

COMPARATIVE BREEDING BEHAVIOR OF LESSER AND LAWRENCE'S GOLDFINCHES

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Studies of comparative behavior are important not only for learning more about given groups of animals but also for clarifying phylogenetic relationships among them. In the avian families Fringillidae and Ploceidae, parallel evolution of morphological and physiological adaptations to a seed-eating existence has made the investigation of their evolutionary relationships quite complex. Studies of the behavior of these birds, emphasizing a comparative approach, have therefore become critical from a taxonomic as well as a strictly behavioral viewpoint. Members of the subfamily Carduelinae (goldfinches and allies) occur in both the Old and New Worlds and have been assigned by most authors to the family Fringillidae. Various facets of the breeding behavior of this group of birds have been studied in several representative species. Aspects of the natural history (such as distribution, habitat preference, attentiveness to nest and young) of these birds have usually been emphasized, while descriptions of the stereotyped displays so important in comparative studies have not. The present paper seeks to provide a better understanding of the relationships between two sympatric species of North American carduelines, the Lawrence's and Lesser Goldfinches (*Spinus lawrencei* and *S. psaltria*). Reference will be made to other members of the subfamily, especially to the American Goldfinch (*S. tristis*), for comparative purposes.

METHODS

Field observations were made during the spring and summer of 1964 (52 days) and 1965 (55 days). Additional observations were made on five days in the spring of 1966. Although observations were made in the field at all times of day, they were usually confined to the morning hours from 06:00 to 12:00. The birds were watched with 7 × 50 binoculars and 20 × telescope. Because natural cover was quite dense and the birds became accustomed to my presence after a few days of observation, a blind was unnecessary.

In addition to studies in the field, eight goldfinches (five *lawrencei* and three *psaltria*) were kept in captivity at the University of California at Los Angeles from August 1964 to January 1965 and eight birds (three *lawrencei* and five *psaltria*) from September 1965 to June 1966.

Agonistic and social behavior of captive birds was observed periodically from August 1964 through March 1966. The birds were separated as pairs in the spring of 1966 in order to allow close-range observations of courtship displays and vocalizations.

Tape recordings of call notes and songs of both species were made in the field and laboratory, using a battery-operated tape recorder (Transflyweight, Amplifier Corporation of America, and Uher 4000 Report-L, Martel Corporation) with tape speeds of 7½ and 15 inches per second, Electro-voice 666 dynamic microphone, and parabolic reflector. These recordings were analyzed with a "Sona-graph," Model R (Kay Electric Company). A detailed treatment of the vocal repertoire of the two species will be reported in a separate paper.

STUDY AREA

Field work was conducted about five miles east of Newhall, California, in Placerita Canyon (latitude, 34°22' N, longitude, 118°27' W, elevation 1800 ft.). This canyon includes a stream that flows year-round, providing a permanent water supply for resident animals. Weather data were obtained from the USDA Forest Service at the Newhall Ranger Station. Temperatures are moderate throughout the year although late-summer highs sometimes reach 42°C and mid-winter lows dip to -5°C. For 1964, a representative year, average monthly highs ranged from 16°C in December to 34°C in July; average lows ranged from 0°C in February to 12°C in July. Rainfall averages about 10-15 inches (25-38 cm) per year, mostly during winter and early spring.

For the most part, Placerita Canyon shares the typical chaparral vegetation common to the surrounding canyons. Dominant plants include chamise (*Adenostema fasciculatum*), wild buckwheat (*Eriogonum fasciculatum*), white sage (*Salvia apiana*), black sage (*S. mellifera*), mountain lilac (*Ceanothus* spp.), and California sagebrush (*Artemisia californica*). The permanent stream supports a restricted riparian community of mule fat (*Baccharis* sp.), willow (*Salix* spp.), western sycamore (*Platanus racemosa*), common cottonwood (*Populus fremontii*), and white alder (*Alnus rhombifolia*). This stream is bordered by oak woodland (mainly coast live oak, *Quercus agrifolia*), within the protected canyon. In addition, the area is bordered on the east by open fields where cattle graze and on the south by a restricted coniferous forest with widely separated big-cone spruce (*Pseudotsuga macrocarpa*). The stream and associated flora support an abundance of animal life including over 70 species of vertebrates.

REPRODUCTIVE BEHAVIOR

All three North American goldfinches in the genus *Spinus* occur in southern California. Although the ranges of these closely related

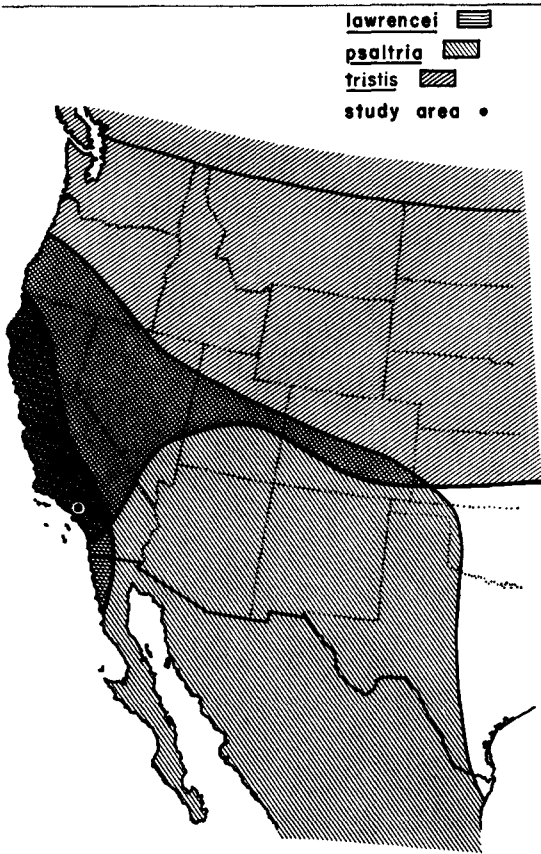


FIGURE 1. Distribution of the three North American goldfinches during the reproductive season.

species overlap (fig. 1), their ecological preferences during the breeding season tend to separate them to some extent. The American Goldfinch occurs in riparian woodland, grassland, or chaparral associations, while the other two species breed mainly in chaparral and oak woodland. Lawrence's Goldfinch is restricted to wooded areas bordering permanent water sources, while the Lesser Goldfinch ranges more widely. In the birds studied by the author, the Lesser Goldfinch was found in dry chaparral at distances as much as one-half mile from water while the Lawrence's remained within a few hundred feet of the stream. During the spring of 1965, the number of birds of each species seen in the oak woodland and chaparral were recorded (figs. 2 and 3). The restriction of *lawrencei* to the oak woodland and the more extensive range of *psaltria* are clearly indicated in these figures. No American Goldfinches were seen at the study area.

Bird-banding records of the United States Fish and Wildlife Service indicate that this breeding segregation is widespread. Nearly 1000 goldfinches were banded west of 100° W

TABLE 1. Stations reporting more than one species of goldfinch banded or recaptured from 1955 through 1963 in the western United States, April through September.

Station		Numbers of goldfinches		
N Lat.	W Long.	<i>lawrencei</i>	<i>psaltria</i>	<i>tristis</i>
33°10'	117°10'	9	68	25
33°20'	117°30'	2	48	—
33°40'	115°40'	155	238	2
34°00'	118°10'	1	10	—
34°10'	117°10'	8	1	—
34°10'	118°00'	119	265	—
35°40'	124°00'	53	8	—
36°20'	121°40'	1	9	—
36°40'	121°30'	4	9	—
36°50'	122°00'	3	268	2
37°20'	121°50'	2	36	—
37°30'	120°50'	22	4	5
37°40'	122°10'	—	2	5
37°50'	122°30'	2	2	—
38°00'	122°00'	—	8	142
39°40'	121°30'	—	29	7
44°30'	123°10'	—	5	330
45°20'	122°30'	—	109	25

longitude between 1955 and 1963. Only 18 localities reported more than one species banded or recaptured during the breeding season (April through September). These reports are summarized in table 1. The data show that, when sympatry occurs during the breeding season, either *psaltria* or *tristis* is abundant but not both. In addition, *lawrencei* and *tristis* seldom occur in the same area, although *lawrencei* and *psaltria* often occur together.

