages of reproductive maturation and ovulation (e.g., Farner and Lewis

1971; Lewis and Orcutt 1971). Temperature or factors related to it may modify the onset of breeding (Lewis and Farner 1973). Perrins (1970) has argued in support of the view that food availability acts as the final determinant governing the timing of egg-laying of many birds. He noted, however, that such is unlikely in most multiple-brooded passerines. Indeed it seems unlikely that the level of nutrition plays a major role as a proximate determinant of the initiation of egg-laying in any of the *pugetensis* populations I studied (see below).

The effect of a male *pugetensis* on the actual time of oviposition is not readily assessed from my data. Presumably, he presents appropriate stimuli that are essential to the culmination of the female cycle. However, because of the regularity with which the first males arrive each year in the lower Puget Sound region (table 2) and because (in the populations studied) males are present well before females and hold territories by the time females arrive, variations in the actual time of egg-laying relate more importantly to the arrival time of females. At a behavioral level, it is clear that the activities of both members of a pair are closely interrelated during the terminal stages
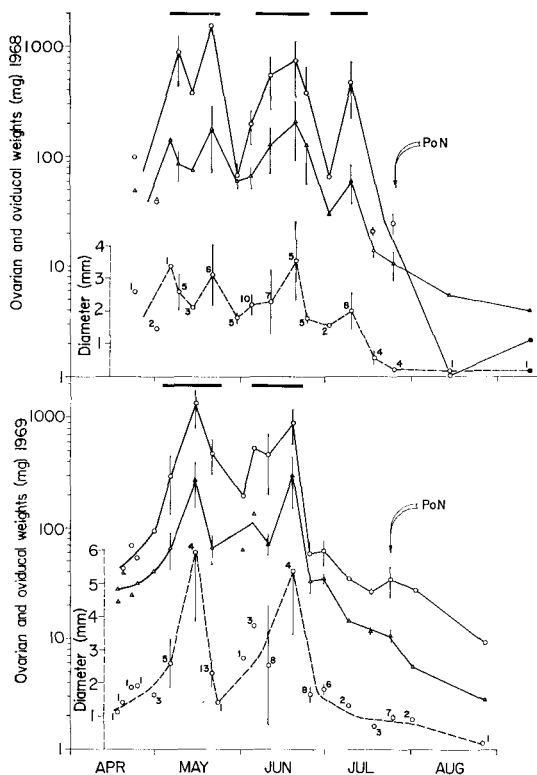
FIGURE 7. The natural ovarian (open triangles) and oviducal (open circles, above) cycles of Camano Island *Z. l. pugetensis*. The dashed lines represent the longest diameter of the largest preovulatory follicle. A single Whidbey Island specimen (shaded circles and triangle) is included. Horizontal bars indicate periods when ovulating females are known to be present in the population. Onset of postnuptial molt (PoN) is also indicated. Numbers indicate sample size.

of reproductive maturation. Pair-formation precedes the onset of the rapid phase of ovarian growth and of nidification.

In the Camano Island population, pair-formation, location of nesting sites, and nest-building take at least 9–12 days, and first ovulations occur approximately 13–15 days following arrival of the first females. Thus, it appears that first ovulations occur about as soon as physiological and behavioral limitations permit. Given the observed time course of these functions, we cannot say that trophic conditions effectively determined the onset of egg-laying on Camano Island, at least in females that laid eggs by mid-May. Some banded females ovulated within 10–11 days of arrival. Body weights and fat levels (figs. 4, 5) are at the seasonal peak during the first ovulatory cycle and are substantially higher than during subsequent cycles. Vitellogenesis begins during the period of nest-building; an earlier onset would be ill-adaptive. First ovulations usually occur within a day of nest com-

pletion (see also Blanchard 1941); thus ovulation and egg-laying take place approximately as soon as there is an appropriate environment to receive an egg. These observations, together with the previously discussed tolerance of foraging by certain conspecifics on the territory, make it highly unlikely that either the level of nutrition or the availability of essential nutrients determines the onset of breeding in the population as a whole. The possibility that nutritional factors may play a role in timing the final stages of ovarian development and ovulation of *pugetensis* nesting in marginal habitat cannot be discounted. Nevertheless, the relatively short spread of first ovulations (ca. 15 ± 2 days) of Camano Island *pugetensis* in 1968 and 1969 is not much greater than the period over which females arrived (ca. 12 days). This suggests that vitellogenesis and ovulation were little delayed in a large fraction of the population. This implies that the most important environmental modifiers of the initiation of breeding are those on the wintering grounds and/or the migration route, and that influence the time of arrival of females which are already disposed to mate and to initiate nesting activities given an appropriate local environment. The data of Lewis and Farner (1973) support this hypothesis.

