THE BREEDING SEASON OF A PARASITIC BIRD, THE BROWN-HEADED COWBIRD, IN CENTRAL CALIFORNIA

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The breeding seasons of birds are usually timed so that the young are reared during a period of abundant food. At high latitudes nearly all small birds may nest within a week or two of each other. In warmer temperate climates where plants grow and insects are active for several months, the breeding seasons are longer, and different species may have different breeding seasons. Birds that feed insects to their young often breed earlier in the year than those reared mainly on seeds. Even the insectivorous species may stagger their breeding seasons when their prey appear during different weeks or months (Davis 1933; Lack 1950). Birds that do not feed their young but instead lay their eggs in nests of other species must generally lay when their foster species do. Synchronizing the breeding season with that of the hosts is no great problem for parasitic birds at high latitudes where all the hosts breed in the same few weeks. Like the brood parasites which lay their eggs in the nests of only one species of fosterer, they simply use the same environmental cues in the same manner to time their breeding as their foster species do. Parasitic species are faced with a more difficult problem when they use many foster species which breed at different times. To remain in breeding condition for a prolonged period may place considerable demands on the resources and on the chances of survival in parasitic birds. Even brood parasites that lay in the nests of several species may reap higher reproductive returns for their laying efforts in the nests of some foster species than in others.

To find how a parasitic bird has adapted its breeding season when its potential foster species breed through several months, I observed Brown-headed Cowbirds (*Molothrus ater*) in central California. Between latitudes 36°30′ and 39°40′ N, small passerines breed every month from February through October, a cumulative breeding season of 9 months. Most, however, breed from April through July. Because the parasitic cowbirds are known to lay their eggs in the nests of many small passerine species, one adaptive strategy in timing their breeding might be to begin early in spring and to continue through autumn until the last possible host had nested. Another possible strategy might be to remain in a condition of near-readiness to breed through the year, or conversely to breed only for a few weeks, when the foster species that most successfully rear the young cowbirds are nesting. The way in which timing of cowbird gonadal activity and egg-laying in relation to their hosts is adapted, whether by one of these strategies or a compromise, may be seen by comparing the breeding seasons of parasite and host, and by comparing the costs in terms of metabolic energy in completing their annual cycle in other times of the year. Recent studies (Lustick 1969, 1970) on Brown-headed Cowbirds in California permit us to make these comparisons.

STUDY AREAS

Brown-headed Cowbirds were observed from 1960–65 for about 200 days in the central valley and the inner coast range of California. Casual field observations were made at other times near Berkeley. In the spring, the most detailed field observations were made at a cattle ranch 4 miles SW of Elk Creek, Glenn County, in the inner coast range, at about 1100 ft elevation. Additional observations were made at East Park Lake in Colusa County, about 20 miles S of Elk Creek. The vegetation in these coast-range habitats is a mixture of open oak woodland (dominated by blue oak, *Quercus Douglasii*), with grasses and some herbaceous plants (especially *Erodium*), as well as chaparral and much *Ceanothus*. The countryside receives 15–20 inches of rain in a year, mostly in winter and early spring. The hills are green with fresh grass from winter to late May or June, depending on the spring rains, and with leaves on the oak from April until late autumn. In summer, autumn, and winter, most field work was done in the central valley in Fresno County near Firebaugh, in Yuba County south of Marysville, and in Colusa County between Colusa and Williams. These valley areas used to be marshland and grassland, with some halophytic shrubs in the poorly drained areas. However, during the early 1960s, they were mostly agricultural lands planted to rice, and this rice attracted thousands of cowbirds and other blackbirds. A few scattered marshes remained in depressions and were used as water reservoirs for irrigation; these and the willows and cottonwoods along the rivers were used as nesting sites by some hosts and roosting sites by the cowbirds. These areas have been described and pictured in

The Condor 75:80–99, 1973

more detail by Orians (1961), Küchler (1964), and Payne (1969a). The vegetation around Berkeley is partly residential, with planted shrubs and grass, and partly a mosaic of disturbed grassland, coastal evergreen-oak woodland, and chaparral.

Within these areas I collected 462 cowbirds for examination. The birds were first weighed; their gonads were then measured or were fixed in neutral buffered formalin in the field and measured after at least 24 hr. Netted birds were held in captivity and were laparotomized and their gonads dissected or (males only) measured within 4 days. An index of reserve energy in the form of body fat deposits was given to each bird, using the scoring of the fat categories described by McCabe (1943). Specimens were examined for molt, as described later, and representative skins of molting birds were prepared for comparison of molt pattern with other icterids. Additional study skins of cowbirds from central California in the collections of the University of Michigan Museum of Zoology (UMMZ) and the Museum of Vertebrate Zoology, University of California (MVZ) also were examined for molt and for information on gonad size and body weight. The laying season of cowbirds was determined by dissection of the birds taken in the field from 1961–65. Females were considered to be breeding if they had an egg in the oviduct or large postovulatory follicles and yellow, yolky growing ovarian follicles in the ovary. The breeding seasons of the cowbirds' foster species were derived from published descriptions of egg dates.

FIELD OBSERVATIONS ON THE COWBIRD CALENDAR

In the winter months, cowbirds fed in flocks in the harvested rice fields of the central valley with other species of icterids, mainly Red-winged Blackbirds (*Agelaius phoeniceus*), Tricolored Blackbirds (*A. tricolor*), and Brewer's Blackbirds(*Euphagus cyanocephalus*). Field observations and examination of stomachs showed that rice spilled during harvest or left for game birds was the main food in winter. Flocks of cowbirds were seen in pastures with cattle and around feed-lots in the central valley. At night, they roosted in marshes near their feeding areas. Usually the only sounds heard from cowbirds were high, whistled calls given in the marsh after the birds had flown to roost at dusk.

The behavior of cowbirds changed gradually through early spring. Singing became more frequent in Berkeley during the last 10 days of February, though the birds gurgled and sang occasionally during the winter as well. Although cowbirds were not seen at Elk Creek and East Park from late summer through winter, they were there in flocks of 10 and 12 birds by 12 March, when they were less numerous around the rice fields at Firebaugh than previously. The change in numbers in these areas suggests some local movements from the valley into the hills in spring. In early March, the males sang mostly in morning and at dusk. During the first week of April, males sang infrequently in early morning. Females began to chatter in April, and I heard them chatter more often in May and June when they were laying. By 25 March, a few males were singing from conspicuous perches: dead oaks at Elk Creek and high levees near Firebaugh where trees were scarce. Males also circled in the air over these sites, one male at a time, giving a call that differed from the song heard when they alighted on their perches. Usually, one lone male sang from a special perch, day after day, though sometimes other males flew to the tree or the levee. When this happened, the two males often stretched their bills and necks skyward, an agonistic display common among the blackbirds. Then one flew away after a few minutes while the other remained and sang.

Cowbirds became attentive toward other small birds during March. In May and June, I sometimes saw lone females watching Song Sparrows (*Melospiza melodia*) and Red-winged Blackbirds building their nests. On the morning of 2 May, I saw a female repeatedly enter a small patch of marsh near Firebaugh. In one hour she was chased out five times by a male and once by a female Red-winged Blackbird, and once by a Song Sparrow. A nest of a Red-winged Blackbird in the marsh on that day held two blackbird eggs and one cowbird egg. Other cowbird eggs were found in the marshes during May in the nests of Red-winged Blackbirds (3 of 13 nests) and Song Sparrows (2 of 5 nests). At Elk Creek and East Park I noted cowbird eggs in only 3 of 72 nests of Red-winged Blackbirds and in none of 3 nests of Song Sparrows. The eggs found were laid in May.

In late April, cowbirds were chattering, a call of the female heard almost exclusively during the breeding season, and they chattered through June at Elk Creek, as well as in the central valley. This chatter, sometimes given by lone females near a nest of a potential host, and often when a male and female flew up from the grass, is part of their courtship sequence. Several complete copulations involved the male singing and bowing, then running toward the female with his wings spread and tilted forward. The female crouched, quivered her wings, and chattered as she was mounted. During May and early June, the cowbirds were abundant at Elk Creek and East Park, where they roosted in marshes. In morning about an hour before

sunrise, I netted females, with eggs in the oviduct, just as they flew from the marsh. A few males were spaced out on their song perches, while others were in flocks near the cattle. Of the eight copulations that I observed, all were at the song perch of a lone male. Although groups of males often display to females in the flocks, females in these flocks are not receptive and do not solicit their attention. All matings occurred between 06:00 and 08:00 in the field, shortly after the egg had been laid [laying takes place only in very early morning in the Brown-headed Cowbird (Hann 1941; Payne 1965)].

Males over a year old probably mate most frequently. Of the five males that I shot from clearly defined song perches, none had any grey juvenal feathers under the wings. My samples, both from marshes and flocks feeding with cattle, consisted of about twice as many adult males as first-year males. Because only some males breed (the adults that hold a song perch) and nearly all the females do, a breeding male cowbird probably mates with more than one female; Darley (1971) found some banded cowbirds in Ontario to be bigamous. Breeding males were shot from their song perches on two occasions at Elk Creek and once at Firebaugh, and all were replaced on the next day by another singing male. No pair bonds seem to be formed. Females were usually alone in early morning, searching for nests and laying, while the males were waiting for them to visit their song perches.

The breeding season at Berkeley began in April, as I heard many females chattering only in April and May. In Strawberry Canyon, a female chattered in a tree several times in a minute, and seen nest-building within a few hundred feet of her was a Song Sparrow. Singing nearby were Orange-crowned Warblers (*Vermivora celata*), Wilson's Warblers (*Wilsonia pusilla*), and Black-headed Grosbeaks (*Pheucticus melanocephalus*), all potential foster species. The dates of ten cowbird eggs and young cowbirds in the care of White-crowned Sparrows (*Zonotrichia leucophrys*) in Berkeley and nearby localities (Baptista 1972) all indicate that cowbirds lay there in May and June.