At Placerita Canyon, Lesser Goldfinches can be found at all times of the year but are rare during the winter months. Large flocks (20–30 birds) begin to arrive in late March, and by April pairs have formed and breeding is under way. The Lawrence's Goldfinches are not found in this area during the winter and arrive after the Lesser Goldfinches have already become numerous. Pairs are formed quickly, however, and nest-building often begins first in Lawrence's Goldfinch. Both species are abundant in Placerita Canyon during the breeding season, and active nests of the two species are sometimes found in the same tree. The reproductive cycles of the two species for 1965 are shown in figure 4.

PAIR FORMATION

In both species, males and females arrive in the breeding area together in large flocks, and pairs are formed within 10–14 days thereafter. Flocks of the Lesser Goldfinch break up through increased activity and agonistic behavior in both sexes. The males are especially aggressive toward one another, and fighting involving body contact is often seen. Two

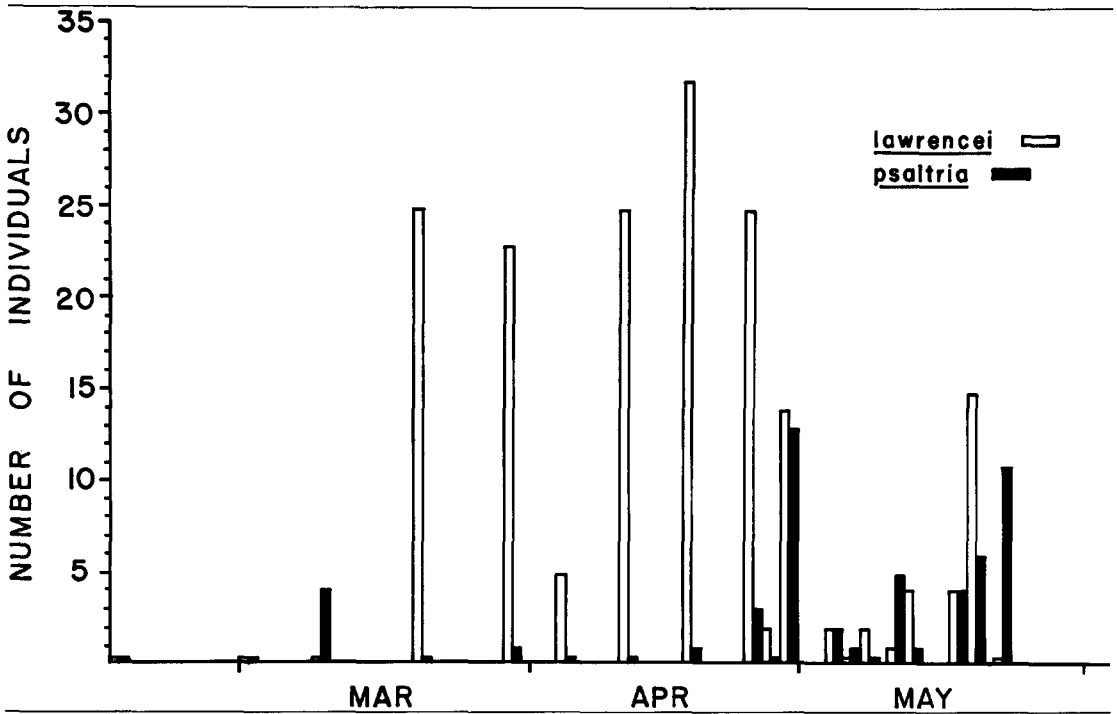


FIGURE 2. Number of goldfinches seen in oak woodland in spring, 1965. Nineteen days of observation, about 3½ hours per day.

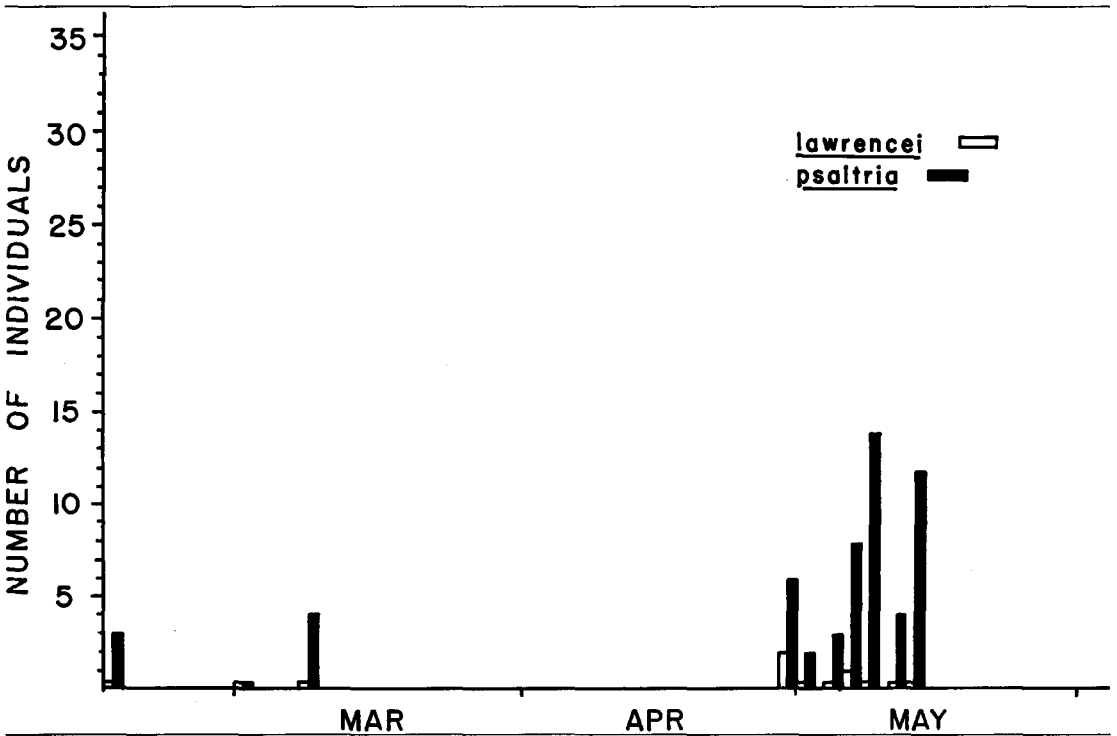


FIGURE 3. Number of goldfinches seen in chaparral in spring, 1965. Ten days of observation, about 3½ hours per day.

