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THE BREEDING BIOLOGY OF THE WESTERN FLYCATCHER

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Many of the species of the tyrannid genus *Empidonax* are so nearly similar in gross outward appearance that they are almost impossible to identify with certainty in the field on the basis of morphology and color alone. In such a confusing group, it is important to have comparative information on the biology of the individual species. Such information, combined with morphologic characters, can be of primary importance in working out the relationships of the species involved. Some biological information is available for certain species; others are poorly known. Those which have been studied in recent years include the Gray Flycatcher, *E. wrightii* (Russell and Woodbury, 1941); the Hammond Flycatcher, *E. hammondii* (D. Davis, 1954*a*); the Least Flycatcher, *E. minimus* (de Kiriline, 1948; MacQueen, 1950; D. Davis, 1959; Nice and Collias, 1961); the Traill Flycatcher, *E. traillii* (Berger and Hofslund, 1950; McCabe, 1951; King, 1955; Stein, 1958); and the Acadian Flycatcher, *E. virescens* (Newman, 1958). The literature prior to 1940 on North American empidonaces has been largely summarized by Bent (1942).

The Western Flycatcher, *E. difficilis,* remains one of the most poorly known species, although it is morphologically one of the more distinct species of *Empidonax*, is readily identified by its vocalizations, is the only representative of the genus in many parts of western North America, and is a common bird over most of its range. Apart from the limited information presented by Bent (1942), Grinnell and Linsdale (1936), and Williams (1942), we know little about this species. Indeed, some of the published information ranges from such inconclusive and unverified statements as: "The period of incubation is said to be 12 days" (Bent, *op. cit.*:249) to misinformation: "The male is remarkably devoted to his mate, feeding her while she is brooding . . . . And she receives this with the same pretty coaxing of wings by which the little ones beg for food" (Wheelock, 1904:438).

This account deals with various aspects of the breeding biology of the Western Flycatcher, first, in order to present some information on the natural history of a common, but poorly known, bird, and second, to provide a basis for the comparison of *E. difficilis* with other members of the genus.

ACKNOWLEDGMENTS

Laidlaw Williams and Louise M. Hatton generously turned over to us information on nests at Carmel Highlands and Corral de Tierra. Mr. and Mrs. George Von Soosten allowed us to observe nests at their cabin in Anastasia Canyon, and Mrs. Von Soosten kept records on some nests in our absence. Dr. Peter Marler and Dr. William R. Fish made the recordings from which the sonograms presented in figures 1 and 2 were made, and Dr. Marler made the sonograms. We wish to express our sincere appreciation to all of these people.

We take this opportunity to acknowledge gratefully the continued support of the program at the Hastings Natural History Reservation by Mrs. Russell P. Hastings.

MATERIALS

Most of the information in this study was obtained at the Hastings Natural History Reservation, two and one-half miles east of Jamesburg, northern Monterey County, California. We spent a total of 1238 hours observing flycatchers during the breeding seasons of 1954 through 1962, but the great majority of data was gathered in 1957, when we spent 1055 hours observing flycatchers from March through August. Throughout the study, we preferred to spend considerable amounts of time watching relatively few pairs. We feel that enough pairs were watched to give a good idea of variability in behavior, and that our observations of individual pairs were sufficiently lengthy to give an adequate picture of their breeding biology. In addition to our own notes, we used the notes of several workers who had previously observed this species at the Reservation. Especially helpful were the records made by John E. Chattin in 1940 and by Ernest L. Karlstrom in 1952.

The nests which we followed most closely will be referred to as follows: Red House 1954 and Red House 1956, Chinchilla House, Barn nests 1 and 2, and Stub nests 1 and 2. The Red House and Chinchilla House nests were built under the eaves or open porches of buildings, Barn nests 1 and 2 were located high inside a large barn, and Stub nests 1 and 2 were placed in cavities in a dead willow stub and a large, dead stub, probably of an oak. The two Barn and two Stub nests were the successive nests of individual pairs. All but the Red House nests were watched in 1957.

We also used unpublished data supplied by Laidlaw Williams for nests at Carmel Highlands, a coastal locality about 25 miles northwest of the Reservation, and by Louise M. Hatton for nests at Corral de Tierra, about 15½ miles north-northwest of the Reservation. In addition, we made some observations on nests at Anastasia Canyon, about three miles south of the Reservation.

SEASONAL STATUS AND HABITAT PREFERENCE

The Western Flycatcher is a summer resident on the Reservation. The earliest dates of arrival were March 11, 1941 and 1957, and the latest record was October 8, 1960. Actually, there is a noticeable decrease in numbers by the end of August, followed by occasional records in September and early October. It seems likely that the local summer residents leave by late August or early September and that records from mid-September on pertain to transients from the north.

At the Reservation, Western Flycatchers are found mainly in canyon bottoms and in riparian situations. Coast live oaks, western sycamores, and willows are good indicators of suitable flycatcher habitat in this area. The higher and drier woodlands, dominated by blue and valley oaks, are not frequented by this species. Buildings are frequently used as nest sites and the presence of buildings may lead to the occupation of territories that appear marginal in most respects.

Difficilis is the only representative of the genus *Empidonax* found at the Reservation with the exception of a few transient Traill Flycatchers recorded in the spring and fall.

DETERMINATION OF SEX

Since the sexes of North American empidonaces are indistinguishable in the field, and since we marked no birds, we were unable to assign sex definitively to the individuals which were watched. This problem has faced all workers dealing with *Empidonax* when unmarked birds were observed. Like most previous workers, we assumed that the female was solely responsible for nest building, incubation, and brooding. Myers

(1911:89) reported an instance of a male Western Flycatcher brooding young for 10.5 minutes, and she assumed that the male probably did some incubating as well, but she gave no indication as to how she told the male from the female. Perhaps this report was the basis for Bent's (1942:249) statement: "Whether both sexes [of *E. difficilis*] incubate does not seem to be known, but both parents assist in the feeding of the young and probably in brooding them also."

We were able to assign certain traits of voice or behavior to the bird that incubated or brooded, and others to the bird that did not participate in these activities. Thus, at the Barn nests, the presumed female almost invariably used a certain approach to, and departure route from, the nest, and the nonincubating and nonbrooding bird used different routes. Observations on this pair away from the nest were not possible since they could not be followed by the observer after they had left the barn. At Stub Nest 1, where it was possible to follow the birds away from the nest more successfully, several differences between the members of the pair were noted. The bird which incubated and brooded almost invariably used *tsit* as a position note off the nest, always went directly to the rim of the nest when returning to it or feeding the young, usually guarded the nest from a nearby perch after feeding the nestlings (when she did not brood them), carried fecal sacs in a particular direction for the first 12 days of the nestling period, and flipped its tail repeatedly when off the nest. The bird that was off the nest during incubation and brooding never used *tsit* as a position note but always used *pee-ist*, never went directly to the rim of the nest with food but always landed first on a small branch stub below it, even when the brooding bird was not present at the nest, never guarded the nest from a nearby perch, carried fecal sacs in a different direction than that used by the brooding bird during the first 12 days of the nestling period, and very rarely flipped its tail. On the basis of these behavioral characteristics, it seemed obvious that one bird did all the incubating and brooding, and that the other bird did none. Both birds fed the young.