In late June, adult cowbirds dwindled in numbers and then disappeared in each of 3 years of observation at Elk Creek and East Park, though juveniles were seen through July. Most adults appear to move out of the area in June, when the hills have become brown and dry. Some may move to higher, cooler elevations, others to the central valley where the irrigated meadows are green through the summer. Breeding appears to continue later into summer in the central valley than in the Elk Creek area. I saw many adult cowbirds, some of them copulating, in Sacramento in early July 1965. In the irrigated residential areas of the city and along the wooded rivers, the cowbirds may find new nests of such hosts as Yellow Warblers (*Dendroica petechia*) and House Finches (*Carpodacus mexicanus*) into mid-July.

During late summer only a few songs were heard, and cowbirds flying overhead had flight feathers missing from the wing. No female chatters and only a few whistled vocalizations given by male cowbirds roosting at dusk were heard during the molting period in August and September. By late October the birds seen flying had completed their molt, as their wings no longer had feather gaps. A resurgence of singing was noted on 26 October 1964, when dozens of cowbirds were singing in the tall cottonwoods around the rice fields of Colusa County, while another flock of 200 was silent, feeding in the rice. This period of singing was short-lived and I noted no chattering females. In November and December, the cowbirds sang only occasionally, though on sunny days a few sang in early morning or at sunset.

These observations on the seasonal changes in behavior suggest that cowbirds begin to breed in central California in late April or early May. They continue to breed into late June in areas that become dry in June, and into July in the wetter habitats of the central valley.

GONADAL ACTIVITY

SEASONAL CHANGES IN TESTIS SIZE

Seasonal activity of the testes of Brown-headed Cowbirds was checked by measuring the left testis in 195 males. Birds examined included live males that were laparotomized and the testes measured, males that were collected and measured in the field, and males that were first dissected in the field and their testes measured after fixation. The testes showed no consistent or marked shrinkage or swelling with fixation, and the data for all males are shown in figure 1. Also included are the birds from the northern half of California in the MVZ skin collection, with testis size recorded on the specimen labels. The size of the testes in passerine birds living in northern temperate regions is well known to be a reliable indicator

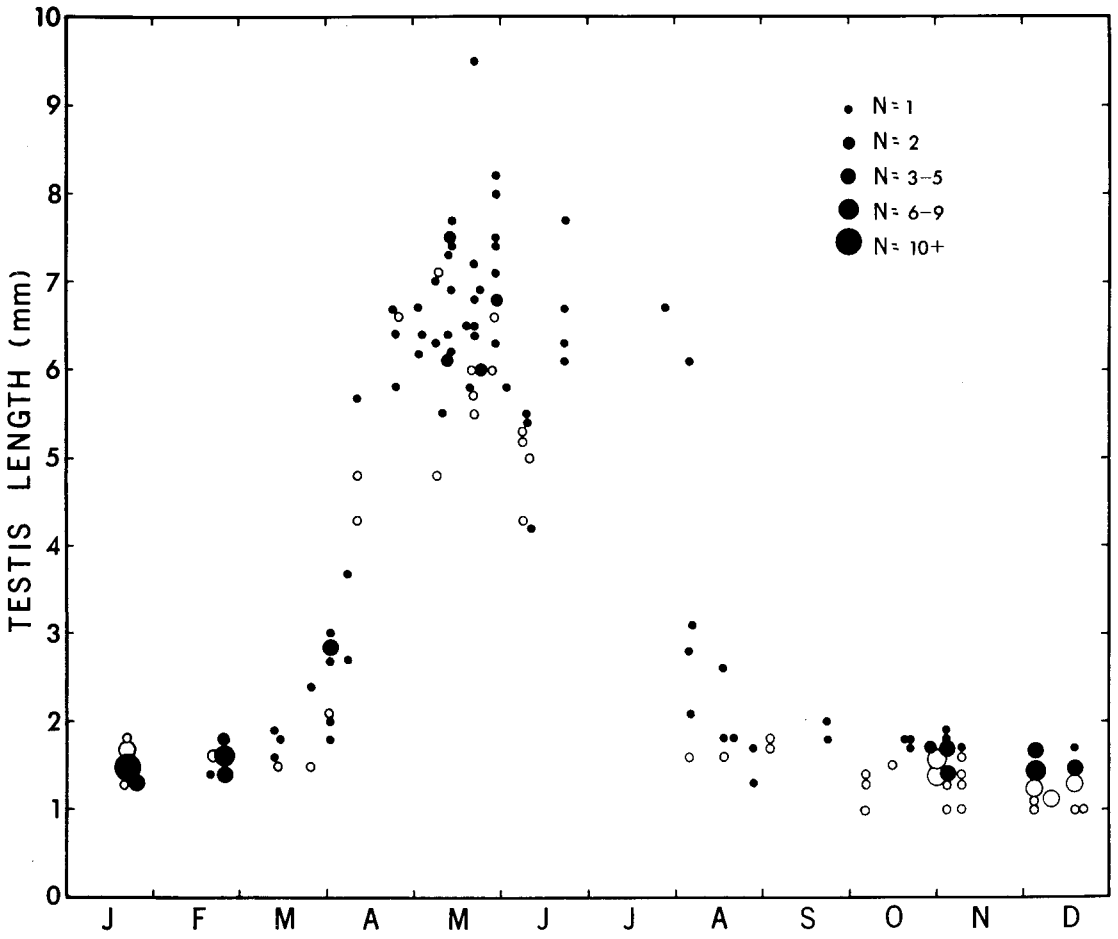

FIGURE 1. Seasonal variation in testis length (mm) in Brown-headed Cowbirds in central California. Open figures refer to males less than a year old, closed figures are older males.

of the spermatogenic activity. Comparison with other icterids living in California suggests that cowbirds with testes less than 2 mm in length lacked any sperm or spermatogonia, whereas birds with testes longer than 5 mm probably all had mature sperm and were in full breeding condition (Payne 1969a). A few testes of cowbirds were sectioned and stained as described in Payne (1969a), and in all cases the above generalizations were supported by the histological material.

The testes of Brown-headed Cowbirds are small and inactive during winter, from December through February. Testis' growth begins in late March, and some birds are in breeding condition by late April. In the samples taken in my field work, no males in northern central California had testes longer than 5 mm before 10 April. By late April, males were in breeding condition, and through the main breeding season, May and June, most males in the sample had large testes. Few birds were taken in midsummer, but apparently some cowbirds maintain their testes in breeding condition to the end of July. By August, the testes had regressed and were small through late summer and autumn. Histological sections of the testes of 15 adult male cowbirds taken in October and November showed no spermatogenic activity (spermatogonia were the only germinal cells in the tubules) and the interstitial tissue had no lipoidal secretory cells, though some lipoidal macrophages that were probably transporting the lipoidal debris from the degenerated tubules from the testis were evident (Payne 1969a:80–81). Testes remained spermatogonially and lipoidally inactive until the following spring.

FIRST-YEAR MALES AND OLDER ADULTS: COMPARISON OF TESTIS SIZE

The male cowbirds less than a year old are similar in plumage to the older males, except that the younger birds usually have several grey feathers among the underwing coverts.

TABLE 1. Testis length of first-year and adult Brown-headed Cowbirds in May and June.

Age of birds	N	Maximum (mm)	Minimum (mm)	Mean (mm)	$t_{.95}\,s_{\bar{x}}$
First-year	15	7.1	4.0	5.37	0.501
Adults	49	9.0	4.2	6.80	0.243

These are juvenal feathers retained in the postjuvenal molt (Selander and Giller 1960: 204). Males in the present study were examined for these grey, loose-webbed feathers. Birds having them were classed as first-year birds; those with only black underwing feathers were called adults. In addition, until January a bursa of Fabricius was evident in all birds with grey feathers as were partially unpneumatized areas on the dorsal surface of the skull. None of the black-feathered males had a bursa or unpneumatized areas of the skull from August through February. Therefore the criterion of grey feathers appears to be a reliable guide to the age of most males up to the time of the first postnuptial molt.

During summer, the young birds hatched in the same year had testes slightly smaller than those of older males (fig. 1). This size difference disappeared in January and February when testis size of the young birds increased slightly. In early April, the testes of first-year males as well as those of adults increase in size quite rapidly. During the breeding period in May and June, the first-year males have somewhat smaller testes, on the average, than the older males, though the two groups overlap in size and some first-year males have testes apparently large enough to indicate the presence of mature sperm. The difference in mean testis size in these two ages is significant ($P < 0.001$, table 1). Scott and Middleton (1968) found first-year male cowbirds to have smaller testes than adults in Ontario. Although the difference in testis size was not significant in the manner in which their data were analyzed, in small subsamples, the difference was probably real.

The age-specific gonadal activity in spring in males may be related to the polygynous mating system of cowbirds. Although the sample of successfully mating males is small, all were birds older than a year. Because all males holding active mating sites were adults and because adults have larger testes than first-year birds, it is unlikely that first-year males mate, at least not in proportion to their numbers in a population. Other icterids with smaller testes in first-year males are polygynous; these include Redwinged Blackbirds, Tricolored Blackbirds (Wright and Wright 1944; Orians 1961; Payne 1969a), and Boat-tailed Grackles (*Cassidix mexicanus*) (Selander 1958; Selander and Hauser 1965). Brown-headed Cowbirds have less conspicuous plumage differences related to age than these other icterids, but the pale wing coverts may be visible to the female when the male courts her with wings open and with their ventral surfaces exposed (see Friedmann 1929:163).