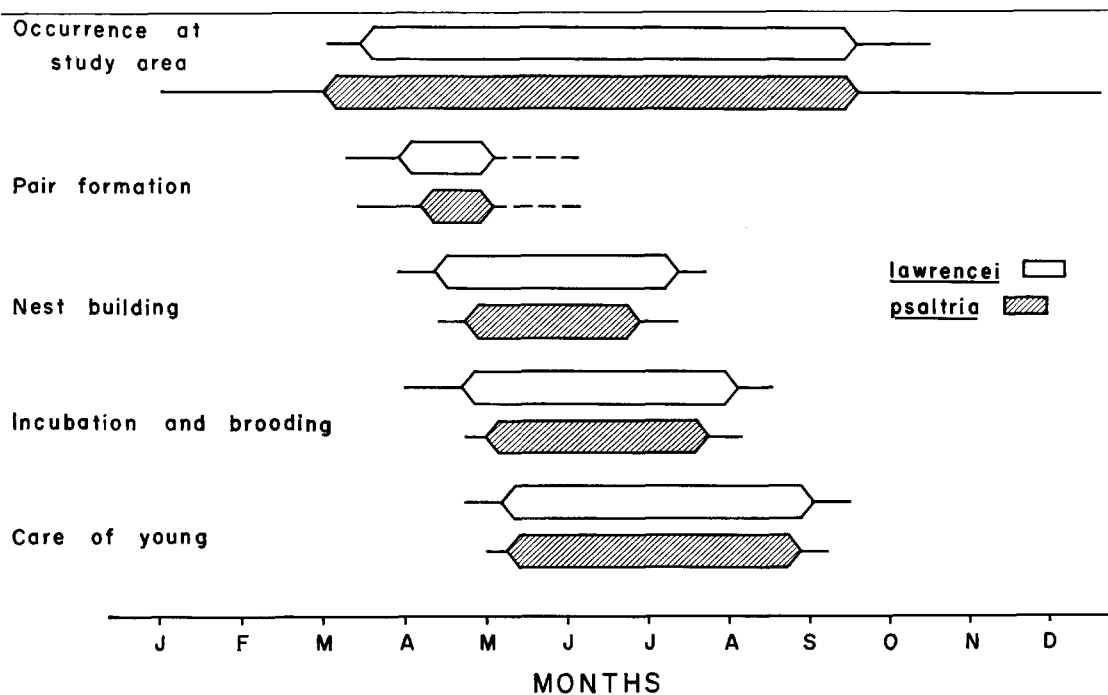


FIGURE 4. Reproductive cycles of Lawrence's and Lesser Goldfinches. Lines = duration of activity in time; bars = peak periods of activity; dashed lines = uncertain dates. Data based on observations of 25 pairs of *lawrencei*, 24 pairs of *psaltria*.

males may flutter upward from three to seven meters with beaks and feet extended toward each other, beating one another with their wings, grappling with the feet, and pecking at each other's heads. In one to two weeks the males have spaced themselves, maintaining a distance of at least 17–20 meters between one another except when foraging or drinking. Each solitary male stations himself near the top of a tall tree and makes himself conspicuous by perching in the open and uttering occasional short songs and penetrating Courtship Calls (figs. 5b and 5d). Females in the area are apparently attracted to the males by both visual and auditory cues. If a female comes near a perched male, he utters the Courtship Call and often follows the female when she flies. At this time, the male and female may be seen flying together, keeping from two to eight meters apart. Although the female usually leads these flights, the male may sometimes be seen ahead of the female. These Following Flights are accompanied by a series of Courtship Calls given by the male. The female is normally silent. As courtship progresses, the Following Flights develop into high-intensity Chasing Flights, the male following the female at a distance of two meters or less and the two birds darting rapidly in and out through dense foliage. The two perch

within one meter of each other; birds are seldom seen alone even in flight.

Pair formation in the Lawrence's Goldfinch is somewhat different from that in the Lesser Goldfinch. The initially large flocks of *lawrencei* (10–15 individuals) soon break up as each male becomes less tolerant of other males and spends more and more time singing loudly from the tops of the trees. For a period of only five or six days, *lawrencei* are extremely active, flying about and vocalizing almost continually. The male song and activity seem to be directed toward females, and extremely noisy groups of five or six individuals are common in the tops of the oaks. These groups usually include two to three females and three to four highly active, singing males. During this period the small groups often fly about in apparent excitement. The males sing loudly, supplant, and chase one another while the females perch quietly nearby. Occasionally a female supplants a male and may chase him. No agonistic behavior was seen, however, between females. In addition to supplanting and chasing, the males occasionally engage in fights as described for *psaltria* in which both birds fly vertically upward for 5–10 meters and then straight down again with much flapping and beating of one another with the wings, grappling with the feet, and pecking. The fights

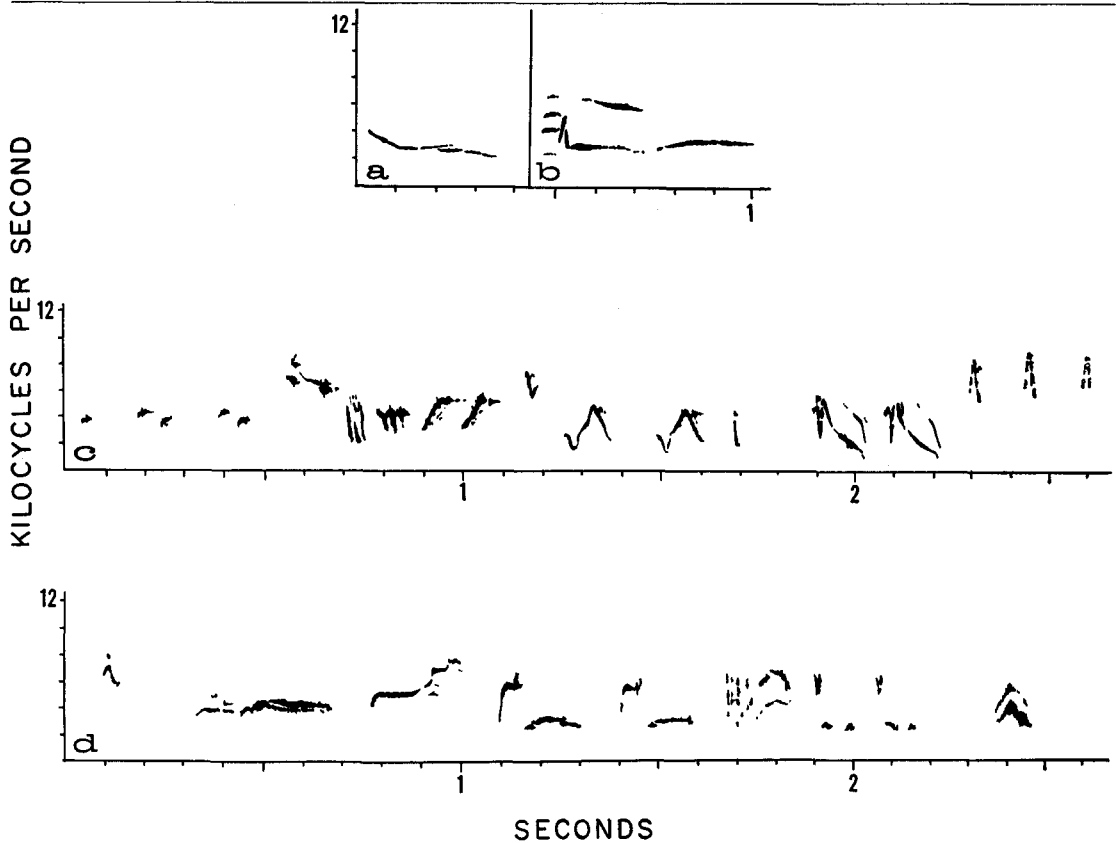


FIGURE 5. Pen-and-ink tracings of sonograms of goldfinch vocalizations. a. Courtship Call of male *lawrencei*; b. Courtship Call of male *psaltria*; c. song of male *lawrencei*; d. song of male *psaltria*. Time (in tenths of seconds) is indicated on the horizontal axis. Frequency in kilocycles per second is indicated on the vertical axis (each mark represents 2 kps).

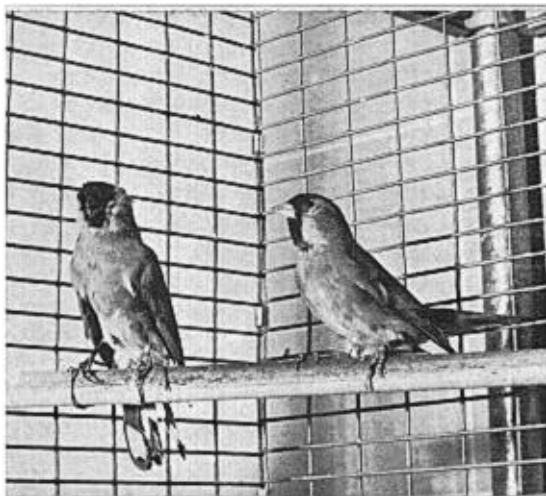
are followed by further supplanting with sharp *caus* and Flight Contact Notes interspersed with song. On alighting, males often flick their closed wings. No more than two males at once were ever seen engaged in such a fight even though the two usually returned to the small group and often flew away with three or four of the associated birds.