MacQueen (1950), using marked Least Flycatchers, found that the female builds the nest, incubates, and broods, and that both sexes feed the young. D. Davis (1959) agrees with MacQueen that nest building, incubation, and brooding are performed by the female Least Flycatcher alone. He established sex on the basis of different vocalizations of the male and female. Nice and Collias (1961) could distinguish the members of the pair of Least Flycatchers that they watched on the basis of appearance, behavior, and voice. The female performed all the incubating and brooding; both sexes fed the nestlings. With regard to the Hammond Flycatcher, D. Davis (1954*a*:167–168) states that: "The nest is built primarily, if not exclusively, by the female . . . . Incubation is done by the female alone. . . . Both adults feed the nestlings. . . . the male begins to feed the young the day they hatch but the female continues to brood . . . ." In a later paper (1959:75), he states: "collections of Hammond's Flycatcher . . . always verified the belief that only the male called." In the Acadian Flycatcher, Newman (1958:131) identified the female "by the repetitive pattern of activity as well as by the call notes peculiar [to her]." Incubation and brooding were performed by the female alone; both sexes fed the young. In the Gray Flycatcher, Russell and Woodbury (1941) state that incubation was performed solely by the female, and that both parents fed the young. Summing up, Skutch (1960:575) states: "Incubation is performed by the female alone in about 27 species of 22 genera [of tyrannids] in which I have given careful attention to this point. The male of a number of North American species is said by various authors to participate in incubation, but the most careful studies indicate the contrary . . . . The nestlings are brooded by the female alone, but normally they are fed by both parents in those species which are regularly mated." Our observations agree with this statement.

HOSTILE BEHAVIOR

Hostile behavior is such a prominent element in the total behavioral makeup of this species that it is evident in the relationships of the individual with nearly every species of bird with which it comes into contact. Hostility falls into three main categories: interspecific, intraspecific, and intrapair.

Interspecific hostility.—At Stub nests 1 and 2, 14 species of birds exclusive of *E. difficilis* were attacked by the resident pair, as follows (number of attacks in parentheses):

Hairy Woodpecker, *Dendrocopos villosus* (1)
Nuttall Woodpecker, *Dendrocopos nuttallii* (3)
Plain Titmouse, *Parus inornatus* (3)
White-breasted Nuthatch, *Sitta carolinensis* (1)
Brown Creeper, *Certhia familiaris* (2)
House Wren, *Troglodytes aedon* (5)
Bewick Wren, *Thryomanes bewickii* (1)
Blue-gray Gnatcatcher, *Polioptila caerulea* (1)
Warbling Vireo, *Vireo gilvus* (3)
Orange-crowned Warbler, *Vermivora celata* (5)
Yellow Warbler, *Dendroica petechia* (1)
Lesser Goldfinch, *Spinus psaltria* (15)
Rufous-sided Towhee, *Pipilo erythrophthalmus* (1)
Oregon Junco, *Junco oreganus* (2)

In addition to the 44 attacks just listed, members of the pair chased several small birds which could not be identified by the observer. There was no correlation between the frequency of attacks and the stage of the nesting period.

Of the 44 attacks, only five were directed at birds considerably larger than the flycatchers (Hairy and Nuttall woodpeckers, Rufous-sided Towhee). The remaining 39 were directed at small birds more or less comparable in size to the attacker. Larger birds came many times to the stubs in which the two nests were located without any response by the flycatchers. Brown Towhees (*Pipilo fuscus*) were consistently ignored although they came many times to the nest trees. Rufous-sided Towhees also visited the nest stubs frequently; the only attack on this species was against a bird foraging on the ground some distance from the nest. Purple Finches (*Carpodacus purpureus*), Black-headed Grosbeaks (*Pheucticus melanocephalus*), and Western Bluebirds (*Sialia mexicana*) were less frequent visitors, and none was attacked.

The large bird attacked most persistently was the Nuttall Woodpecker, which was driven out on each of its three observed appearances in the territory. Twice these woodpeckers came to the nest tree, each time landing well below the nest cavity, and each time the intruder was chased out at once. One flew toward the nest stub at nest level, but when it was about six feet from the tree, both flycatchers attacked, diving at the woodpecker's head and snapping their bills. Single Hairy Woodpeckers came to the nest stub twice. One was ignored and the other was driven out. Thus, woodpeckers were attacked on four of their five visits to the nest stub.

With regard to the smaller birds, the significance of the numbers of observed attacks on individual species is greatly lessened because of the inability of the observer to know the total number of times birds came to the area when they were not attacked and, in the case of birds which were apparently ignored, because of the observer's inability to know whether or not they had actually been seen by the flycatchers. Individuals of nearly every species which was attacked came to the area at other times and were either ignored or not noticed. Thus, it was not possible to predict whether or not an intruding individual of any species would be attacked. Nonetheless, two features are apparent. The great majority of attacks was directed against small birds, and large birds, with the exception of the woodpeckers, were virtually ignored. Second, despite our lack of information on the total number of visits, the Lesser Goldfinch apparently stimulated hostile behavior more than any other species. According to Beal (1910:73–74), the diet of this goldfinch is 98.3 per cent vegetable and 1.7 per cent animal food. Of the 476 stomachs examined, only 50 (10.5 per cent) contained animal food. Of the animal food, 94 per cent consisted of plant lice. The 157 stomachs of *E. difficilis* examined by Beal (1912:55–56) contained 99.31 per cent animal matter, and none contained plant lice. On the bases of these analyses, the Lesser Goldfinch does not compete for food with the Western Flycatcher. Information given by Linsdale (1957:6–9) on nest sites of *Spinus psaltria* at the Reservation indicates that this species does not compete with the flycatchers for nest sites. It is possible that the overall coloration of the goldfinches, greenish above and yellow below, and thus vaguely resembling the general coloration of the flycatchers, may have served as a stimulus for the flycatchers' aggressive behavior.