SEASONAL ACTIVITY OF THE OVARIES

Breeding condition in females was determined by examination of the ovaries and oviducts. The largest ovarian follicles were measured under a dissecting microscope; the number and size of large visible atretic follicles and postovulatory follicles in breeding birds were noted. Figure 2 shows the size of the largest ovarian follicle in each female.

Ovaries of cowbirds were small in late autumn and winter and showed no sign of laying until spring. In late March and early April, most females in the sample developed ovaries with follicles larger than 1 mm, and by late April and early May, some females had yolky, yellow follicles larger than 6 mm which likely would have been ovulated in a day or two (compared with *Agelaius* blackbird ovaries, Payne 1969a:52, 55). From mid-May through June, nearly every female had large, yolky follicles. Of the 65 females taken from May 15 through June 30, nearly all had recognizable postovulatory follicles, indicating ovulations within the previous 10 days (Payne 1966); the four exceptions were ovaries that had dried after fixation and had changed so much that no structures were clearly visible, but these four were all from females that had an egg in the oviduct. Most females had three or more postovulatory follicles longer than 2 mm, and nearly all had one or more large, yolky follicles growing in the ovary. Because the postovulatory follicles of icterids regress rapidly after ovulation (Payne 1966), the California cowbirds evidently were laying on the average four or more eggs per week through the breeding period from mid-May to late June. Many birds were laying also from 1 to 14 May, as 14 of the 26 females in this period had eggs in the oviduct or had large, recognizable postovulatory follicles. Some females may begin laying in late April in central California; one of the four birds taken from 23 to 25 April had a large, yolky follicle which

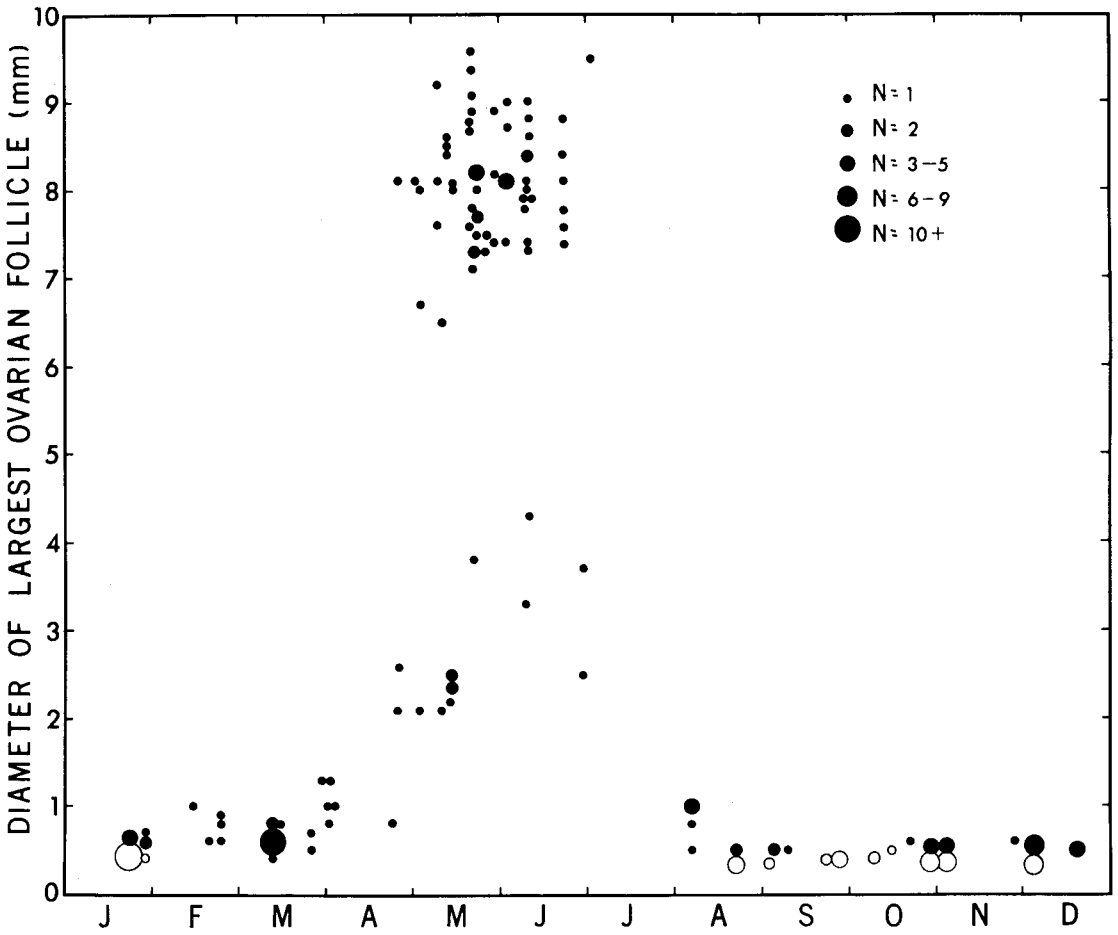

FIGURE 2. Seasonal variation in ovary size in cowbirds. Open figures are birds between 1 and 8 months of age, solid figures are older females. All the females with ovarian follicles from 3–5 mm in May and June had laid, as evidenced by their postovulatory follicles.

measured 8.1 mm and also two large postovulatory follicles.

In addition to these April, May, and June birds, I collected one other female (RBP 3695) in adult plumage (taken on 20 May 1965 at Elk Creek) that had a rudimentary oviduct, thread-like and straight without the convolutions of a bird that had laid earlier in its life, and it had no visible gonad, even under the microscope. The bird appeared to be normal in every other way.

Only one female was collected in July, and by early August most had undergone regression of their ovaries, though four females taken on 5 August still had slightly enlarged ovaries, with follicles 0.8 to 1 mm. Through August and September, the ovaries of cowbirds remain small, with the largest ovarian follicles measuring 0.5 mm or less in almost all adult females. A female taken on 21 October 1962 near Colusa had an ovary with a slightly enlarged set of follicles measuring 0.6 mm and with a translucent, glassy appearance. This female may have experienced a slight recrudescence of the ovary in October, but this slight increase in ovary size was unusual. Generally, the ovaries of female cowbirds are quiescent through fall and winter.

LAYING SEASON

The laying period of Brown-headed Cowbirds in the Elk Park area begins about the last week of April for some females, but most do not lay until May. In 1963, only one of eight females taken from 10 to 13 May had laid; in 1964, four of six females taken from 1 to 9 May had laid; and in 1965, six of seven females (besides the female that lacked an ovary) had laid by 13 May.

The laying season at Firebaugh, more than a hundred miles south, appeared to begin at the same time as at Elk Creek. All four females taken on 3 May 1964 had large, postovulatory follicles, and one bird had only one post-

ovulatory follicle, indicating that laying had just begun. Cowbirds in the inner coast range breed through May and June, and the adults disappear in July when the hills are dry and few hosts are likely to begin nesting. In the central valley, cowbirds continue breeding into early July. A female taken near Firebaugh on 2 July 1964 was laying and had large, yolky follicles. At Sacramento cowbirds copulated on 26 and 27 June and on 3 July in 1965, though none did here on 10 and 11 July. Laying may continue a few weeks longer in the green lawns, orchards, and marshes of the central valley than in the dry hills. Breeding is completed by late July or early August.

From the dates of laying indicated by the ovaries of females collected, as well as from the time of regression of the testes of the males and the end of mating behavior, the laying season of the Brown-headed Cowbirds in northern central California begins in late April and early May and ends in late June and early July. On the average females appear to lay for about 7 or 8 weeks.

BREEDING ACTIVITY IN FIRST-YEAR AND IN OLDER FEMALES

During August and September, the ovaries of females with bursae and partially unpneumatized skulls were minute. Ovarian follicles of these birds were barely recognizable in low relief as granular protuberances on the small ovaries. Through autumn and early winter, the ovaries of young birds were less well developed than were the ovaries of older birds. After early February, the first-year birds could no longer be distinguished from older females, for by that time their skulls had fully pneumatized and the bursae had regressed. Female cowbirds often retain some juvenal lower wing coverts, as do the males. The under coverts of juveniles and of adult females are both light greyish-brown, and it was not possible to distinguish juvenal feathers from later feather generations in the females in winter or spring. Selander and Giller (1960:204) similarly found it impossible to age the female cowbirds taken after March because the juvenal and adult covers are indistinguishable by that time.

Nearly every female was laying in May and June, and this indicates that female cowbirds breed when they are just less than a year old. If the females did not breed in their first year, or if proportionately fewer of them bred than did the older females, one would expect to find some females that were not laying during late May and June. The sample of females taken in the laying season probably included the first-year females though they could not be aged individually. Female cowbirds older than a year have a higher annual mortality rate than do adult males, but the mortality rates of the two sexes in their first year of life are said to be the same (Fankhauser 1971; Darley 1971). From the survival data of first-year and adult cowbirds one would expect somewhat more than a fourth of the females in spring to be birds less than a year old, or about 20 birds in the sample of 65 females collected in the laying season. Because all but one female cowbird taken in late May and in June were laying, it is evident that female Brown-headed Cowbirds regularly breed in their first spring. The younger females may begin laying slightly later in the spring since their ovaries are smaller in late winter and have further to develop to laying condition, and consequently they may lay fewer eggs in a season than the older birds.