Aggressive song (fig. 5c) is usually very loud and accompanied by the high-intensity Song Display. The male perches facing his opponent with body feathers sleeked, throat feathers fluffed, neck extended, wings lowered, and tail raised and fanned (fig. 6a). The bird often pivots alternately to the right then left while facing forward, sometimes bending the tail stiffly to one side or the other.

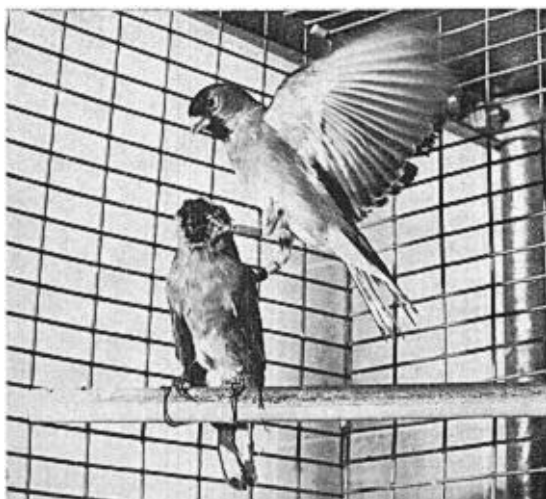
As Linsdale (1957) points out, *lawrencei* males are considerably less aggressive on the whole than are *psaltria* males. In the birds that I studied, however, the *lawrencei* males were extremely aggressive (more so, perhaps, than *psaltria* males) for the short period of five or six days while flocks were disintegrat-

ing. In fact, during three hours of observation on 13 April 1965, at the height of pair-formation activity, there was only one male *lawrencei* observed for at least five minutes which did not engage in combat or agonistic displays with another male. In a laboratory situation a stuffed male mounted in the high-intensity song posture was presented to a pair of *lawrencei* in a small (1 m × ½ m × ½ m) cage. After giving loud song accompanied by the typical high-intensity Song Display, the male flew at the stuffed bird, pecked feathers from it and tore at its head with its feet (fig. 6b). The *lawrencei* male is therefore capable of intense aggression, but this aggressiveness is usually not manifested under natural conditions since subordinate birds retreat quite readily.

Attraction of the female, as in the Lesser Goldfinch, depends on a specific Courtship Call (fig. 5a). A male *lawrencei* approaches a female, perches within one meter of her, and utters the Courtship Call. The female responds with a short series of Contact Notes,



a



b

FIGURE 6a. High-intensity Song Display of male Lawrence's Goldfinch (right) to stuffed male in simulated singing posture; b. male *lawrencei* attacking stuffed male.

and the two often perch or fly together, both giving Contact Notes. The male occasionally repeats the Courtship Call when perched near the female. Following Flights as seen in the Lesser Goldfinch are common, and may be led by either the male or the female. Pairs of Lawrence's Goldfinches, however, were not seen in high-speed, darting chases.

In the birds studied at Placerita Canyon, small flocks broke up into pairs over a period of only about one week. After this time they were found perching or flying in pairs, the male and female usually about a meter apart.

COURTSHIP

Repeated chasing between the two members of a pair as described above characterizes the initial stages of courtship in the Lesser Goldfinch. This is replaced by Billing as the members of the pair become more tolerant of each other. Since the two birds perch, fly, and feed together, they are very near each other at all times. Billing is usually initiated by the female. She gives a series of very soft calls while facing the male. He may approach her immediately, but usually in the early stages of courtship he first becomes agitated, preens and flicks his tail. Soon, however, he leans toward the female with neck outstretched, and they move toward each other. When the tips of the bills touch, a very soft, continuous *tee-tee-tee* is heard, and the two mandibulate rapidly, each opening and closing the bill about one millimeter. This Billing may continue for as long as five seconds before one or the other flies away. After two or three days, Billing develops into true Courtship Feeding in which the female takes regurgitated food from the male's bill. In all cases, although the birds are perched close together, the female apparently induces Courtship Feeding, indicating her readiness to the male by giving the soft *tee-tee call*.

The male *lawrencei* are subordinate to the females and approach them only hesitantly. In the field, the male usually alights one to two meters from the female. He then hops or sidles toward her a few centimeters at a time until he is only about five to six centimeters away. He usually approaches with legs flexed and with the side of his body toward the female. This stance not only indicates a nonaggressive attitude but also may directly inhibit aggressiveness in the female, who is likely to peck at the male as he comes closer. Although the male shows readiness to engage in courtship behavior by uttering the Courtship Call or song, it is again the female who initiates Billing and Courtship Feeding by flying to and perching near the male. The two face each other, and the male approaches the female slowly. Each bird stretches its body toward the other to the fullest extent until at last the tips of the bills are in contact. As in *psaltria*, mandibulation results only in Billing during these first attempts. Soft Contact Notes are given continuously. The first periods of Billing are extremely short (three or four seconds) and may be terminated by the female's sharp pecks at the male's head. When this occurs, the male retreats a few centimeters and adopts a submissive posture with legs fully flexed, neck flexed, and body feathers fluffed. In

some instances, both birds may fluff the body feathers and lower and quiver the wings. Contact Notes are given by both, and the male may give a short song. After several repetitions, food is regurgitated by the male and is taken by the female. In addition the two become more tolerant and do not fly away or show agonistic behavior unless one or the other makes a sudden movement.

Feeding of the female by the male is continued throughout nesting in both species. It thus serves to maintain and strengthen the pair bond as well as to provide food for the female during incubation and the first few days of brooding.

NEST-SITE SELECTION

As soon as pairs have separated from the flocks, they begin inspecting potential nest sites, hopping and flying about and peering into forks among the branches. In both species the female leads these explorations, hopping in and out of prospective crotches, making nest-building movements in some by crouching and moving her abdomen from side to side, and carrying bits of nest material. During these activities, the male is always close by and continually calls and sings. There seems to be no definite restriction of the area which the female frequents, and she does not seem to be conspicuously restrained by the activities of the male. On 9 June 1964, for example, a pair of Lesser Goldfinches was seen inspecting branches and was followed for over 100 meters along a stream, the female hopping in and out of crotches and leading the male from one tree to another. There were no other goldfinches nearby, however, and this probably allowed more freedom of the pair under observation.

The nest is placed in a fork of three to five branches usually only one or two meters from the tip of a main branch, and often in drooping branches. Early nests of the Lawrence's Goldfinches are often found in sycamores or mistletoe clumps, but as the season progresses oaks are used more and more commonly. The Lesser Goldfinches, on the other hand, select sycamores and large shrubs as well as oaks throughout the breeding season. The nest sites of *lawrencei* for the years 1964 and 1965 averaged 7.60 meters above the ground (range, 3–13 m; $N = 25$); *psaltria* sites for these years averaged 3.79 meters above ground (range 2.7–8 m; $N = 24$).

NEST CONSTRUCTION

The open, cup-shaped, compact nest typical of goldfinches is constructed by both Lawrence's and Lesser Goldfinches. The nest is

built almost entirely by the female, and only occasionally does the male even carry nest materials. In both species the female makes regular trips as much as 100 meters from the nest site in order to collect building materials, and she is usually accompanied by the male. Nest construction requires four to eight days.