Examination of the list of species attacked reveals that the next largest number of attacks was directed against House Wrens (5) and Orange-crowned Warblers (5). The House Wren is a well-known destroyer of other birds' nests, eggs, and young, and many species react intolerantly to it. The Orange-crowned Warbler is olive-green above and greenish-yellow below. It is a ground nester and its foraging habits would not make it a particularly serious competitor of the Western Flycatcher, certainly no more so than the Blue-gray Gnatcatcher or the Warbling Vireo, species which entered the territory of the flycatchers much more frequently than did the Orange-crowned Warbler, yet which were attacked less frequently than that species. It seems more likely that the flycatchers reacted primarily to the general coloration of the warbler. Richardson (1908:67) has also recorded an instance of a Western Flycatcher chasing an Orange-crowned Warbler.

At Barn nests 1 and 2 the flycatchers were not subjected to intrusion by the great variety of birds noted at the Stub nests. Most of the attacks by the pair resident in the barn were directed at Plain Titmice, White-breasted Nuthatches, and House Finches (*Carpodacus mexicanus*); the latter nested commonly in the barn. At a nest watched by John E. Chattin in 1940, most attacks were directed against Lazuli Buntings (*Passerina amoena*), a species that was never attacked by the Stub pair despite repeated intrusions which included frequent use of the nest stub as a song perch by a male.

Examples of intolerance of animals other than birds were rare. One of the Chinchilla House adults, accompanying two newly fledged young, chased a wood rat (*Neotoma fuscipes*) over 30 feet through the crown of a coast live oak, forced it down the trunk, and drove it across open ground to a building under which it took refuge. The flycatcher then returned to the oak and repeated the entire performance with a second rat. Both chases were silent save for repeated bill snaps by the pursuing flycatcher. At the nest watched by Chattin, the adults attacked western fence lizards (*Sceloporus occidentalis*) four times after the nest had fallen and the nestlings, unable to fly, were being fed by the adults on the ground.

The generally aggressive nature of the Western Flycatchers observed by us agrees with the intolerant nature of the flycatchers studied by Williams (1942). This species seems to resemble the Song Sparrow (*Melospiza melodia*), which is intolerant of other species of similar size (Nice, 1943:160).

Intraspecific intolerance.—Encounters between flycatchers were observed frequently but, because of pronounced hostility between the members of pairs watched over long periods of time, it was often difficult to tell whether two individuals in combat represented members of a pair or one member of a pair attacking a third, intruding flycatcher. At the Stub nests, several encounters between flycatchers were noted while the female was on the nest. The reaction of the male to such intruders was always immediate, and a swift chase followed at once, often accompanied by series of *chrrips, bzzt* notes, squeaks, and bill snaps. Rarely, the intruder would stand his ground and the two contestants would lock in mid-air and flutter slowly to the ground. Territorial chases were also observed in March between early arrivals, presumably males. As would be expected, these flycatchers are highly intolerant of intruders of their own kind.

Intrapair hostility.—Hostile behavior was noted between the members of every pair that was watched over a long period of time. Such behavior varied from simple displacement of one member of the pair by the other to violent attacks which ended with both birds locked together and fluttering to the ground. This latter type of contact was noted once in the pair at Barn Nest 2 while the fledglings were being cared for by the adults.

The best documented intrapair intolerance was noted at Stub nests 1 and 2, where the pair could be followed by the observer better than at any other nest. During the incubation and nestling periods, including the pre-incubation period of three days at Stub Nest 2, 80 aggressive contacts were noted during a total of 53 days of observation between May 8 and July 16. Frequent and extended periods of observation were needed to see these contacts, as evidenced by the fact that no aggression was noted on 29 of the 53 days. The 80 contacts were recorded during a total of 376 hours of observation, an average of 0.21 contacts per hour, or one every 4.7 hours of observation. Obviously, short and widely spaced periods of observation have little chance of turning up such behavior. We know of only two observations of possible intrapair hostility reported in *Empidonax*. MacQueen (1950:199) noted a male Least Flycatcher which came to the nest to feed the incubating female, but the latter, instead of remaining on the nest, flew off, "flying wildly about the territory with the male in chase. After a few seconds of flight the female landed on a branch ten feet from the nest where the male fed her, after which she flew back to the nest." Wheelock (1904:440) says of the male Traill Flycatcher: "When there is no one else within scrapping distance, he contents himself with scolding his mate on the nest;" and that after hatching, when the male is feeding the nestlings, "No time has he now for scrapping or bullying his little wife." Skutch (1960:571–577), in his "General Summary of Information on the Tyrannidae," does not mention intrapair hostility for any tyrannid.

Plotting the number of intolerant contacts per hour of observation at Stub Nest 1 shows no particular trend toward increasing or decreasing frequency as nesting progressed. There was a great difference between nests 1 and 2. At Nest 1, contacts were noted on 18 of the 23 days of observation between May 8 and June 5. At Nest 2, contacts were noted on only six of the 30 days of observation. At Nest 1, the frequency of contacts was 0.34 per hour of 190 hours of observation, whereas at Nest 2 the frequency was only 0.08 per hour for 186 hours of observation. In most cases, it was impossible to tell whether the male or the female was the aggressor. Nearly all contacts came when the female flew from the nest to a shrub or tree in which the male was perched. Since the actual contact was often obscured by foliage, it was not until the birds came into view, one chasing the other, that the observer could note the hostile behavior. In 36 instances, it was possible to follow the female long enough to establish the identity of the aggressor. Thirty-three of these instances occurred at Nest 1. When they are plotted against time, three well defined periods are evident. From May 15 to 26, the male attacked the female eight times and was attacked four times by her; from May 27 to 29, the male attacked the female five times and was attacked six times; and from May 30 to June 5, the male attacked twice and was attacked eight times. Thus there was a period of male dominance, followed by a short period of shifting dominance with intolerant behavior at about the same level of intensity in both members of the pair, and this was followed in turn by a period of female dominance up to the destruction of the nest by a snake on the fourteenth day of the nestling period. At Stub Nest 2, only three contacts were noted in which the aggressor could be determined, a sample too small to support any analysis.

Reversal of dominance has been described for a number of species. In the Song Sparrow, the male dominates the female until the start of laying (Nice, 1937:84). In the Chaffinch (*Fringilla coelebs*), the reversal may occur before, or at, the start of nesting (Marler, 1956:99). No observations were made of the pair at the Stub nests until shortly before the start of laying of the first clutch. The male was dominant through the entire incubation period and the first four days of the nestling period. The great drop in attendance by the brooding female occurred between the fourth and fifth days of the nestling period, and it was on the fifth day that the reversal of dominance started. In this pair, at least, reversal started when the female was free of her close attendance at the nest. By the time of the second nesting, hostility was apparently at a low ebb, judging by the sharp reduction in the number of hostile encounters recorded.