NUMBER OF EGGS LAID IN A BREEDING SEASON

A rough estimate of the number of eggs laid by each female cowbird during the breeding season may be made from the number of eggs laid in each 10-day period and from the duration of the breeding season. From measurements of the larger postovulatory follicles and the growing ovarian follicles of each bird, it seems that most females lay on most days of the breeding season. In 57 females taken from 15 May to 30 June, an egg was noted in the oviduct in 49 (83%). Others had yolk in their body cavities because of eggs shot in the duct or in disrupted large, unovulated follicles. Because these two measures of the day-to-day frequency of laying in female cowbirds both indicate that females lay on more days than they do not, probably most females laid six to eight eggs in a 10-day period, or several dozen eggs during a single breeding season. The details of the number of eggs in each series will be discussed elsewhere. The California birds seem to lay more eggs in a season and also more in a series or clutch than the sample of breeding cowbirds collected in northern lower Michigan (Payne 1965).

To get an idea of the effort involved in laying this large number of eggs, I weighed the ovaries and oviducts of breeding and nonbreeding birds. Breeding females included all laying birds taken May 1964 and 1965, for which both the ovaries and oviducts were un-

TABLE 2. Weights of ovaries, oviducts, and bodies of breeding and nonbreeding Brown-headed Cowbirds.

Sample	N	Weight (g); mean (min., max.)		
		ovary	oviduct	body[a]
Laying	10	0.80 (0.5, 1.2)	2.69 (1.3, 3.7)	37.8 (34, 41)
Nonbreeding	12	0.049 (0.02, 0.09)	0.041 (0.02, 0.06)	37.8 (32, 42)

[a] Total body weight (including reproductive organs).

damaged by shot. The organ weights for nonbreeding females were taken from the first 12 adult specimens with weight data selected at random from the months December through March. The weights of the reproductive organs and of the birds are shown in table 2. In the nonbreeding season, the reproductive organs comprise less than 1% of the weight of a cowbird, whereas in the laying season, the ovaries and ducts (including in some cases eggs in various stages of albumen deposition and shell formation) were about 10% of the total body weight. The only local egg weight available is one taken at 01:30 from the oviduct of a female that had been netted earlier in the night. The egg had several splotches of brown pigment deposited on the hard shell and it would have been laid about 3 hours later. The egg weighed 2.4 g, or about 7% of the nonbreeding weight of cowbirds (total body weight less the weight of the reproductive organs). Since a female lays about 30 eggs in a breeding season in California, her total laying effort involves producing eggs that add up to 200% of her body weight.

MOLTING SEASONS

Birds were examined in the hand for feathers in sheath, remiges and rectrices that were only partially grown, and missing flight feathers that had dropped but had not been replaced. In winter, the growing feathers were seen only in an asymmetrical pattern, and then in only a few birds in each sample. In early spring, most specimens were molting the head and neck feathers, and during the breeding season no feathers were growing. In late summer and early autumn, cowbirds molted all or nearly all of their feathers during the postjuvenal molt of the young birds and during the postnuptial molt of the older birds.

To describe the stage of molt in cowbirds, molt scores were determined for each specimen collected in the summer and autumn from 1961–64. By scoring the degree of completion of selected feathers and feather tracts in the same manner as in other icterids in California (Payne 1969a), the molt of various ages, sexes, and species of icterids may be compared. The proportion of the molt completed (as shown by the molt score) at various dates in late summer and autumn is shown in figure 3. A molt score of 0 indicates that molt had not begun, a score of 60 indicates that molt was approximately 60% completed, and a score of 100 indicates that the plumage had been completely replaced, except for some underwing coverts in the young birds. The pattern of feather replacement within the feather tracts and the synchronization of molt of the various tracts were identical in all details studied with the pattern of molt in other North American icterids described by Selander (1958) and Payne (1969a).

Postnuptial molt in male and female cowbirds in central California usually begins by the first week of August and is completed in some birds by mid-October. The earliest birds taken in molt were netted on 4 August, and the earliest birds taken with the molt completed were shot on 20 October, suggesting an average time to complete the postnuptial molt of about 75 days. The duration of molt is similar in males and females.

Postjuvenal molt begins at the same time in some young as does postnuptial molt in the adults, but in other young the molt may not begin until a full month later (fig. 3). Some young birds complete the summer molt at about the same time as the adults; no great difference in the duration of molt in first-year or older birds is apparent. Birds beginning the postjuvenal molt later in the season may be those hatched late in the breeding season, but unfortunately the degree of skull pneumatization of the young birds in the sample was not noted for many. Those Brown-headed Cowbirds in Texas which undergo a more complete postjuvenal molt have more of the skull pneumatized (Selander and Hauser 1965), though again these data only indirectly suggest an effect of age upon the time of molting.

The postnuptial molt of cowbirds is completely separated in time from the breeding season, inasmuch as the July birds with large gonads were not molting, and the August birds that were molting had small gonads. Whether

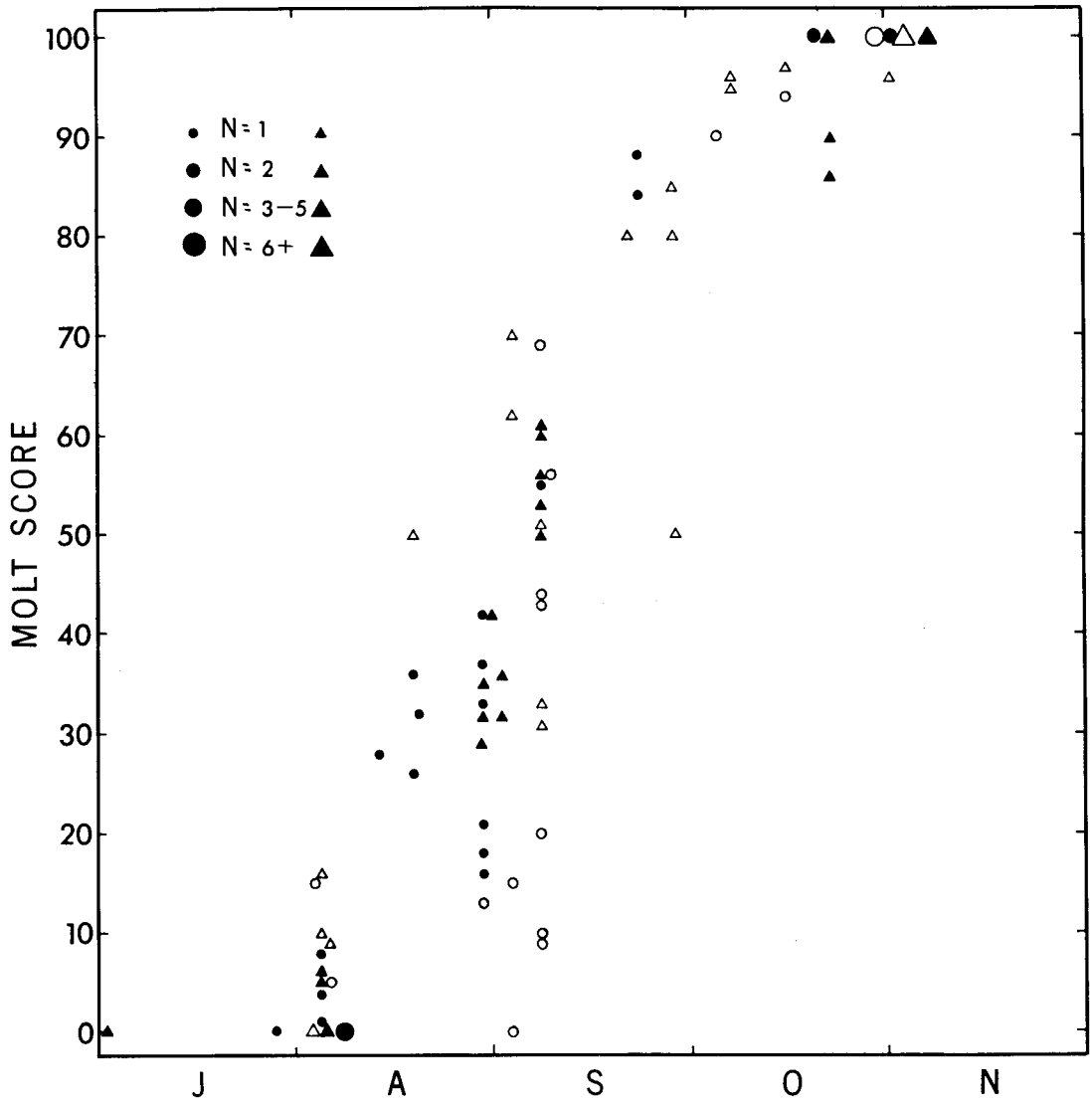

FIGURE 3. Time of molt in cowbirds in central California. The molt score for each bird gives the proportion of molt that had been completed. Open figures are birds in postjuvenal molt, closed figures are birds in postnuptial molt. The circles are males and the triangles represent females. Dates run from July through November.

the molt of individual cowbirds begins earlier in those whose gonads regress earlier is not known. Additional samples of birds taken in July would be useful in determining the relationship of breeding condition to molt in the individual bird.

Duration of the molting season of Brown-headed Cowbirds is about the same as in Red-winged Blackbirds and Tricolored Blackbirds in the same areas of California, as all of these birds molt in late summer and early autumn over a period of 2–3 months. Molt in the cowbirds begins and ends about a month later than in these marsh blackbirds, however, reflecting the later breeding season of the cowbirds.

In late winter and early spring, the cowbirds in central California regularly molt their head feathers and often also feathers on the neck. A few also molted feathers in the scapular and spinal tracts. The proportion of birds taken with the head feathers in sheath are listed in table 3. Molt begins in some birds in late January, and more than half of the birds taken during February and March were molting the head feathers. Both sexes and first-year and older birds molt the head feathers in late winter. During March and April, both fresh, dark feathers and pale, worn feathers are seen on the heads of both sexes; the difference between the fresh and the worn feathers is more conspicuous in the males.