Psaltria females collect oak leaves, catkins, strips of bark, cocoons, and webs for their nests. A loose part of the plant or web is grasped with the bill; the neck is then extended as the female raises her head. If this movement is not effective, the female leans away from the attached piece and tugs by bending her neck sharply away from it while grasping the free end in her bill. A branch near the perched female may be held with the feet as she strips pieces from it. The bird may also move along a branch or *Yucca* leaf as she strips off long fibers, releasing the strip and grasping it again near her feet, pulling it upward as before, and repeating the process until the strip is as long as 45–50 centimeters. Tall grasses which can be collected by a female perched in a low bush may also be included in the nest.

The *lawrencei* females in Placerita Canyon searched on the ground for nest materials, and the male sang loudly from a perch one or two meters above his mate or accompanied her closely on the ground. When the female is about to fly, she utters the Flight Contact Note, and the male immediately joins her as they fly off together. Nests of this species included leaves and shoots of small forbs (especially Geraniaceae) in addition to short pieces of grass. *Lawrencei* females were often seen grasping small forbs and grasses with the bill and tugging at them until they broke off at the base. The entire shoot (3 to 5 cm in length) was then added to the nest.

In both species a few fine fibers, hairs, or feathers are added as a lining to complete the nest.

COMPETITION FOR NEST SITES

Although apparently suitable sites for nest placement seem numerous, activity of one nesting pair usually attracts other goldfinches. Since nest sites are often similar in both species, some interspecific competition is apparent. In one instance on 1 May 1965, a nest under construction (about one day old) was visited regularly by two females, one *psaltria* and one *lawrencei*. Each hopped into the nest and moved about in it for several seconds before hopping out. Only the *psaltria* female, however, was seen to add materials to the nest. Both females were accompanied by their mates who sang from nearby perches while

the females were in the nest. If both pairs were present at the same time, the *lawrencei* were chased away by the *psaltria*, the latter giving sharp alarm cries as well as pecking and chasing the *lawrencei* pair. When the nest was visited three days later, no *lawrencei* were found in the vicinity, and the resident birds were *psaltria*.

As a rule the resident pair repels congeneric intruders as well as predators. In *lawrencei* the female is the more active in this respect at the beginning of the period of nest construction, but a strange pair of *lawrencei* may approach to within two meters of the nest before being pecked at and chased by the resident female. Her mate follows in the chase but does not usually participate actively at this stage of nesting. Later, the male plays the most active role in defending his territory and the included nest site. Nest-construction activity of *lawrencei* pairs, especially late in the season, attracts others members of the species, and individuals or paired birds sometimes fly with the nesting pair as materials for the nest are being collected. Although the nesting pair is fairly tolerant of these onlookers, one or both of them may show aggression if the intruding birds come near the nest site and chase them away with sharp *caws*.

Early *psaltria* nests are usually defended by the male, who fights with and chases intruding males. The female usually perches nearby and may give soft *tee-tee-tee* calls, but she seldom joins the fighting. If she does so, she directs her aggression toward the female member of an intruding pair. It may be noted that although *psaltria* pairs were on several occasions seen approaching *lawrencei* nests which were under construction, the reverse was never observed (except perhaps in the case cited above on 1 May 1965).

PRECOPULATORY AND COPULATORY BEHAVIOR

During nest building and until the clutch is complete (three to five eggs), precopulatory and copulatory behavior occurs in addition to Courtship Calls and Courtship Feeding. This behavior usually takes place near the nest, among the branches of the nest tree, and in all cases observed was between 06:00 and 09:00.

In the Lesser Goldfinch precopulatory activities are extremely intense, with both members of the pair calling loudly and flying about near the nest. The female crouches with her legs fully flexed, neck flexed and head raised, giving constant *tee-tee-tee* calls. Meanwhile the male flies about excitedly, keeping at least one meter away from her at all times, and uttering the Courtship Call or Courtship Song while he moves from branch to branch, flicking his wings and tail. When perching, he often assumes the Pre-

copulatory Display with legs extended, body erect, contour feathers sleeked, and tail lowered and fanned. The female's activity becomes progressively more intense until it reaches a peak, and she constantly utters the *tee-tee-tee* call, raises her head and tail, and flutters her wings. The male then flies to her and mounts, continually fluttering his wings to maintain balance. Actual cloacal contact is maintained for only two or three seconds and then the male flies away. Copulation is usually attempted several times in rapid succession while the pair is extremely active as described above. During this series there may well be more than one successful copulation. As the female becomes quieter, the male ceases to approach her, and both usually fly off together, the female often in the lead, giving constant Flight Contact Notes.

Only one copulation of a *lawrencei* pair was observed. As in *psaltria* the pair flew about excitedly in the nest tree, giving constant vocalization. The female uttered *chee* notes at regular intervals of about one second, vibrated her wings, and raised her head and tail when she alighted. The male gave Contact Notes and led the female in short flights from one tree to another. The female seemed to initiate copulation, however, and flew to within three meters of the male, facing him while soliciting, before copulation was attempted.

INCUBATION AND BROODING

The details of incubation and brooding will only be summarized here since nesting studies of the North American goldfinches have already been published (see, for example, Shepardson 1915, and Linsdale 1950, for *lawrencei*; Chambers 1915, for *psaltria*; Walkinshaw 1938, and Gross 1938, for *tristis*). In all three species, one egg is laid each day. Incubation begins intermittently after the first two or three eggs have been laid, and continuous incubation is begun before the clutch of three to five eggs is complete. This means that the eggs do not hatch at the same time and that there may be a one- or two-day difference in age between the youngest and oldest nestling. Unlike many passerines, the female is in almost continuous attendance at the nest during the 12-13 days of incubation. In a pair of *lawrencei* observed by Linsdale (1950), for example, the female was on the nest for 97 per cent of the time during 56 hours of observation over a period of 13 days. She made only 27 trips away from the nest during this time and was gone less than six minutes on 23 of them. During incubation, the female goldfinch is fed regurgitated food by her mate about once an hour. Since she seldom leaves the nest, we must assume that this food provides practically all her nourishment. The male always gives Contact Notes as he approaches the nest and often gives Courtship Calls or song. The female responds with a typical Begging Note and vibrates her wings as the male approaches.

Very young nestlings are brooded almost

continually. The male continues to feed the female about once each hour, and she, in turn, feeds the young a portion of this food. After about five days, the female begins to spend time off the nest foraging with the male. At this time the adults' diet consists primarily of seeds, but insects (mostly Aphidae) are also taken. The pair usually returns to the nest together, and the adults take turns feeding the young. Fecal sacs are eaten by the adults (usually the female) for the first four or five days after hatching. Subsequently the young birds void over the edge of the nest, and the outside of the nest soon becomes caked with droppings. The young remain in the nest for 12-15 days before fledging.

CARE OF FLEDGLINGS

For the first few days after fledging, the young stay near the nest. They are usually quiet and motionless until they become hungry. Loud Begging Notes are then given even if adult birds are not in sight. The adults usually arrive shortly to feed them, and the young immediately begin fluttering their wings and hopping about while calling loudly. In both species the adults and young fly about excitedly until feeding is completed. The adults then fly off to forage while the young return to quiet perching. By the end of the first week or so after fledging, however, the young birds accompany the adults to foraging areas and are fed whenever they give the insistent Begging Calls. These small family groups do not return to the nesting territory, and they remain together until the end of the season when large flocks are again formed as migration begins. Linsdale (1957) indicates that the family groups of *psaltria* at the Hastings Reservation disbanded early and that separate groups of males and of juveniles were common before migration. In the *psaltria* I observed, groups of juveniles were also common; but there was usually a single adult male or female in the vicinity, and these were therefore assumed to be family groups.