Although our observations were best documented at the Stub nests, such intolerant behavior was also noted at the Barn, Chinchilla House, and Red House 1956 nests, and it is apparently typical behavior of the Western Flycatcher.

Pair formation.—Only one instance of possible pair formation was noted in this study. On April 9, 1959, two flycatchers were seen moving about within an area that had been patrolled by a single bird on the preceding day. Several hostile contacts took place between these two, although most were confined to simple displacement of one bird by the other. A few short chases were noted, but they were not vigorous and the pursued bird never left the territory. At times the two called back and forth, and several times they foraged in close proximity with no display of hostility. During the observation period, one bird became involved in several prolonged chases of another flycatcher near the boundary of the territory. These chases were considerably longer and more violent than those involving the two birds which remained well within the territory. It seems likely that the prolonged chases at the periphery of the territory were attacks on a third, intruding flycatcher, and that the displacements and brief chases that occurred well within the territory represented low intensity hostile contacts between a male and female in the early stages of pair formation.

VOICE

The functions of some of the vocalizations of the Western Flycatcher are easily understood; others are given under such a wide variety of circumstances that their functional significance is difficult to interpret. The important vocalizations are the song, the position notes, the alarm note, the *chrrip* note, and the *pik-pik-pik* note.

Song.—The song of the Western Flycatcher has been most accurately described by Hoffmann (1927:205) as "*ps-séet ptsick*, and after a slight pause *sst*." Peterson's (1961:197) description is also good: "*pseet-trip-seet*! (*seet* highest); arrangement varies." A combination of these two descriptions, *ps-séet ptsick seet* (*seet* highest), describes accurately the song of the population at the Hastings Reservation. In addition to the variable arrangement of the three elements noted by Peterson, the interval between the second and third, or between the first and third in songs in which the second is omitted, can be highly variable. As Grinnell and Storer (1924:373) point out: "the pauses between songs seem no greater than the intervals between the constituent notes." Actually, the pauses between songs are often considerably shorter than the pauses preceding the delivery of the third note. The first and third elements are often repeated, and such repetition, together with the variability of the pause preceding the third note, sometimes makes it difficult to assign a particular note as the beginning of a song. The following sequence, with "1" representing the *ps-séet*, "2" the *ptsick*, "3" the *seet!*, and "P" a male position note (*pee-ist*), will suggest the variability inherent in the singing of this species. The sequence was taken from a tape recording made at the Hastings Reservation by Dr. William R. Fish on April 16, 1954: P P P-1-2 3 P-1-2-3 3 1-3 1-3 1-P-1-2-3-P 1-2-3 1-3 1-P-1-2 3-1-3-P 1-3 P 1-3-1 P 1-P-1-2-3 P P P 3-1-3 P 1-3-1-3 P 1-2-3-3 P 1-2-3-3.

In this sequence, *seet!* was given twice as an isolated note, once representing the completion of 1-2 after a long pause, and once representing a repetition, after a long pause, following a sequence of 1-2-3. Two songs start with *seet!* In one instance 3 follows 1-2 after a long pause and is immediately followed by 1-3, thus 1-2 3-1-3. This we interpret as belated completion of one song and immediate rendition of another. In the second case, 3-1-3 was given after three position notes and probably represents a new song starting with 3. The great majority of songs start with 1, and in many cases in which a bird resumed singing after a lengthy interruption, 1 was almost invariably the first note given. The sequence of *ps-séet ptsick seet!* or of *ps-séet seet!* is thus an accurate description of the great majority of songs, with *seet!* the true first note only rarely. The variable nature of the singing of this species has led to such erroneous descriptions as *see'rip, sip, see'rip* (Grinnell and Storer, 1924:372), apparently 1-3-1, and *set! p-swoit! putzit!* (Jewett *et al,* 1953:431), apparently 3-1-2.

The first phrase of the song, the *ps-séet*, is reminiscent of the male position note, *pee-ist*, and sonograms of the two (figs. 1, 2*a*, *b*) show that there is considerable similarity between the *pee-ist* and the terminal note of the *ps-séet*. The terminal *seet!* is a simple, high-pitched note, reminiscent of the female position note, although not particularly closely related to it (figs. 1, 2*e*). The middle phrase of the song, *ptsick* (fig. 1), does not suggest any other vocalization of the population considered here. Significantly, *ptsick* is given far less frequently than either of the other two elements. Of 431 individual phrases given by two singing males, regardless of sequence or repetition of phrases within individual songs, 181, or 42.0 per cent, were *ps-séet*, 169, or 39.2 per cent, were *seet!*, and only 81, or 18.8 per cent, were *ptsick*. Of the 153 individual songs given by these two males, disregarding repetition of individual phrases within songs, 79, or 51.6 per cent, were the full *ps-séet ptsick seet!*, 72, or 47.1 per cent, were *ps-séet seet!*, and two, or 1.3 per cent, were *ps-séet ptsick*. In these 153 songs, *ps-séet* was given in all, *seet!* was given in 151, or 98.7 per cent, and *ptsick* was given in 81, or 52.9 per cent. The *ps-séet* and *seet!* elements were repeated frequently within individual songs, but the *ptsick* was never repeated. It seems obvious that *ptsick* is used far less frequently than the other two phrases.

Although the song itself does not seem to vary in the course of the breeding season, singing can be divided into two well-defined categories, daytime singing and dawn singing. Daytime singing appears to be confined almost entirely to unmated birds. In 1957, three pairs were followed through their nesting programs. Two pairs raised two broods each. The male of one pair did no daytime singing at all; the male of the other pair sang briefly a few times during the first nesting and not at all during the second. The third pair raised one brood and the male did no daytime singing during this nesting. However, shortly after this male's mate had started construction of the second nest, she was found dead within the pair's territory on June 17. Her mate was kept busy caring for the two young of the first brood, but on July 3 he began occasional daytime