The efficiency of evolved mechanisms (e.g., early arrival of males and establishment of territories prior to the arrival of females; rapid segregation of newly arrived females and pair-formation) that support a rapid initiation of breeding, as well as the probable early abundance of food, is apparent also from the fact that the entire period from the onset of rapid follicular growth to hatching of the first egg in Camano Island *pugetensis* occupies 20–24 days.

MULTIPLE-BROODEDNESS: CYCLES WITHIN THE SEASON

The number of broods reared. Z. l. pugetensis that breed in the lower Puget Sound Region and other populations that have been studied (see also Blanchard 1941) rear two or three broods per year. The fraction of the Camano Island population that rears, or attempts to rear, three broods varies from year to year. Furthermore, the number of clutches laid varies locally, implying that local environmental information plays a role in determining the number of broods reared or the duration of breeding. This number apparently depends in part upon the time when breeding begins, a phenomenon that may be relatively common among multiple-brooded birds (see Kluijver

1933; Lack 1950, 1954, 1966; Tolenaar 1922; Wolda 1926, 1929). This suggests that Camano Island *pugetensis* breed annually for as long as the environment is favorable and further implies that selection favors early onset of breeding.

While it is possible that breeding is under strict local control once it begins, one may reasonably infer that controls are redundant and that termination mechanisms have some endogenous or annually periodic components (Lewis 1971).

The internesting period. Of particular interest to the control of reproduction of multiple-brooded populations is the physiology of the internesting period. In this regard, the gonadal cycle of the single-brooded *gambelii* (King et al. 1966; Kern 1972) may be compared with that of *pugetensis*. Following a single nesting cycle, the reproductive systems of both male and female *gambelii* undergo extensive involution and become temporarily refractory to photoperiodic stimulation. In contrast, although the reproductive tract of the female *pugetensis* undergoes a similar involution following egg-laying, rapid progressive changes leading to a new series of ovulations typically begin after fledging the first brood (fig. 7). Similarly, there is a small but statistically significant reduction of gonad size between nestings in male *pugetensis*. This mid-season minimum in male gonadal weight is reached at about the time when the first young become fully independent. Testicular weights of *gambelii*, however, are maximal until the broods are fledged, and then rapidly decrease essentially to resting levels.

The internesting gonadal regressions of male and female *pugetensis* are somewhat out of phase with each other (figs. 6, 7) and appear to be associated with decreasing pituitary gonadotropic potencies (Lewis, unpubl. data; Mikami et al. 1973).

The bimodal ovarian cycle in *pugetensis* is not a sampling artifact; ovary and oviduct sizes are closely correlated with the stages of the ovarian and nesting cycles. Indeed, ovarian and oviducal involution begin immediately following the last ovulation of the clutch, and within a day both ovarian and oviducal weights have diminished appreciably. The need for further analysis of the male cycle is indicated, however. It is possible that the male curve is the product of some sampling bias or that a complex population is being sampled. A bimodal cycle in testis weight or function has been reported for several other multiple-brooded bird populations (Collias

1950; Davis 1958; Selander and Hauser 1965; Threadgold 1960). Various interpretations of the mechanism of this mid-season partial regression of the testis have been made (e.g., Davis 1958; Lofts and Murton 1968; Threadgold 1960). Such speculation is, however, premature in the case of *pugetensis*. It is sufficient to note that the internesting gonadal and oviducal involution and the recovery from them occur while photoperiod is increasing, and without the induction of postnuptial molt. These facts suggest that the endocrine state of an internesting bird differs importantly from that of a postseasonal bird. Primary photoperiodic populations such as *pugetensis* that terminate reproduction in a photorefractory state (Lewis 1975) and are multiple-brooded may thus afford an unusual opportunity to advance our knowledge of the mechanisms that terminate reproduction. Furthermore, since the time of termination in multiple-brooded species may vary substantially from year to year, careful investigation may provide information on proximate environmental factors that sustain reproductive condition.