RESPONSE TO ENEMIES

The most common nest predators in the study area are Cooper's Hawks (*Accipiter cooperii*), Scrub Jays (*Aphelocoma coerulescens*), and Grey Squirrels (*Sciurus griseus*). In addition, goldfinch nests are parasitized by the Brown-headed Cowbird (*Molothrus ater*). On one occasion a Cooper's Hawk called and alighted in an area where *psaltria* nests were abundant. About 20 *psaltria* gathered in a loose flock about the hawk—both in the same tree and in adjacent trees—and gave continual, drawn-out

Hawk Calls. These continued for nearly half an hour before the birds apparently became habituated to the perched hawk and dispersed gradually.

Jays, squirrels, and cowbirds were chased from the nest sites by *lawrencei* and *psaltria*, usually both male and female participating. If the male was not nearby, however, the female did not seem to hesitate to chase intruders alone and often followed them from the nest tree, giving repeated *caws*.

FLOCKING

Throughout the nesting season, small flocks of four to six goldfinches are regularly seen at foraging areas or near water. Although there is usually some agonistic behavior, the social tendency of the birds allows fairly peaceful intraspecific group feeding. Where the water supply is limited, it is not uncommon for small groups of both *lawrencei* and *psaltria* to be drinking and bathing side by side at these neutral areas.

AGONISTIC BEHAVIOR

TERRITORIAL BEHAVIOR

As soon as the nest site has been selected, male goldfinches begin to establish a territory which includes the nest. As mentioned above, the female actively defends only the area immediately surrounding the nest and becomes restricted almost exclusively to it as soon as the eggs are laid. The male, however, defends a larger area against other males of the same species.

The Lesser Goldfinch male defends an area about 30 meters in diameter, and his behavior is very similar to that of the American Goldfinch (see, for example, Drum 1939). He perches atop the highest branches of the trees within his territory, periodically giving very loud advertising song. Circling Song Flight Displays are made with wings and tail spread, showing their white areas effectively. Although singing occurs at fairly regular intervals throughout the day, it is characteristically triggered by song from other males or the presence of another male near the territory. If a strange male enters the territory, the resident male flies toward it with the Song Flight Display. If the intruder does not leave, the resident flies directly at it and the two may engage in a grappling fight, flying together vertically upward or downward, beating each other with the wings and feet, and pecking. When the intruder has been routed, the resident male usually gives the circling Song Flight Display. The grappling fights are seldom seen after the first few weeks of nesting,

and song seems sufficient to defend the territory of the Lesser Goldfinch after this time.

The male *lawrencei* maintains a much smaller territory, only about 10–15 meters in diameter, and is much less active in its defense than is the male *psaltria*. He often sings while perched near the nest when he comes to feed the female. No elaborate circling Flight Displays or Song Flights are given, as is the case in Lesser and American Goldfinches. The male Lawrence's Goldfinch may, however, begin flight away from the nest tree a few seconds before completing his song. The territory is usually defended solely by high-intensity singing if a strange male enters it. In only a few instances was a resident Lawrence's male seen to fly toward a strange male. Even in these cases, however, fights or chases were not always forthcoming. The resident male often merely sang loudly while facing the intruder, body erect, and tail turned to one side. In only one case was a grappling fight seen in this context.

Both species show a tendency to nest in a loose colony, as do other cardueline finches. Although territories are maintained by each male, the birds tend to group together even though the apparently suitable habitat may be more extensive than that occupied by nesting birds.

Interspecific encounters between nesting males were observed in the field on only three occasions. These occurred when active *psaltria* and *lawrencei* nests were within 10 meters of each other, once in the same tree. In all three cases, the males chased each other about near the nests and sang. No actual attacks were made, however. Although this behavior may indicate poor species recognition, it must be remembered that the males did not fight continuously and that both nests seemed successful. On the other hand, most interspecific territories did not overlap, but seemed to be mutually exclusive. It would seem, then, that there is some competition between the species and that pairs whose nesting territories overlap may be subject to interspecific encounters.

Laboratory studies indicate that *psaltria* is dominant over *lawrencei*, at least outside the breeding season. In mixed flocks, *psaltria* displaces *lawrencei* from perches and food by aggressive displays or pecks. Of 19 encounters between adults of the two species, *psaltria* was the victor in 18. In addition, when food was supplied to a mixed flock of hungry goldfinches, the *psaltria* always ate first, and the *lawrencei* seldom attempted to approach the food until the *psaltria* had flown away

from it. Field observations included six inter-specific encounters during the breeding season. In these, *lawrencei* was the victor only once. This apparent dominance relationship of the smaller species over the larger probably affects the formation and maintenance of territories in wild birds. It may also account for the lack of overlap of territories of the two species.

Field observations reveal a seasonal diminution of territoriality that is particularly evident after the eggs have hatched. Song Flight Displays are less and less frequent, and fights are not seen late in the season. There seems to be little violation of territorial boundaries, however, and males confine their activities rather strictly to the nest instead of to the whole territory. When they come to the territory, they often go directly to the nest, feed the female, and fly away, giving only call notes and no song at all.

GENERAL AGONISTIC BEHAVIOR

In both species, the female is dominant, at least during the early part of the breeding season, displacing the male from food and perches, supplanting him, and pecking at him when he approaches. This situation is common among carduelines (see, for example, Hinde 1955–56; Thompson 1960; Dilger 1960). Hinde suggests that it is due to a decrease in aggressiveness of the males as they approach breeding condition. The result is a greater tendency to flee from the females at this time rather than to attack them. Hinde indicates that the cardueline females he studied also show this change in drive but that it occurs later, making them more aggressive than the males during copulatory and precopulatory activities. In the Lesser and Lawrence's Goldfinches in southern California no encounters were observed between members of a pair after the female began incubating. It may be that females of these species also become less aggressive as the breeding season progresses.

Except for the unique high-intensity Song Display of the male *lawrencei* (fig. 6a), the agonistic displays are similar in both species and are like those of the American Goldfinch (for detailed descriptions, see Coutlee 1967). The birds utilize the Carpals-Raised, low- and high-intensity Head-Forward (figs. 7a and 7b), and Wing Fluttering (fig. 7c) displays accompanied by grating *caw* calls which indicate aggression. Dilger (1960) describes repeated chin-lifting in the Common Redpoll (*Acanthis flammea*) during displays with high attack valency and points out that several other black-chinned carduelines also exhibit chin-lifting. The Lawrence's Goldfinch, which pos-

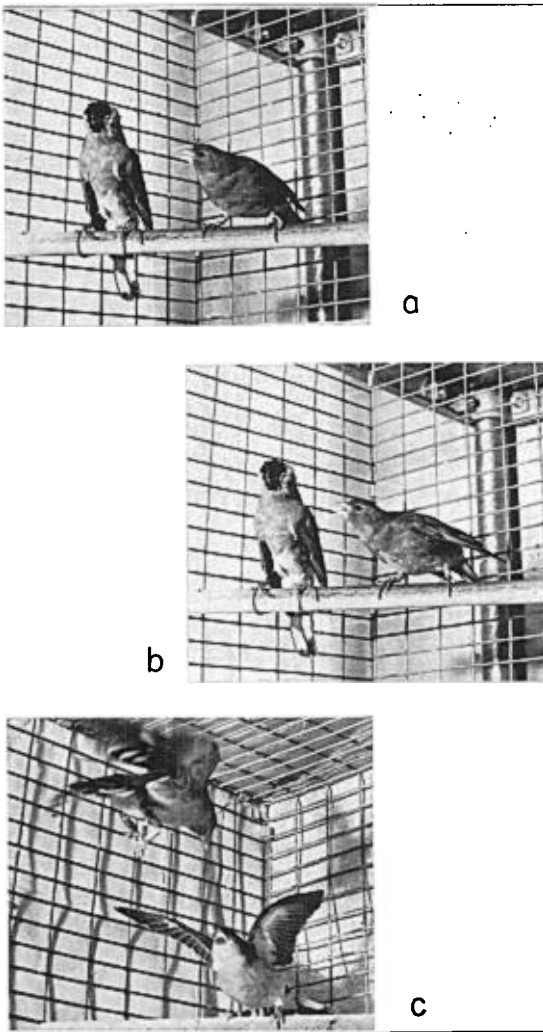


FIGURE 7a. Low-intensity Head-Forward by female *lawrencei* toward stuffed male; b. High-intensity Head-Forward with aggressive *caw* by female *lawrencei* toward stuffed male; c. High-intensity Head-Forward with Wing Fluttering and aggressive *caw* by a male and female *psaltria*.

esses both a black chin and facial region, does not show this ritualized behavior. Instead, the neck is extended and the head raised during aggressive displays, making the entire black facial region and sharply contrasting pale bill clearly visible to the opponent. The highly fluffed contour feathers of attacking European Goldfinches (*Carduelis carduelis*) (Conder 1948; Hinde 1955–56) were not seen in either species. Submissive individuals of both *lawrencei* and *psaltria* usually simply crouch and flex the neck, but may also fluff the contour feathers and lean away from the aggressor (both adults and juveniles show these patterns). These fairly subtle submissive displays are similar to those of the American Goldfinch (Coutlee 1967).