TABLE 3. Proportions of cowbirds in molt in late winter and early spring.

Age and sex	Molting or not	Number of birds in each sample						
		Dec.	Jan. 16–31	Feb. 16–29	Mar. 1–15	Mar. 16–31	Apr. 1–15	Apr. 16–30
Adult ♂	Molt	0	7	9	1	0	2[a]	0
	No molt	15	7	2	2	1	8	1
1st-year ♂	Molt	0	10	1	1	0	0	0
	No molt	14	10	0	0	1	4	1
Adult ♀	Molt	0	4	4	18[b]	1[c]	0	0
	No molt	10	10	0	2[d]	1	5	3
1st-year ♀	Molt	0	2					
	No molt	2	9					

[a] One on 2 April, 60 head feathers in molt; the other on 1 April, 15 crown feathers in molt.
[b] Two nonmolting birds had ovarian follicles (O.F.) of 0.8, 0.6 mm, whereas molting birds had O.F. < 0.5 mm (one bird) or 0.6 to 0.8 mm (all other birds)—no difference between groups.
[c] Molting bird, skull pneumatized, O.F. 0.7 mm. Nonmolting bird, skull 30% unpneumatized, O.F. 0.5 mm.
[d] One molt completed, new feathers.

As few specimens taken in later April and May had two colors of head feathers, the molt may involve most or all of these feathers.

Because birds taken in late winter may have been out of phase in their molt, with some molting while others had not begun or had completed the molt, I checked the plumage at fortnightly intervals in eight captives held on natural daylengths in Berkeley. All of these birds molted most of their head feathers, though early birds began their molt more than 2 weeks before the latest birds. The molt of these captives indicates that all or nearly all individual wild cowbirds in central California molt the plumage of the head in late winter and early spring. The two nonmolting adult females taken in early March had molted earlier as their heads showed some dark, fresh brown feathers as well as older worn feathers; these birds indicate that molt occurs in nearly all local cowbirds in late winter or early spring. This partial prenuptial molt is completed in most cowbirds in California before the end of March, and the only two birds recorded as molting in April were taken in the first 2 days of the month and had few feathers (60 in one, 15 in the other) in sheath.

Cowbirds in the east and south-central parts of North America are said not to have a prenuptial molt (Dwight 1900; Bent 1958; Selander and Giller 1960). On the other hand, Phillips found Brown-headed Cowbirds taken near Tucson, Arizona, to molt their head and neck feathers in March (Phillips et al. 1964: 172). I have examined museum specimens of cowbirds taken from January through April in eastern North America and from California in the collections of the UMMZ and MVZ, and no eastern birds were molting, though molting feathers were evident in museum specimens from California as well as in most males and females taken from February through April in the states of México and Guerrero in México.

Perhaps the molt in late winter in the southwestern cowbirds and the apparent lack of molt in the East is related to differences in their winter habitats. In most of the Southwest, the climate is dry and the vegetation harsh and abrasive. Perhaps wear of the plumage in these ground-foraging birds is greater there than in the greener East. Another possible explanation of the geographic difference in molt of different populations living at the same latitude is that winter climate of the Southwest is milder and more energy is available to the birds living there. Sunny days are frequent in the Southwest in winter, and cowbirds are known to have lower rates of oxygen consumption (implying lower food requirements) when exposed to radiant energy comparable to sunlight (Lustick 1969). The ability of cowbirds to use solar radiation may decrease their food requirements for maintenance activities and may make additional energy available for molting.

The adaptive significance of the molt in spring may involve the role of the head feathers in display. Males in worn plumage have paler heads than males in fresh plumage. Comparing museum series of April and July males shows that although the iridescent greens and purples of the body plumage do not change with wear during the breeding period, the head fades from dark brown to paler tan, increasing the contrast between the head and the body. The distinctive color of the head of males may be important in courtship display when they bow, setting the brown head against the glossy black body plumage. The new, longer nape feathers may be significant by increasing the size of the ruff in the

displaying male. The head molt in the female as well as in the male may simply reflect the result of selection for fresh plumage in spring in males with no counterbalancing selection against molting in females. The appearance of the head and nape may also be important in the behavior of cowbirds toward their hosts, as both male and female may sidle up to a potential host and lower the head toward it, exposing the nape, in a display that may appease the host adult (Selander and La Rue 1961) and increase the likelihood that the cowbird will be tolerated and may find a host nest in which to lay.

THE RELATION OF PRENUPTIAL MOLT TO GONAD DEVELOPMENT

Molt is completed in late March or early April, the time when gonadal growth is first evident. As most passerines of northern temperate regions do not molt and breed at the same time, the physiological state of molting birds may inhibit gonadal development (though other species molt and enlarge their gonads at the same time, Payne 1973a, b). To test whether molt seemed to have an inhibitory effect on gonadal development in early spring in the California cowbirds, I compared the gonad size of birds that were still molting or that had completed molt in March. In the 18 molting females taken from 1–15 March, size of the largest ovarian follicles ranged from just under 0.5 mm to 0.8 mm, and in the two birds that had completed molt the follicles were 0.6 and 0.8 mm. These figures suggest no important differences in follicle size in birds that had completed molt. The four molting birds with follicles of 0.8, 0.7, 0.7, and 0.7 mm possibly were birds that had undergone some gonadal growth in late winter just before molting and then had arrested the gonadal development, however, so the relationship between gonadal development and molt in early spring females is unclear. In the nine adult males taken in the central valley on 1 and 2 April 1963, the two males with the head still in molt had testes of 2.7 and 2.9 mm, whereas the seven nonmolting birds had testes ranging from 1.8–3.0 mm. Again there seems to be no clear evidence of inhibition of gonadal development by molt.

BODY WEIGHT AND BODY FAT

Because the breeding and molting seasons of many birds are sharply separated in time, avian biologists have often proposed that each of these processes demands a considerable increase in the energy requirements, and that the two events use up so much energy that they may not occur simultaneously without harming the bird. Molting increases the metabolic rates of cowbirds (Lustick 1970), but no information is available on the energy requirements of breeding in this species. Probably making eggs, displaying, etc., use somewhat less than the basic energy requirements of living from day to day, as in other small songbirds in temperate regions (Helms 1968; Payne 1973b). In the absence of direct physiological measurements of the energetic cost of both breeding and molting in cowbirds, we may compare their body weights and their energy reserves in the form of body fat deposits. The weights and fat indices for adults collected in this study are shown in figure 4.

The body weights of Brown-headed Cowbirds in central California change but little during the year. Males and females have slightly lower body weights in early April and in early summer than in the late winter. In early April, they move locally from the central valley into the foothill region, and perhaps the drop in body weight is related to this movement. The females increase in body weight during the breeding season, and this increase is nearly all accounted for by the development of large ovaries and oviducts (table 2). At the end of the breeding season, weight decreases as the reproductive organs regress, though the difference between breeding weights and the early July weights appears to be about 2 g more than can be accounted for by these structures. During the molting period, the cowbirds may increase slightly in weight. Additional sampling would be required for a test of any change in weight at the end of molt, when the birds might perhaps be exhausted from molting. By late October when some birds are just completing molt, the body weights appear to be slightly lower than during the next 2 months.

Seasonal deposition of body fat in these California residents appears to account for much of the change in body weight, as these rise or fall together. The only time of year when no cowbirds were "fat" or "very fat" was during the breeding season and shortly after it in July. Early in the molting season several birds were at least "moderately fat" and one was "fat," a male with a molt score of 32 and a body weight of 44.2 g. At most other times of year a few birds were taken with "little fat" or "no fat," but most birds from October