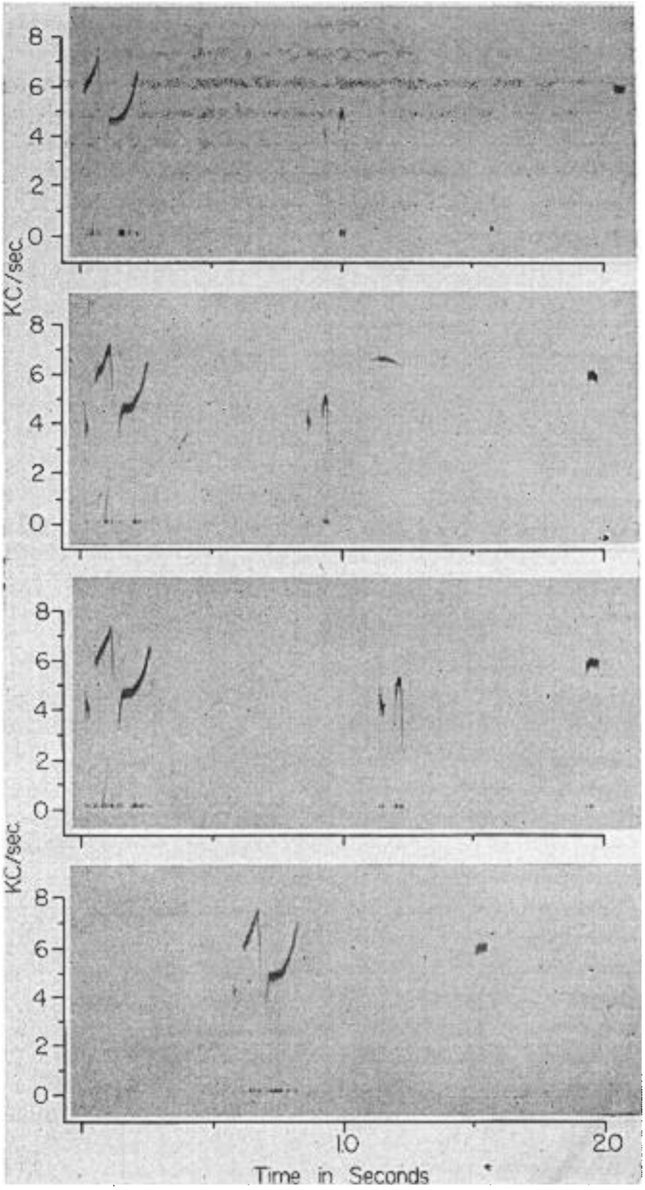

Fig. 1. Sonograms made by Peter Marler of four songs of the Western Flycatcher, recorded at Hastings Reservation by William R. Fish.

singing and sang nearly every day until July 19. In 1958, an unmated male sang in the daytime on all days of observation from April 12 until May 20. From the time observations were resumed on May 26 he did not sing. On July 22, a pair of adults was seen feeding a single juvenile in this male's territory. Allowing time for pair formation, selection of a nest site, building, laying, incubating, and fledging, it seems likely that this male had quit daytime singing as a result of pairing. In contrast, in 1958, an unmated male occupying the territory in which the female of a nesting pair had been found dead in 1957, sang in the daytime on many occasions between April 17 and June 26. This male was seen up to July 20, but only transient flycatchers were seen in his territory.

The virtual absence of daytime song in paired males and the persistence of such song in single males suggest that daytime singing functions primarily in mate attraction and ceases at the time of pair formation. Such singing may also function as territorial advertising, but this function appears to be secondary, since the cessation of daytime singing is controlled by the acquisition of a mate, and the resumption of daytime singing by a mated bird was triggered by the loss of the mate. Surely, in this latter case, territorial limits had been well established before the loss of the mate, and no other flycatcher had been seen in this male's territory other than the members of the pair and their young. A few playbacks of song to a nonsinging, and presumably mated, male always resulted in the immediate approach of the bird to the playback device; he either took a perch nearby or hovered over the recorder, sometimes within a few inches of it. At no time did this individual respond to playback by singing, suggesting rather strongly that the response of a male to an intruding flycatcher is immediate investigation and direct attack rather than singing back to the intruder.

Dawn song, on the other hand, is heard from mated males throughout the nesting period. Most of our records of dawn song were made in 1956, in the territory of a mated pair whose nest, probably a second nest, was followed from June 21 until the young were force-fledged on July 17. The male of this pair probably arrived on March 22, when dawn calling, but no singing, was first heard from his territory. Although his first dawn singing was heard on May 19, it probably started well before that date, as will be explained later. We have two records of dawn song in 1958 from males known definitely to be unmated. Since such single males do considerable singing in the daytime, it seems likely that most, or all, of them also sing at dawn.

The dawn program of the mated male observed on 43 mornings between March 22 and August 2, 1956, was similar to that of male Rufous-sided Towhees. In these towhees, early and late season dawn singing was preceded by considerable calling, and mid-season dawn singing was preceded by little or no calling (J. Davis, 1958:328, fig. 5; 329). Thus, in the flycatcher, calling was the first, and only, dawn vocalization on all 20 mornings of observation between March 22 and May 17; between May 19 and June 29, the first vocalization was song on nine of 13 mornings of observation, with one to five calls preceding song on the other four; and between July 3 and 17, the first vocalization on all five mornings of observation was calling (from two to 31 calls) followed by song. Since these dawn observations were concerned primarily with the Rufous-sided Towhees, which gave their dawn vocalizations at about the same time as did the flycatchers (*op. cit.*:325), since the towhees had virtually eliminated calling prior to dawn song by May 1 (*op. cit.*:328, fig. 5), and since the observer left the area as soon as towhees within earshot had started their dawn singing, it seems likely that on many mornings in April and May on which only flycatcher calling was recorded, singing after calling would also have been recorded had the observer remained in the area longer. Other records made of dawn singing involving males whose status was not known indicate that dawn singing is done by most, if not all, males.

We have no evidence of flight song or evening song, as has been reported for some other empidonaces, nor do we have any evidence that females ever sing.

The position notes.—There are two position notes, one given primarily, but not exclusively, by the male, and the other given exclusively by the female. The first of these is a sharp, clear *pee-ist*, or *see-ist* (fig. 2*b*). It is described by Hoffmann (1927:

205) as "*pee-ist*" and is apparently the note described by Peterson (1961:197) as "a sharp lisping *pseet*? or *seest*? with rising inflection (male)." The second note is a sharp *tsit* (fig. 2*e*); this is not described by Peterson (*loc. cit.*) and may be the note described by Hoffmann (*loc. cit.*) as "a low *whit*."