TERMINATION OF REPRODUCTION

Current concepts regarding mechanisms that terminate the reproduction of annually breeding birds have been reviewed by Farner (1970), Farner and Lewis (1971), and by Lofts et al. (1970). We are largely ignorant of the mechanisms that terminate breeding. Even the selective factors that have been effective in shaping termination mechanisms are poorly understood. Clearly, various selective factors that influence the survival of both young and/or adults may be involved, and no doubt termination mechanisms are central to the temporal exclusion of breeding and energetically intense postbreeding functions. That the postnuptial demands (e.g., postnuptial and postjuvenal molts; autumnal migration; energetic demands of young birds during the days or weeks following abandonment by their parents) are the most critical in many cases is suggested by the fact that many small passerines *appear* to terminate breeding well before the time that their food ceases to be abundant (Lack 1950, 1954).

In the Pacific Coast races of *Zonotrichia leucophrys*, the span of the breeding season varies both with race and with the latitude of breeding. Even so, the natural termination of the breeding season takes place at very nearly the same time annually in all three races (Lewis 1971). This is especially interesting because only in *gambelii*, and perhaps in some of the more northern *pugetensis* populations,

would a somewhat longer breeding season be ill-adaptive. The date at which breeding terminates in the arctic and subarctic populations of *gambelii* allows little more than sufficient time for postnuptial/postjuvenal molt, the deposition of migratory fat reserves, and departure prior to the first autumn storms (DeWolfe 1967; King et al. 1965; Oakeson 1954). Interestingly, however, breeding in the non-migratory *nuttalli* terminates as early as in *pugetensis* (Blanchard 1941; DeWolfe 1968a, b), suggesting that termination in these races is not related primarily to the energetic demands of autumnal migration.

SUMMARY

Resident male *Zonotrichia leucophrys pugetensis* arrive in the lower Puget Sound Region in the early days of April. Both males and females arrive in Island and King counties, Washington, over a period of many days, the first resident males arriving about two weeks before the first females. Sporadically throughout April, small flocks of *pugetensis* are temporarily present. Most of these birds appear to be migrants, though in late April, some do remain and establish territories. The resident males rapidly establish territories onto which the females segregate on the day of their arrival. Territorial conflicts are infrequent; indeed, nearest neighbors often show nearly complete tolerance of one another and temporary foraging associations of two to four pairs are frequently seen during the first half of May. The first eggs of the initial clutch are laid at a median date of about 13 May and the first eggs of second clutches are laid at a median date of about 14 June. The eggs are generally laid daily until the clutch of two to five eggs is complete. Incubation begins with the laying of the ultimate or penultimate egg of the clutch, and the last egg of the clutch hatches about 12 days after the clutch is completed. Nestlings remain in the nest until about ten days of age, but may leave earlier in response to disturbances near the nest. The young are able to fly when 11–12 days old and are strong fliers by the 15th day. They may become independent of their parents by the time that they are about 30 days old.

Two or three clutches are laid; both parents attend the young of the first brood until the second clutch of eggs is complete, after which time the male generally assumes all care of the young. This adaptation favors earlier laying of the next clutch.

The combined weight of the testes of first arrivals is less than 100 mg. The testes attain a mean maximum weight of 520 mg by about 15–20 May. Testicular weights remain high until about 10 July and then regress rapidly, starting about one week before the onset of postnuptial molt. The ovarian cycle is more complex than the testicular cycle. Ovarian weight at the time of arrival averages 30–40 mg and the ovary is still growing slowly. It begins to grow rapidly soon after arrival. This culminates in ovulation and egg-laying, following which the ovary and oviduct regress until the second nesting commences. The cycle is then repeated. Following a second or third nesting, ovarian and oviducal weights remain low.

ACKNOWLEDGMENTS

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