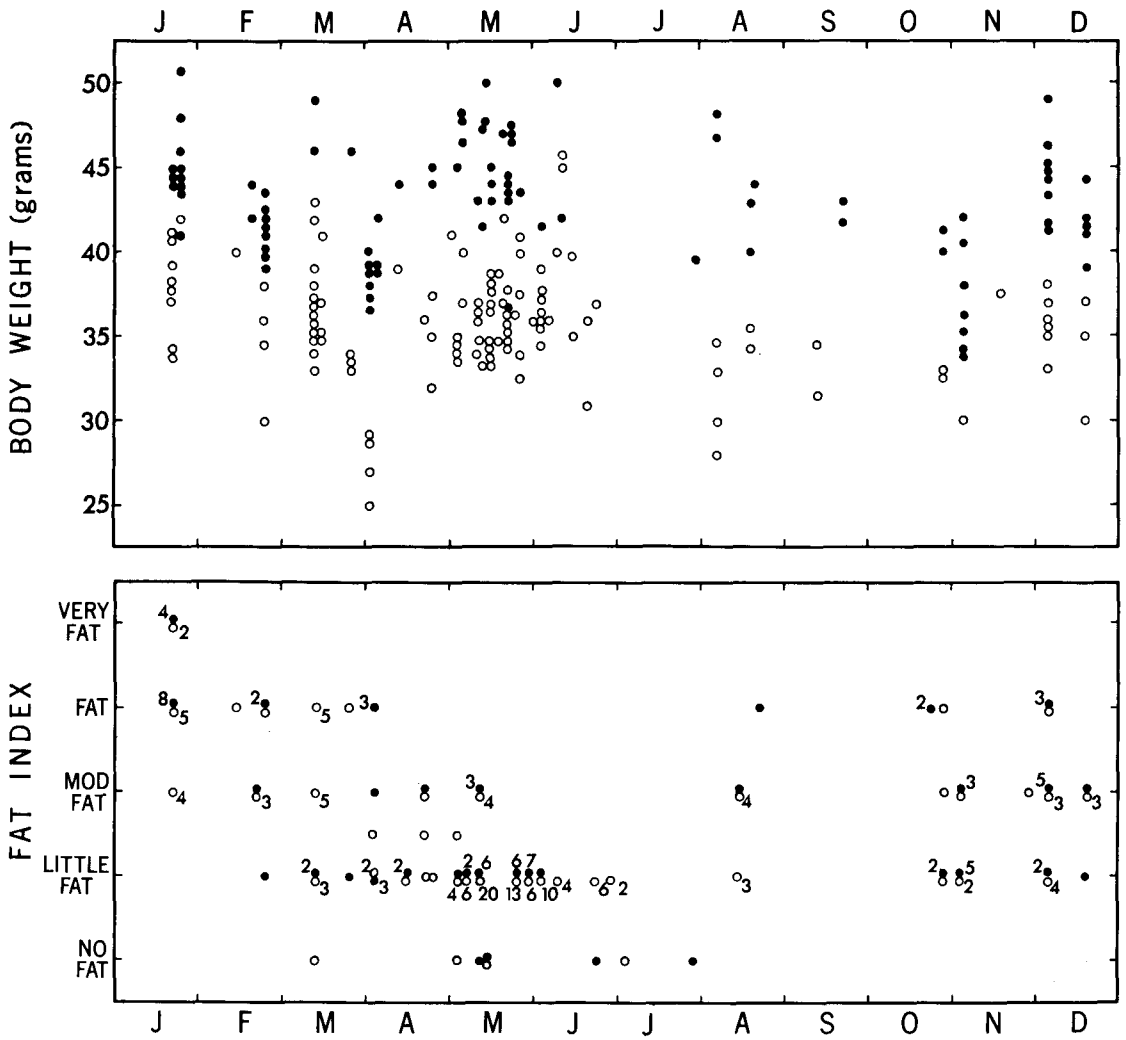

FIGURE 4. Seasonal changes in body weight and in body fat index in adult cowbirds. Closed figures indicate males, open figures are females. Fat classes are described by McCabe (1943).

through March were "fat" or "moderately fat."

The seasonal changes in body weight and in body fat in the cowbirds do not show clearly that breeding or molting directly exhaust the abilities of the birds to keep up their energy intake for several weeks at a time at the level required for these activities. Although body fat is relatively low during the breeding season, body weight is higher then than in early spring and in early summer. Even without the reproductive organs, the body weights of females are greater than before breeding. The rather low body weights of females in July (lower than the body weights less the reproductive organ weights of laying females), however, suggest a degree of exhaustion at the end of the laying season. Molting itself does not tax greatly the energy resources of cowbirds, as birds increase slightly in body weight and fat while they are molting in late summer. In this increase the cowbirds are similar to most other small passerines that have been studied, at least the forms which have a relatively prolonged molt lasting between 45 and 90 days. Increases in body weights and, in some forms, in body fat during molt have been noted for several species of small shorebirds, Old World warblers, icterids, sparrows, and buntings (Payne 1973b).

COWBIRD HOSTS AND THEIR BREEDING SEASONS

Brown-headed Cowbirds lay their eggs in the nests of many birds. Friedmann (1963, 1971) has compiled the records of eggs and young of cowbirds found in the nests of North American birds. More than 200 species are parasitized, some of them only occasionally

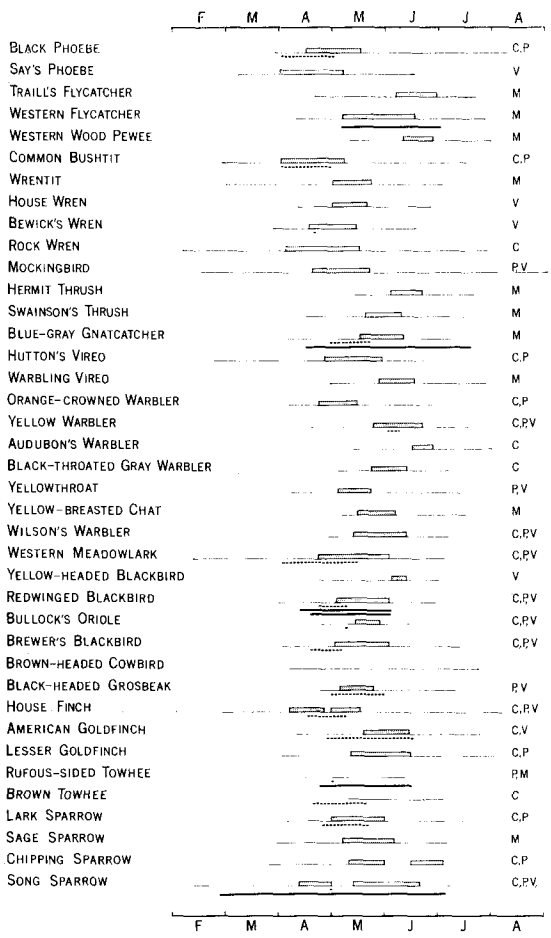

FIGURE 5. Breeding seasons of cowbird hosts and of cowbirds in California. Solid light lines join the earliest and latest egg dates and give the total laying season, and hatched figures show the peak of laying as defined by Bent et al. (1942–68). Dotted lines are dates for the Sacramento Valley by Davis (1933). The heavy lines show the breeding season as determined in life history studies mentioned on text p. 93. Letters for the hosts indicate whether they bred at Elk Creek (C), East Park (P), the central valley (V), or (M) in similar habitats in other localities (Miller 1951).

and some of them in nearly half of the nests of some host populations. Most records of parasitism, however, are of four families of passerines: the sparrows, warblers, vireos, and flycatchers. Also every record of successful fledging of cowbird young from a host nest has been from the nest of a passerine.

To determine which birds were important locally as hosts of the cowbirds in central California, I recorded the passerines that I noted in the study areas in the inner coast range and the central valley. Although no attempt was made to find the nests of hosts (except for the *Agelaius* blackbirds), the local lists give a good sample of species likely to be important as cowbird hosts. At the Elk Creek and East Park areas, 52 species of passerines were recorded and in the central valley, six additional species were seen. Both the inner coast range and the central valley study areas were in the Sonoran life zones and were characterized by late winter and spring rains, hot dry summers, and cool winters. The vegetation was mainly grassland and open deciduous oak woodland. The Elk Creek study area was only 2 km from the edge of an evergreen mixed coniferous forest, with patches of chaparral at a higher elevation. I have also included birds of these vegetation zones, the former including the lower part of the Transition life zone (Miller 1951; Küchler 1964). Since I saw color-banded female cowbirds up to 2 km from the place where they were ringed 3 weeks earlier in the breeding season, it seems likely that some of the females in the Elk Creek sample were laying in the nests of birds of this coniferous forest-chaparral mosaic. For this reason I have added to figure 5 a few species of small songbirds from the lower Transition zone coniferous forests and chaparral from Miller (1951). I have excluded the birds known locally only in winter or in migration and the birds breeding locally but not used as hosts by the cowbirds, the species with no known published instances of cowbird parasitism in California. Of the 52 passerines noted in the Elk Creek-East Park area, 24 species were probably hosts of the Brown-headed Cowbirds. Of the others, some have occasionally been noted to have cowbird eggs in the nest, but none has had recorded instances of successful parasitism. These include several birds that build their nests in dark holes or in covered nests. The other passerines of the area not known to be significant hosts are mostly birds of body size considerably larger than cowbirds and birds whose large eggs would probably prevent successful incubation of the cowbird eggs. Some of the unparasitized larger passerines are also either predatory (shrikes, corvids) or strongly aggressive toward other birds (kingbirds). Barn Swallows (*Hirundo rustica*) and Tree Swallows (*Iridoprocne bicolor*) are occasionally parasitized and fledge young cowbirds, but no records of parasitism are known for California (Friedmann 1963, 1971), and they are omitted from the list of hosts in figure 5 although they bred at Elk Creek.

The other local passerines at Elk Creek and East Park are known to be occasional or

regular hosts of Brown-headed Cowbirds either in California or in other western states (Friedmann 1963, 1971). Also included are the additional host species that I recorded in the cowbird study areas in the central valley and the other small passerine hosts common in similar habitats in central California as listed by Grinnell and Miller (1944) and Miller (1951). Breeding seasons of the species seen in the hills of the coast range at Elk Creek and East Park, those from the central valley, and the birds that I did not see in the cowbird study areas but did see in similar habitats elsewhere in central California and that were noted by Miller (1951) are shown in figure 5.

The nesting season for each species was determined mainly from the records of eggs found in California as published in the species accounts of Bent's *Life History* series (Bent et al. 1942–68). For most birds, this includes data on the peak of laying also, the period during which eggs were laid in about half of the nests. I have included also in figure 5 the nesting dates of W. B. Davis (1933) from the northern Sacramento Valley. For the Red-winged Blackbirds, the breeding dates for the Elk Creek, East Park, and Sacramento Valley areas from Orians (1961) and Payne (1969a) are shown. Other passerine hosts of oak woodlands and grasslands of central California with recent life history information on breeding seasons in figure 5 are the Western Flycatcher (*Empidonax difficilis*) as studied by Davis et al. (1963); Blue-gray Gnatcatcher (*Polioptila caerulea*), by Root (1969); Rufous-sided Towhees (*Pipilo erythrophthalmus*), by Davis (1960); and Song Sparrows, by Johnston (1954).