In pairs formed early in the season, although we could not assign sexes to the individuals involved, the difference in voice between the members of the pair was noticeable. On April 9 and 11, 1958, one member of a pair gave only the *pee-ist*, the other member only the *tsit*. On April 8, 1959, both members of a pair gave the *pee-ist*, and in addition one member also gave *tsit* notes. On April 22, one member of this pair gave

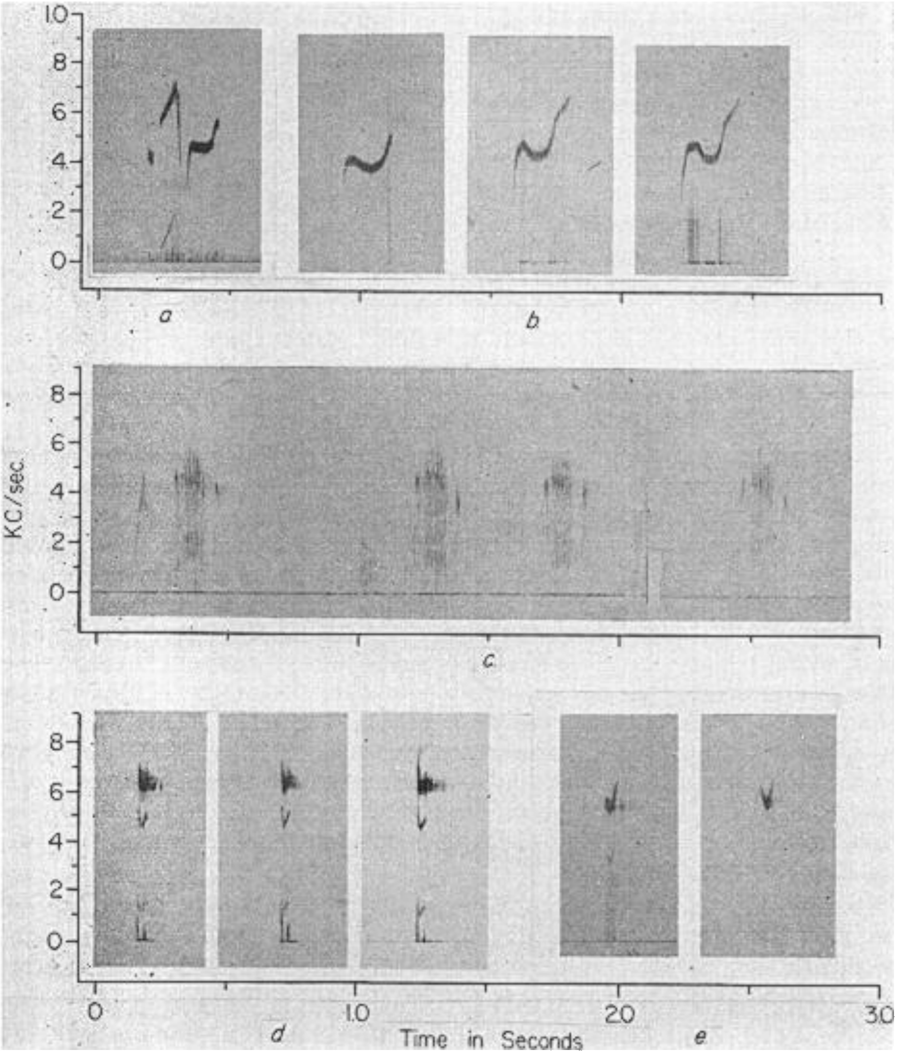

Fig. 2. Sonograms made by Peter Marler of vocalizations of Western Flycatchers, recorded at Hastings Reservation by Peter Marler; *a*, the opening phrase of a song, showing the similarity of the terminal note to the male position note; *b*, three male position notes; *c*, a series of four *chrrip* notes; *d*, three alarm notes; *e*, two female position notes.

frequent *pee-ist* notes, the other gave frequent *tsit* notes and only occasional *pee-ist* notes. The same was noted for a pair followed on March 18, 1960. It is obvious that both sexes give the *pee-ist,* and that one member of the pair gives this call more frequently than does the other, and does not give the *tsit.*

On April 17 and 18, 1958, one bird, presumably a female, was watched as she worked on a nest. After leaving the nest cavity, she gave the *pee-ist* on three occasions, but never more than two notes, and on three occasions she gave the *tsit* note, once only a single note, and twice in long series. On May 5, 1957, a nest was found, apparently near the beginning of the laying period, as incubation began on May 8. On May 5, 6, and 7, one member of the pair gave *pee-ist* notes while the other answered on three occasions with *tsit* notes. Twice, one bird gave both types of notes. Once the female left the nest and gave both types of notes. The two nests of this pair were watched for long periods of time (Stub nests 1 and 2). After the start of incubation the female gave the *pee-ist* note only rarely *during her periods off the nest.* After leaving the nest she almost invariably gave her position with *tsit* notes which were often given throughout her off period. The male, while the female was sitting, gave only *pee-ist* notes. When the female was *on* the nest, however, she frequently engaged in lengthy exchanges of *pee-ist* notes with the male. One example will suffice. On May 9, the female returned to the nest at 6:34.5 a.m. At 6:39, a lengthy exchange of calls began between the male and the incubating female, as follows (all notes *pee-ist* unless otherwise specified):

male, 1; female, 2; male, 1; female, 1; male, 1; female, 1; male, 2; female, 1; male, 1; female, 1; male, 1; female, 1; male, 4; female, 1; male, 5; female, 1; male, 4; female, 1; male, 5; female, 1; male, 1; female, 1; male, 2; female, 1; male, 1; female, 1; male, 2; female, 1; male, 1; female, 1; male, 4; female, 1; male, 1; female, *tsit*; male, 1; female, *tsit*; male, 1; female, *tsit*; male, 1; female, 1; male, 1; female, 1; male, 1; female, 1; male, 3; end of calling.

Exchanges of this type were noted frequently at all nests followed over long periods of time throughout both incubation and the period of heavy brooding; such exchanges must be considered typical nesting behavior in this species. The calling was usually started by the male and only rarely by the female. Often, a male would call many times without any answer from the sitting female, and then, at his next call, the female would answer and a lengthy exchange would follow. Most of the female's on periods were not marked by such exchanges, but communication of this kind was by no means uncommon at any of the nests at which lengthy observations were made. It seems likely that such exchanges between the members of the pair at the time when the female is largely confined to the nest serve to maintain the pair bond. The use of the *pee-ist* note by the female, rather than the *tsit* note, makes the exchanges effective. The *tsit* note would carry only a few feet beyond the confines of the nest, which is usually placed in a sheltered location. The louder and more penetrating *pee-ist* can undoubtedly be heard farther from the nest. Sonograms of the male and female position notes are given in figure 2*b, e.*

The alarm note.—This is a sharp *tsit,* much like the female position note, but noticeably louder and more emphatic (fig. 2*d*). It was given by both sexes in response to hawks flying overhead, to snakes and Scrub Jays (*Aphelocoma coerulescens*) near the nest, and in other circumstances in which one or both members of the pair became alarmed.

The chrrip.—This is a harsh note that may be rendered as *chrrip, prrit,* or *chrrr* (fig. 2*c*). It is used in a greater variety of circumstances than any note of the repertoire and some of its functions are difficult to interpret.