As mentioned above, some agonistic behavior is noted at neutral areas during feeding, drinking, or gathering of nest materials. In most cases such behavior involves two females or a female and her mate. Only very early in the season, before pair bonds are well established, are males seen in agonistic encounters toward each other in neutral areas. After territories are established, agonistic behavior between males rarely occurs except in the territories.

DISCUSSION

COURTSHIP AND PAIR FORMATION

The close association of goldfinches in large mixed flocks during the winter, coupled with the common arrival of males and females at the breeding grounds, makes studies of pair formation especially difficult. It was necessary to study captive birds in order to observe courtship displays accurately, and it was sometimes difficult to integrate these observations with those in the field. The American Goldfinch appears to form pairs at the wintering grounds, during migration, and early in the breeding season. Birds arriving at the breeding areas are sometimes already paired (Stokes 1950). In southern California where goldfinches are less migratory than in the colder regions of North America, pairs are formed just after arrival at the breeding area. Pair formation depends in large measure on the Courtship Calls of the males, which serve to identify them and to attract females.

Although Linsdale (1957) indicates that *lawrencei* pairs were already formed in north-central California while the birds were in large flocks (30–50 birds), this certainly was not the case at Placerita Canyon. As described above, increased activity in smaller flocks seemed definitely to give rise to pairs within a period of a few days. Since the birds had been associated in large flocks, probably for several months, it is possible that some individual preferences for mates had already been established and that this hastened the final formation of pairs.

Vigorous Courtship Chases are seen in both *tristis* (Stokes 1950) and *psaltria* as members of the pair dart in and out among dense foliage, the male giving a loud Courtship Song. This behavior was not noted in *lawrencei* pairs either in captivity or in the wild. Billing and Courtship Feeding occur regularly in all three species and function in both formation and maintenance of the pair bond.

It is most interesting that disintegration of large winter flocks in all three North American goldfinches is coincident with pair formation

and, unlike the case in many passerines, territories are not established until after nest sites have been chosen. This pattern may be related to the social nature of these birds and to their strong tendency to flock even during the nesting season. Both sexes flock together in winter and arrive simultaneously at the breeding areas. It appears, then, that disintegration of the flocks is the direct result of pair formation, rather than of territory establishment as with many other species. This means that the male's efforts are concentrated on attracting a female rather than on choosing a territory, and selection acts to develop distinctive courtship calls and elaborate song as well as bright plumage in the male. The female, on the other hand, is not restricted in her choice of a mate by the territory which he occupies, and also has great freedom in nest placement. The two sexes are highly specialized at this point in nesting, the female building the nest essentially unaided by the male and the male establishing a territory around this site. The close cooperation of the birds in the successful completion of a nest and rearing of the young is assured by the strong pair bond that is formed and maintained throughout the season by Courtship Feeding. In total, this pattern allows maximum advantage to be taken of the flocking habit (for instance, in discovery of food and protection from predation) while still providing for isolation of pairs for nesting. The close pair bond may, in addition, serve to inhibit flocking tendencies in both birds which would, of course, result in unsuccessful nesting.

NESTING

In the goldfinches studied in southern California, the *lawrencei* and *psaltria* females showed definite preferences when gathering nest material, *lawrencei* taking grasses and small forbs from the ground, *psaltria* taking grasses and plant and animal fibers while perched in shrubs or trees. These distinct preferences were not shown in the goldfinches observed by Linsdale (1950, 1957). In fact, in the birds Linsdale observed, the major part of most *lawrencei* nests was constructed of lichens which the females gathered from nearby oaks. These goldfinches were not seen collecting nest materials on the ground. It would seem that the texture and size rather than the location of the nest material is important in Placerita Canyon. No foliose lichens were growing on the oaks there, and female *lawrencei* were not seen collecting nest materials in the trees.

Although the American Goldfinch characteristically lines its nest with a thick layer of

thistle down, this was not seen in Lawrence's and Lesser Goldfinch nests in southern California. Their nests usually contained a few fine fibers of plant down or insect webbing within the outer cup, but lacked a thick lining. Most goldfinches at the study area had nested before any composites were ripe, and no soft fibers were available. Even late nests, however, were never completely lined. The few fibers present may be homologous to the final coarse fibers used in the nest lining of the American Goldfinch (Nickell 1951), the thicker down cup being omitted entirely.

Even though *lawrencei* nests tend to be built higher above the ground than do those of *psaltria*, the pattern of nesting is the same in both species as well as in *tristis*. The female builds the nest and remains on it almost continuously for over two weeks while the male spends most of his time feeding and makes regular trips to the nest to feed the female by regurgitation. This behavior seems characteristic of carduelines and has also been reported in the House Finch (*Carpodacus mexicanus*) by Thompson (1960) and the European Goldfinch by Conder (1948). Again, the highly social nature of the species in this group may have given rise to this closeness of the female to the nest. Since the birds readily flock together, selection may have favored females who remained at the nest for long periods, since only these would be successful in raising young. If the attachment for the nest were not strong, females might actually desert the nest and join a flock of foraging birds.

TERRITORIALITY

Extensive summaries of definitions and functions of territory have been given by Nice (1941) and Carpenter (1958) and will not be repeated here. Although goldfinches nest in a loose colony, the males maintain fairly large (10 m to 30 m in diameter) nesting territories. These territories are established only after pairs have been formed and a nest site has been selected, and are seldom used for foraging. They thus seem to function (1) to isolate the female and prevent strange males from courting her during early incubation, (2) to prevent interruption of feeding of the female or young on the nest, and (3) to maintain isolation of the pair and inhibit flocking tendencies. Since the calls given by the adults during feeding make the nest site conspicuous, the spacing of nests may also prevent mass predation.

Although fights sometimes occur when territory boundaries are violated by conspecific males, territories are defended primarily by

aggressive song and accompanying displays. In *lawrencei*, this display consists of posturing while perched, but *psaltria* and *tristis* males perform an elaborate Song Flight Display. Both of these displays define territorial boundaries and cause retreat of intruders without combat. The territory seems always to remain intact even though the males may be foraging $\frac{1}{4}$ to $\frac{1}{2}$ mile away from it for from 30 to 45 minutes of each hour while the female is on the nest. The male actively defends his territory if intruders are present when he comes to feed his mate, and he often sings after he has fed her.

Toward the end of the nesting period the territories are not vigorously defended. This finding supports the idea that territories serve primarily to isolate the females. By the last week of nesting, the female accompanies her mate to forage, and the two birds spend a large part of the time caring for their young. Defense of the female from other males and isolation from the flock are unnecessary at this time since her parental drive is very strong. The pair bond is maintained by close contact of the pair and by occasional courtship feeding.