Several common host species begin their breeding season several weeks before the cowbirds are in breeding condition, and these early nests escape parasitism. Birds with early, unparasitized nesting by early April include the Black Phoebe (*Sayornis nigricans*), Say's Phoebe (*S. saya*), Bushtit (*Psaltriparus minimus*), Wrentit (*Chamaea fasciata*), Bewick's Wren (*Thryomanes bewickii*), Rock Wren (*Salpinctes obsoletus*), Mockingbird (*Mimus polyglottus*), Blue-gray Gnatcatcher, Hutton's Vireo (*Vireo huttoni*), Orange-crowned Warbler (*Vermivora celata*), Yellowthroat (*Geothlypis trichas*), Western Meadowlark (*Sturnella neglecta*), Red-winged Blackbird, Brewer's Blackbird, House Finch, Lesser Goldfinch (*Spinus psaltria*), Chipping Sparrow (*Spizella passerina*), and Song Sparrow. Except for the gnatcatcher and warblers these are all locally resident species (including Say's Phoebe at Marysville). The early nestings of the Song Sparrows are of particular interest as these sparrows are important fosterers of cowbirds later in the season.

The breeding season of cowbirds in central California begins shortly after the insectivorous migrants have returned and begun nesting and while the resident birds are nesting as well. Bullock's Orioles (*Icterus bullockii*) arrived at Elk Creek between 6 and 15 April during 1963, 1964, and 1965, and Lark Sparrows (*Chondestes grammacus*) were first seen in pairs on 10 and 11 April during these years. Red-winged Blackbirds built their first nests in the Elk Creek area in these years on April 12 to 25. The beginning of cowbird laying in late April also matched the time of intensive singing in Yellow Warblers, though I did not find their nests. Laying of cowbirds coincides with the peak of nesting of many small passerines. The peak of laying of the cowbirds themselves in Bent's data falls within June, though at Elk Creek the season is somewhat longer, as nearly all cowbirds taken in May as well as in June were laying. A few foster species continue laying after the cowbirds stop. Some of these are birds whose peak of laying falls well within the period of cowbird laying, and the late nests probably do not represent a large proportion of the nests of these foster species. Thus cowbirds are laying for nearly all of the laying season of the Warbling Vireos (*Vireo gilvus*), Audubon's Warbler (*Dendroica auduboni*), House Finch, Western Wood Pewee (*Contopus sordidulus*), Western Flycatcher, and Traill's Flycatcher (*Empidonax traillii*). Because few cowbirds were collected during July and early August and because Bent's egg dates for California cowbirds extend to 21 July, some may continue breeding through the month of July. Locally, at Elk Creek and East Park, breeding evidently stopped by late June because the adult cowbirds all disappeared by then.

A few small passerines continue nesting into late July and August and one host species (the Mockingbird) may lay into early September. In addition, in the central valley, the Tricolored Blackbirds often have a second season of breeding in late September and October, occasionally laying as late as November (Payne 1969a). These late summer and autumn breeders do not appear to be parasitized.

DISCUSSION

The breeding season of Brown-headed Cowbirds in central California begins in late April and early May and ends in late June and July. Because each species of icterid in California has a slightly different breeding season as well as a different ecological niche, the time of breeding of the cowbirds appears to be an adaptive compromise between two major ecological factors: the breeding season of their fosterers, and the metabolic cost of the breeding and molting schedules. The time of laying is relatively long (2 months or more) and this coincides with the peak of breeding of most small songbirds. It seems likely that the availability of host nests has led to the observed timing of breeding in the cowbirds. On the other hand, the lack of breeding in early April and especially through July may follow from the greater energy strains that a more prolonged breeding season or a later scheduling of molt would involve.

BREEDING SEASONS OF COWBIRDS AND THEIR FOSTERERS

The seasonal changes in the numbers and kinds of breeding songbirds appear to have determined to a large degree the time of the breeding season in the parasitic cowbirds. Breeding coincides with the peak of egg-laying of most of the local host species (fig. 5), however, a few host species nest several weeks earlier than the earliest cowbird eggs are laid. Some passerines lay for several weeks after the last cowbird.

The apparent failure of cowbirds to breed when some of their hosts are laying early in the season may be in part due to early nesting dates for the hosts from southern California, where breeding may be a few weeks earlier than in the Sacramento Valley. Southern Californian culture more than northern includes egg-collecting, especially in the early part of the century. The nesting dates of 15 foster species of the cowbirds at Oroville, at the northern end of central California, nearly all begin in April or May and end by June (Davis 1933; fig. 5). Thus locally the cowbirds lay when almost all of their hosts are breeding. A tendency for the early egg dates in Bent to come from southern California may account for the early dates of the Mockingbird and House Finch, as I found eggs of these birds in central California no earlier than 17 April. The early egg dates for Song Sparrows probably come from the coast, where breeding begins earlier than inland. Johnston (1954) found most nests of Song Sparrows around San Francisco Bay in late March and April, with a few nests completed by late February, whereas the birds further inland in California did not nest until April. I found nests of Song Sparrows and Red-winged Blackbirds with eggs no earlier than 16 April in the central valley. However, even in southern California and along the coast, the cowbirds are not known to lay early in spring. Bent (1958) records no cowbird eggs earlier than April in California, so their apparent failure to parasitize the early nests is not entirely due to the wide area from which the nesting dates are taken.

The reason that cowbirds do not lay in early nests may be due in part to the poor quality of the early-nesting birds as foster species. Of the 18 birds mentioned above that are known to be hosts but are not parasitized in their first nestings, only half are species known to rear the young cowbirds to fledging.

The breeding season of cowbirds around San Francisco Bay in March and early April is of interest because an important foster species of cowbirds elsewhere, the Song Sparrow, breeds there in early spring (Johnston 1954). The molt and the minute gonads of all eight specimens of cowbirds taken in March in Alameda County in MVZ indicate that the Bay-area cowbirds, like those of the central valley, are sexually inactive in early spring. At Berkeley, the wild cowbirds are sexually active only after mid-April, laying mainly in May and June (Baptista 1972). Cowbirds caught in the valley and held in outdoor aviaries on local Berkeley daylength were active in singing as well as in gonadal development at the same time as free inland birds (Payne 1967). Similarly, in coastal Marin County, the Point Reyes Bird Observatory nesting records show only May and June egg dates for the cowbirds (R. M. Stewart, pers. comm.). Although cowbirds have been known in central California for less than 60 years (Grinnell 1934; Grinnell and Miller 1944), a lack of time to evolve a coastal race adapted to an earlier breeding season has probably not been very important causally in their nonparasitism of the early breeding sparrows. Even along the east coast and the Gulf coast of North America, where cowbirds have long occurred, the local salt-marsh sparrows, the Sharp-tailed Sparrow (*Ammospiza caudacuta*) and the Seaside Sparrow (*A. maritima*), are not parasitized, although the sparrows breed

in the same months as the local cowbirds (Friedmann 1963; Bent 1968).

The failure of cowbirds to parasitize these salt-marsh sparrows in California is probably due in part to the difficulty of finding nests in low, extensive marshes. Lone females that I have watched in other habitats spend considerable time looking about on elevated perches in shrubs and trees and occasionally, when other small birds flew into the vegetation beyond, I have seen female cowbirds turn their heads and follow their flight. They seem to find their hosts' nests by watching their hosts' activities from a high perch. Salt marshes on coasts on both sides of North America are low, flat expanses of vegetation almost exclusively of a single species of rooted plant, either *Spartinia* or *Salicornia* (Johnston 1956; Teal and Teal 1969) and there are miles of marshy land with no standing trees or shrubs from which a female cowbird might observe a bird building its nest. Searching in flight for nests or investigating each clump of plants most likely would take too much time and energy. The only instances of parasitized salt-marsh nests that Johnston found were both near the landward edge of the marsh near shrubby plants (Johnston 1960); perhaps those shrubs provided the lookout from which the cowbirds found the nesting birds.

Cowbirds that did successfully parasitize the early nesting songbirds might leave a few offspring to be reared by these fosterers, but those adults might not have any selective advantage over cowbirds that waited longer. Though she might leave a few young with the early hosts, the early female cowbird might well be somewhat exhausted looking for their infrequent, scattered nests. Her reproductive output later in the season or in future years might be lower than that of females that waited for the mass of spring migrants to nest. Probably the risks attending the search for nests and the production of eggs in early female cowbirds would outweigh the reproductive gains that her few early young would represent.

Cowbirds do not extend their breeding season much beyond mid-July because the birds that nest later in the summer in central California are too few in number and make poor foster parents. Cowbirds may parasitize the American Goldfinches and the House Finches in July, as both are successful fosterers in California earlier in spring and summer, but seldom parasitize the other late-nesting species. Those birds include the Black Phoebe, Rock Wren, Mockingbird, and Lesser Goldfinch. The phoebe is probably not an important foster species of cowbirds even in May and June because it is not numerous, and very few of its nests are parasitized (Friedmann 1963). Lesser Goldfinches are uncommon hosts, and Ellen Coutlee (pers. comm.) noted only one parasitized goldfinch nest among several dozen nests in southern California. The Rock Wren and Mockingbird also are uncommon hosts and rarely raise young cowbirds; no successful cowbird fledgings from Mockingbird nests and only one from the Rock Wren have been reported (Friedmann 1963, 1971). It is interesting that the Black Phoebe, Mockingbird, and Rock Wren in California all have a prolonged breeding season, extending from February or March into the last week of July to early September. The cowbird ignores these species in postponing its own laying in early spring, and they are inadequate as fosterers for the advance of the cowbird breeding season.