The use of *chrrip* as an aggressive note is well documented. Males used this note routinely in chases of, or actual combat with, other birds. Birds of unknown sex also used the *chrrip* in this fashion. We have relatively few records of the note accompanying hostile behavior of females but this is probably because it was much more difficult to identify females as such when aggressive behavior was noted. The difficulty was not so serious with males, as aggressive contacts were noted many times involving flycatchers whose mates, presumably females, were either incubating or brooding. In low intensity aggression, as in displacement or a brief chase, the note is given singly or as a doublet; in aggression of moderate intensity, as in a prolonged chase, the note may be given in a rapid series of four to seven or eight; and in high intensity aggression, as in the chase of, or actual combat with, another flycatcher, not the mate, the initial, rapidly given series of *chrrips* may be followed by a series of harsh *bzzt* notes and finally by several high-pitched squeaks. In some cases, *chrrip* notes were followed by a rapidly given series of bill snaps. Some chases were silent or accompanied by bill snaps only.

Single *chrrips* were sometimes given by the male at Stub nests 1 and 2 while his mate was on the nest. These were given when the male was perched or moving about his territory and they were unaccompanied by any overt hostile behavior. It is possible that these notes were territorial and they may have been directed at intruders which the male could see but which the observer could not. The function of these notes is not clear.

The most confusing use of the *chrrip* occurred when both members of the pair came together at or near the nest. At the Red House 1956 nest the female frequently gave a single *chrrip* after feeding the young as she passed the male coming to the nest with food. At Barn nests 1 and 2 the female frequently gave a single *chrrip* as she left the nest when the male came in to feed. At Stub nests 1 and 2 the male frequently gave a *chrrip* as he exchanged at the nest with the female, and he often gave single or double *chrrips* when the female left the nest after a session of incubation or brooding.

Notes given by other species of *Empidonax* under similar circumstances have been construed as "greeting notes." Of the Hammond Flycatcher, D. Davis (1954*a*:167) states: "Greeting Note. The female at the nest may chatter or twitter as the male comes near. The greeting is also used when the birds meet away from the nest, probably by both sexes." The same author (1959:79) says of the Least Flycatcher: "*Greetings.*—Both male and female may chatter and twitter when they meet away from the nest or at the nest. Typically the greeting is given when the female comes off the nest during incubation or comes from the nest during feeding of the young." Of the same species, Nice and Collias (1961:146) state: "All of us recorded soft *tsips* and *whits* from both parents, as well as twitters and chatters, and also a gentle and melodious trill lasting one or two seconds and barely audible from the blind. All these notes seemed to be greetings to the mate or young."

In the Western Flycatcher, in every pair that was watched over a long period of time, there was obvious hostility between the members of the pair. Further, the *chrrip*, which was used by *difficilis* under the circumstances described by other authors for the "greeting notes" of *minimus* and *hammondii*, is definitely the threat note used by *difficilis* when chasing or fighting with other birds, including the mate. Finally, most of the hostile contacts between members of pairs of *difficilis* occurred when the male and female came into close proximity either at or near the nest or newly fledged young. Therefore, we conclude that the *chrrip* used when the members of a pair came into close contact, whether followed by chasing or not, was not a greeting but an expression of hostility between male and female. The functional significance of the "greeting notes" of other species of *Empidonax* must be evaluated over long periods of observation of individual pairs, since hostility between the members of a pair of *difficilis*, although it may be demonstrated from time to time throughout the nesting and postfledging periods, is rather infrequently documented by actual chasing or fighting (see p. 342).

The *pik-pik-pik*.—This note is frequently given when an adult of either sex feeds the young in the nest or approaches the nest with food. Adults may also give this note when approaching dependent young with food. The series of *pik* notes is sometimes followed by a complex warble. All these notes apparently serve to notify the young of the parents' approach with food and to arouse the young when the parent wants to feed them, although many trips to the nest were silent.

The male of one pair (Stub nests 1 and 2) sometimes gave these notes during the incubation period. They were usually given just after the male had changed perches. Their significance is not known. The female at Barn nests 1 and 2 also gave this note during the fledging of the young.

Other vocalizations.—Adults gave a variety of warbles, squeaks, chirps, and other notes, the functions of which are not known.

Vocalizations of juveniles.—Recently fledged juveniles repeatedly give a scratchy *eep* when an adult comes with food. The young also give a *peep* which seems to serve as a position note, and as they mature the *peep* develops into a *tsit* which is much the same as the female position note.

Voice on the wintering grounds.—Two of us (J. and B. S. Davis) made brief observations of Western Flycatchers near Manzanillo, Colima, México, in October and November, 1957. These birds were not of the nominate race and pertained to one of the Mexican populations (J. Davis, 1960*a*:216). Several individuals gave the *pee-ist* note. The *tsit* note was heard very commonly. It did not seem likely that all these *tsit* notes were given by females; probably most were given by first-year birds, since we know that juveniles at the Reservation were giving this note at the time of their departure in August. Several chases were noted in which both birds gave *chrrip* notes. Most surprisingly, single males were heard singing on October 28 for at least two minutes; on October 29 for about 30 seconds; and on November 5 for several minutes. It seems likely that some gonadal recrudescence occurs in males of this species in the fall.

NESTING BIOLOGY

Nest site.—Considering natural situations first, 28 nests of the Western Flycatcher averaged 10.9 feet above ground, ranging from 0 to 25 feet up. Only one nest was terrestrial, placed on the shelf of a creek bank 10 inches below the top of the bank and three feet above water. The remaining 27 were in trees, including coast live oaks, valley oaks, maul oaks, black oaks, western sycamores, buckeyes, and willows. Of the 27, 15 were in willows or sycamores, suggesting a preference for riparian vegetation at this locality.

Nests were usually placed so that they were supported below and at the rear, sometimes in a crotch or between the main trunk of a tree and a limb or limb stub projecting from it. Six nests were placed behind flaps of loose bark slanting out from the main trunks of willows (2) or sycamores (4). Four nests were placed in cavities in main trunks or main forks of trunks.

In addition to natural situations, this flycatcher makes frequent use of buildings for nest sites. A variety of situations was used. The only prerequisites appeared to be a supporting surface with some shelter above. One nest at the Hatton Ranch in Corral de Tierra was placed in a tin cup hanging from a nail on the side of a house, and at the Reservation one female built in a small brass flower pot hanging from a nail on the wall of an unscreened porch.