TAXONOMIC AND HISTORICAL FACTORS

Although a detailed consideration of taxonomic and historical factors is beyond the scope of this paper, a few salient points may be noted. It is generally accepted that the North American goldfinches are, in contrast to most New World seed-eaters, derived from Old World forms (see Sushkin 1925; Mayr 1946). This hypothesis of common origin seems to be supported by the courtship and agonistic behavior observed in the genus *Spinus*. The highly stereotyped pivoting behavior seen in Courtship Displays of the European Goldfinch (Conder 1948), Greenfinch (*Chloris chloris*; Hinde 1955), and several other carduelines (Hinde 1955-56) also appears in less intense form in *lawrencei*. In this species, however, it occurs during agonistic encounters and indicates a fairly high-intensity aggressive drive. It is interesting that there appears to be no evidence of this display in *psaltria* or *tristis* either in agonistic or sexual encounters. Displacement Breast Preening, common in cardueline displays (Hinde 1955-56), is also frequently observed in all three North American goldfinches during conflict situations.

On the basis of the morphology of the skull and axial skeleton, Tordoff (1954) places the goldfinches in the family Ploceidae, owing to their close resemblance to estrildine finches. The Courtship Displays of some representative

estrildines as described by Morris (1958) and Immelmann (1965), however, show a considerable difference from the cardueline group. For example, males of most estrildine species engage in nest-building and carry nest material during some or all Courtship Displays. Among carduelines this behavior is found only in the Bullfinch (*Pyrrhula pyrrhula*). Bobbing up and down or bowing to the female while displaying is very common among estrildines but has not been reported for any cardueline species. Furthermore, Courtship Feeding is very important among carduelines in the maintenance of the pair bond, and is found in all species thus far investigated. Estrildines, on the other hand, do not participate in Courtship Feeding but instead maintain body contact and preen each other, thus enhancing the pair bond. From a behavioral point of view, then, the members of the genus *Spinus* are more closely allied to the European carduelines than to estrildine finches.

The morphological and behavioral similarity of *tristis* and *psaltria* indicates a close relationship. It seems probable that *psaltria* diverged from *tristis* during the Pleistocene as a form adapted to the drier climate then developing in western North America. *Lawrencei*, however, seems much more closely related to Old World carduelines, and differs from *psaltria* and *tristis* in morphology and, especially, in behavior. Its present breeding range is restricted mainly to oak woodland on the west coast of the United States. This restricted New World range of a species that seems to have closer affinities with Old World forms than with its sympatric congeners is puzzling. The evolutionary pathways that could account for this pattern include the following: (1) *lawrencei* may have been derived from an Old World population that reached North America from Eurasia after the arrival and differentiation of the *tristis-psaltria* stock; (2) *lawrencei* may be a relict form derived from a population that was formerly more widespread and less differentiated from the presumed Eurasian ancestral stock. In the absence of a fossil record or any other direct evidence bearing on the origin of the three species, these suggestions are necessarily speculative.

SUMMARY AND CONCLUSIONS

A field and laboratory study of behavior of the sympatric *Spinus lawrencei* and *S. psaltria* was conducted during 1964-1966 in southern California. Both species are small, seed-eating finches, but they are able to occupy the same habitat despite some competition for nest sites

and despite similar patterns of reproductive behavior, including vocalization. The problem of species identification and integrity in these two goldfinches thus becomes of great interest. Studies of behavior patterns showed the following.

1. Pairs are formed as mixed winter flocks disintegrate, and territories are not established until the nest site is chosen. Males are subordinate to their mates, at least during the early part of the reproductive cycle.

2. Although *lawrencei* nests are usually higher above ground than *psaltria* nests, there is some interspecific competition for nest sites. This is probably due in part to the highly social nature of both species and their attraction to nest-building activities.

3. Female *psaltria* collected nest materials while perched in bushes or trees, while *lawrencei* females collected nest materials on the ground.

4. A strong pair bond is maintained by Courtship Feeding throughout the nesting season and may be related to the necessity for isolation of the pair and inhibition of flocking tendencies for several weeks.

5. The unusually close attention of the female to the nest may insure breeding success by inhibiting her tendency to join groups of goldfinches.

6. Territories of *lawrencei* are about 10-15 meters in diameter, those of *psaltria* about 30 meters in diameter. The territories of *lawrencei* and *psaltria* are mutually exclusive.

7. Pair formation is promoted by species-specific Courtship Calls, close association of a male and female, and Following or Chasing Flights.

8. Male song is quite variable in pattern but retains species distinctiveness and serves

mainly in courtship and to defend a nesting territory.

9. Agonistic displays are similar to those of the American Goldfinch; *psaltria* appears to be dominant over *lawrencei*.

10. Since *psaltria* is morphologically and behaviorally so similar to *tristis*, it is suggested that *psaltria* arose as an offshoot of *tristis* stock adapted to the drier conditions of western North America.

11. *Lawrencei* has a very limited breeding distribution and is very similar, behaviorally, to Eurasian carduelines. Some possible pathways of its evolution are discussed.

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LITERATURE CITED

- CARPENTER, C. R. 1958. Territoriality: a review of concepts and problems. Pp. 224-250, in A. Roe and G. G. Simpson, Behavior and evolution. Yale Univ. Press, New Haven.
- CHAMBERS, W. L. 1915. History of a nest of the Green-backed Goldfinch (*Astragalinus psaltria*). Condor 17:166.
- CONDER, P. J. 1948. The breeding biology and behaviour of the continental goldfinch (*Carduelis carduelis carduelis*). Ibis 90:498-525.
- COUTLEE, E. L. 1967. Agonistic behavior in the American Goldfinch. Wilson Bull. 79:89-109.
- DILGER, W. C. 1960. Agonistic and social behavior of captive Redpolls. Wilson Bull. 72:115-132.
- DRUM, M. 1939. Territorial studies on the eastern goldfinch. Wilson Bull. 51:69-77.
- GROSS, A. O. 1938. Nesting of the goldfinch. Bird-Lore 40:253-257.
- HINDE, R. A. 1955. The courtship and copulation of the Greenfinch (*Chloris chloris*). Behaviour 7:207-232.
- HINDE, R. A. 1955-56. A comparative study of the courtship of certain finches (Fringillidae). Ibis 97:706-745; 98:1-23.
- IMMELMANN, K. 1965. Australian finches. Angus and Robertson, Ltd. Sydney.
- LINSDALE, J. M. 1950. Observations on the Lawrence Goldfinch. Condor 52:255-259.
- LINSDALE, J. M. 1957. Goldfinches on the Hastings Natural History Reservation. Amer. Midl. Nat. 57:1-119.

- MAYR, E. 1946. History of the North American bird fauna. *Wilson Bull.* 58:3-41.
- MORRIS, D. 1958. The comparative ethology of grassfinches (Erythrurnae) and mannikins (Amadinae). *Proc. Zool. Soc. London* 131:389-439.
- NICE, M. M. 1941. The role of territory in bird life. *Amer. Midl. Nat.* 26:441-487.
- NICKELL, W. P. 1951. Studies of habitats, territory, and nests of the eastern goldfinch. *Auk* 68:447-470.
- SHEPARDSON, D. I. 1915. Nesting habits of Lawrence's Goldfinch. *The Oologist* 32:59-60.
- STOKES, A. W. 1950. Breeding behavior of the goldfinch. *Wilson Bull.* 62:107-127.
- SUSHKIN, P. P. 1925. A preliminary arrangement of North American genera of Fringillidae and allied groups. *Auk* 42:259-261.
- THOMPSON, W. L. 1960. Agonistic behavior in the House Finch. *Condor* 62:245-271; 378-402.
- TORDOFF, H. B. 1954. A systematic study of the avian family Fringillidae based on the structure of the skull. *Misc. Pub. Mus. Zool. Univ. Mich.* 81:1-41.
- WALKINSHAW, L. H. 1938. Life history studies of the eastern goldfinch. I. Jack-Pine Warbler 16:3-11.

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