Tricolored Blackbirds are not parasitized by cowbirds in spring or in fall, though in spring at Elk Creek and Firebaugh several laying females were shot and netted at roost in the same marshes where Tricolored Blackbirds were nesting. Although thousands of clutches of Tricolored Blackbirds have been examined during the breeding season in spring, there have been no cowbird eggs found in their nests (Orians 1961; Payne 1969a). The closely related Red-winged Blackbirds are sometimes parasitized in California and, at least in other parts of North America, successfully fledge young cowbirds. The density of nesting Tricolored Blackbirds in a breeding colony may confuse or intimidate a cowbird much as it drives other species of blackbirds, such as Red-winged Blackbirds or Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), from the marshes (Payne 1969a), and this behavior may account for the lack of its parasitism by cowbirds.

BREEDING SEASONS AND ENERGY REQUIREMENTS

The breeding season of cowbirds is less directly imposed by the seasonal availability of food than it is in other species in which the parents feed their own young. In nesting birds, the breeding season as well as the brood size are determined in large part by the seasonality of food which the parents provide to the young. Since cowbirds parasitize many species throughout the seasons, the potential

duration of their breeding season might be considerably longer than that of nesting species that are dependent on certain seasonal foods for rearing their young. Cowbirds, like their hosts, require nutrients and minerals to make eggs. Perhaps also the breeding males require more energy to maintain their mating sites than the nonbreeding males do simply to exist, and female cowbirds may spend much of their time searching for nests instead of feeding.

Indirect evidence for a considerable amount of expenditure of energy in breeding in the cowbirds is available not only in the time available for feeding and the energy used for breeding activities but also in the molt cycles and in the seasonal changes in body weight and fat deposition in these year-round residents of central California. In cowbirds gonadal development is delayed in comparison to the time of gonadal development of other blackbirds. In contrast to the cowbirds, two marsh blackbirds living in the same habitat in central California lack a prenuptial molt and begin their seasonal gonadal development in January and may have sperm by late February (Payne 1969a). The separation in time of molting and gonadal development may suggest that each of these processes involves ecologically significant increases in energy requirements. Similarly, the nonoverlap of the onset of late summer molt with the laying schedule suggests that breeding and the postnuptial molt are incompatible events. The decreases in body weight and fat deposits of females at the end of the breeding season and the beginning of molt also imply heavy taxation on their energy reserves as a result of a long breeding period. Perhaps a relative shortage of energy before and after the observed intensive laying season constrains any extension of the breeding period in cowbirds even though some hosts breed before and after the cowbirds. The higher annual mortality of adult females than of adult males (Fankhauser 1971; Darley 1971) also may be a result of their intensive laying efforts, involving production of 72 g of eggs by a 36-g female.

Because few songbirds nest later than July and because these largely are not good foster species at any time of year, the reproductive gain of extending breeding into August and September would be small. Extending its breeding season would involve more time searching for food in a drying, deteriorating habitat (central California is brown by summer) and the energetic cost of postnuptial molt would be greater at the same time. Cowbirds in California require considerably less increase in their energy requirements for molting at temperatures typical of late summer than they do at temperatures of late October and November, a difference of about 100% in the increase above the standard metabolic rates of nonmolting birds at the same temperatures (Lustick 1970). Molting at colder temperatures involves considerably more production of metabolic heat than at warmer temperatures because of the lesser insulation and the greater area of vascularized skin when the plumage is dropped and new feathers are grown (Lustick 1970). Late summer is also a time of clear skies in the central valley. Since Brown-headed Cowbirds may exist with lower food requirements under direct radiation of sunlight than under cloudy skies (Lustick 1969), the sunshine as well as the warm temperatures may enable the cowbirds to molt at a season when molting is least demanding on the birds' resources. The increased energy cost of molting that would accompany extended breeding would provide stronger selective coercion for ending the breeding effort of cowbirds by midsummer than the low returns of late deposits of eggs in the nests of late-nesting fosterers would for continued laying.

COWBIRD BREEDING SEASONS IN OTHER AREAS

Brown-headed Cowbirds in northern lower Michigan have a shorter breeding season than do those in central California. They begin breeding in late May, 3 or 4 weeks later than in central California, most likely because the vegetation does not leaf out until mid-May and most migrant birds return and nest in late May and June (Payne 1965). The cowbird breeding season in Michigan ends at about the same time as in California, and as on the West Coast, they miss some of their later-nesting foster species, probably because late July and August is the optimal time for an energetically economical molt. In Kansas and Oklahoma, the breeding season of cowbirds outlined by Johnston (1964) and Sutton (1967) is nearly the same as in California at the same latitude, in spite of the extreme temperatures of the midcontinent. Again, the timing may be due to the nesting of resident birds and the return of nesting migrants in April and May, as well as the energy requirements of molt at various temperatures. If any adaptive differences in breeding seasons of cowbirds in North

America occur in regions where birds have a prolonged but generally later season than in California and the Great Plains, these might be expected in Arizona. Here several potentially good foster species breed with the late summer rains, but the dates of independent young of cowbirds reported by Phillips et al. (1964), August and September, suggest laying in May and June, and Brandt (1951) found eggs only in May and June. In the Palouse hills of eastern Washington, cowbirds lay from mid-May to early July (King 1954). Evidently cowbirds across the continent are closely tied to a schedule of breeding in late spring and early summer.

COMPARISON OF BREEDING SEASONS WITH OTHER PARASITIC BIRDS

The breeding season of other species of parasitic birds have been studied in less detail than have those of Brown-headed Cowbirds. Some interesting differences between species should be pursued in further studies. Lack (1963) notes that the common Cuckoo (*Cuculus canorus*) in England arrives and breeds after several foster species have already laid. He suggests that cuckoos must await an abundance of caterpillars before they can build up the energy reserves necessary for the formation of their eggs so that they can begin to lay. In southern Africa, some species of parasitic cuckoos may retain large gonads throughout the year (Payne 1969b; Immelmann 1969), and some honey-guides have large gonads and also maintain their call-sites and mating-sites throughout the year as well (Payne 1969b). The host-specific parasitic finches in the indigobird species complex (*Vidua chalybeata* and its relatives) breed across different latitudes of Africa at the same time as their respective local populations of hosts, and they are in breeding plumage only during the breeding season of their local hosts (Payne 1973a). The less host-specific finch *Vidua macroura* in Rhodesia develops its gonads seasonally a few weeks before one of its common foster species, *Estrilda astrild*, in apparent anticipation of the foster finches' breeding season (Immelmann 1969). These brief sketches available from other parts of the world suggest a diversity of timing mechanisms in parasitic birds which enable them to breed at the same time as their hosts. Brown-headed Cowbirds are known to respond experimentally with gonadal growth to long daylengths, and hence they synchronize their breeding cycles with those of their hosts by responding to precisely the same environmental changes, the increasing length of days in spring, as do the host species (Payne 1967, 1969a). It would be of interest to determine the way in which other kinds of parasitic birds time their breeding seasons to fall at the same period as the breeding of their hosts.

SUMMARY

Brown-headed Cowbirds in central California breed in late spring and early summer, mainly from early May to late June. Local differences in the time when breeding ceases were related to the time of local seasonal droughts, with activity lasting for a few weeks longer in the irrigated central valley than in the dry inner coast range. The gonads of both sexes are small and inactive through late summer, autumn, and winter. Seasonal gonadal development begins in March, when some other icterids in central California are already in breeding condition. A partial prenuptial molt in late winter is associated with the delay in the start of gonadal development in spring. A complete postnuptial molt follows the end of breeding in late summer. Seasonal changes in fat and weight suggest that breeding may be energetically costly to the cowbirds.

Observations of the behavior of cowbirds indicate that they may be polygynous, with a few adult males servicing several females. Mating is restricted to special perches that are usually used by single adult males. First-year males appear not to hold mating sites, and they have significantly smaller testes in the breeding season than do the older adults. The numbers of females with eggs in the oviduct and the frequency of laying indicated by gross examination of the ovaries of cowbirds indicate that each female lays about 30 eggs in each breeding season; the weight of the eggs laid in a season is about twice that of a female.

The Brown-headed Cowbirds begin laying in late April and early May; they miss the hosts that nest earlier. About half of the species breeding before May are poor fosterers that have never been recorded to rear a young cowbird successfully. The breeding season of cowbirds coincides with the peak of nesting of both residents and migratory species such as the flycatchers, vireos, and warblers. Cowbirds continue nesting later in summer than other icterids in the same area, and this late phase of their nesting coincides with the late nests of some of their important foster species such as the Blue-gray Gnatcatcher, Warbling

Vireo, and Yellow Warbler. Small passerines nesting after mid-July are mostly species that are poor fosterers for cowbirds. The loss of late eggs laid in nests of these birds would probably result in a selection against late summer breeding in the parasitic cowbirds, because the late-breeding cowbirds would have expanded considerable energetic cost and risk of mortality with little reward. Breeding is terminated before the latest hosts have nested also because of the economic advantages of summer molt; the experimentally demonstrated energetic cost of molt at late summer and early autumn temperatures is only half what it would be at late autumn or early winter temperatures. The breeding season of Brown-headed Cowbirds appears to be a compromise between the reproductive gains to be expected in terms of young fledged from hosts breeding in the different seasons, and the increased survival risks and energetic costs that would be associated with an earlier onset and a later termination of breeding.

ACKNOWLEDGMENTS

Most of the field work and collections were made while I was at the Museum of Vertebrate Zoology, University of California, and I am grateful especially to the late A. H. Miller and to H. A. Bern for their advice. Examination of MVZ specimens was provided by N. K. Johnson. R. M. Stewart made available cowbird laying records of the Point Reyes Bird Observatory. The illustrations were prepared by Martha Lackey. During part of the study, I received financial support through predoctoral fellowships from the National Science Foundation.

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Accepted for publication 20 October 1971.