There is a definite tendency for individuals to use a particular type of nest site, either in successive years or for successive nestings within a single season. Thus, certain sites in buildings at the Reservation have been used for several successive years, although it is not possible to say whether the same builder was involved. Bent (1942:249) has also noted this apparent attachment to a particular nest site over long periods of time. This reaction of the builder to a particular set of environmental features in choosing a nest site is exemplified by a bird that built its first nest in 1957 in a west-facing cavity 17 feet 9 inches up a dead willow stub which was 19 feet 3 inches high. This bird's second nest was placed in a west-facing cavity 15 feet 8 inches up a dead stub, probably oak, 16 feet 8 inches high. The following year, on April 17, an early date for the start of nest building, a flycatcher, possibly the same bird, was seen to make several visits to the cavity in which the second nest of 1957 had been built, apparently refurbishing the old nest. Subsequently the bird was seen to work on this old nest many times over a long period, but eventually the site was abandoned. Another site was chosen some time later, in a west-facing cavity 18 feet up on a large, main fork of the trunk of a huge, living willow which was within the territory occupied in 1957. The cavity had been formed where a limb had broken off and the base of the limb had rotted out. A nest was built here but this, too, was abandoned, and the bird returned to the site of the second nest of 1957 and resumed its building there. Eventually this site was also abandoned, and the pair evidently did not breed during the season of 1958. But the definite partiality to build in west-facing cavities in dead wood was apparent. Another pair in 1957 built successive, and successful, nests inside a barn; the second nest, a refurbished old nest, was a few feet from the first and was placed in an identical situation.

In 1956, a pair built under the roof of an open porch; the nest was placed in a nearly complete and unlined, but abandoned, nest of the Black Phoebe (*Sayornis nigricans*), attached to the porch wall just below the roof. The first egg was laid on June 23, suggesting that this was a second nest. In 1957, a pair built in an abandoned chinchilla house within the territory of the pair of 1956 and not far from the house which had been used as a nest site by that pair. When the pair using the chinchilla house in 1957 had successfully completed the first nesting, we expected that their second nest would be built on the porch used by the pair in 1956. Within a few days construction had started there. The old phoebe nest had fallen during the winter, and the new nest was placed in a small, brass flower pot hanging from a nail in the porch wall, an excellent substitute for the mud cup used by the pair in 1956. Although we have no evidence that the same pair was involved in both years, the similarity of nest sites in 1956 and 1957 suggests rather strongly that the same birds were involved.

The variety of nest sites used by the population at the Reservation indicates that the species is not restricted to any particular type of nest site, but the placing of successive nests in one season in nearly identical sites, and the similarity of nest sites found within a given territory in successive years, indicates that individual birds seek out a particular type of nest site.

Building.—The nest is built by one member of the pair, presumably the female. Periods of observation in which the builder could be followed to and from the sources of material indicated that only one bird was involved. Karlstrom (MS) followed the construction of one nest for nine and one-half hours between June 20 and 23, 1952. In each period of observation, only one bird was noted. Fifty-one sessions at the nest while the builder placed material averaged 42.7 seconds, and 50 sessions away from the nest, while the builder gathered material, averaged 129.1 seconds. There appeared to be a tendency for the builder to remain longer at the nest as construction progressed. On

June 20, nine periods at the nest averaged 31.3 seconds; the corresponding figures for June 21, 22, and 23, respectively, were: 10 periods, 34.0 seconds; 18 periods, 44.3 seconds; and 14 periods, 54.4 seconds. No trend was evident in the periods spent gathering materials.

On June 4, 1958, a flycatcher building a nest was watched for 35 minutes. During this period 15 trips to the nest were made, and again, only one bird was involved.

Two nests, found shortly after construction had started, took four and five days to complete.

The nest.—The materials used for nests are highly variable. Bent (1942:247–249), citing the observations of several ornithologists, leaves the reader with the impression that green moss is a very prominent element in nests of this species. This may be true in more humid localities where green moss is relatively abundant during the nesting season, but at the Reservation, where the supply of moss near most nest sites was restricted, this material was either absent from, or present only sparingly in, most nests. In only a few could it be considered a prominent element. Materials used in nests included moss, lichens (*Ramalina, Usnea,* and others, unidentified), outer bark, strips of inner bark (of *Aesculus californica, Salix* sp., and others, unidentified), dry and green leaves (of *Ceanothus ramulosus, Rhamnus crocea, Robinia pseudo-acacia, Quercus agrifolia, Q. lobata, Salix* sp., and others, unidentified), midribs and veins of large leaves (of *Platanus racemosa,* and others, unidentified), seedheads of *Rumex acetosella,* stems and heads of dry grasses (*Avena* sp., *Elymus glaucus,* and others, unidentified), dry tendrils of *Marah fabaceus,* the dry, spirally-coiled portions of the fruits of *Erodium* sp., small, dry annuals, twigs, spider web, and feathers. The cup was almost invariably lined with fine, dry grass, alone or in combination with lichens and/or strips of inner bark. Near houses and barns, artificial materials were widely used, including thread, string, burlap, paper, dust kittens, human hair, yarn, horsehair, straw, wood chips, and onion skin. Often the pieces of string or burlap had been frayed out to form a soft matting. One nest was composed mainly of spider web, a tough, spongy, and beautifully fashioned structure. A nest on the Hatton Ranch at Corral de Tierra was made mainly of dog hair, obtained from a nearby hedge against which dogs had scratched themselves, leaving tufts of hair available to the nest builder.

In general, availability was the most important factor governing the use of nest materials. The variety used, not only in the entire series of nests examined, but in individual nests as well, indicates that these flycatchers do not rely on certain rigidly selected types of materials but use whatever may be handy.

In size and general appearance there is less variability among nests than in the materials used in construction. The mean longest diameter of the inside cup was 2.1 inches (7 nests, range 1.75–2.50), the mean shortest diameter was 1.8 inches (7 nests, range 1.50–2.25), and the mean depth was 1.1 inches (4 nests, range 0.75–1.25). The mean longest outside diameter of four nests was 4.7 inches (range, 4.0–5.0), and the mean shortest outside diameter of three nests was 4.0 inches (4.0–4.5). Characteristically, nests are placed against a vertical surface so that the rear outside wall is flattened. Some nests thus appear to be somewhat triangular in shape, while others are broadly oval with one long side flattened. The combination of size, shape, and proportion of cup to outer supporting structure served in most cases to identify nests of this species at the Reservation, where only one species of *Empidonax* occurs.

Clutch size and laying.—Thirteen clutches at the Reservation consisted of from three to at least five eggs. Of these, three were of three eggs, nine were of four, and one nest contained five young. A nest at the Von Soosten cabin held four eggs, two at the

Hatton Ranch contained three and four eggs, and three nests at Carmel Highlands contained four eggs each. Of the four three-egg clutches, three were from second nests. In this area, the usual clutch is four in first nests and three in second nests. These figures agree in general with those given by Bent (1942:249), who did not distinguish between first and second clutches.

The earliest date for the laying of the first egg of the first clutch at the Reservation was May 4, or before. Linsdale (MS) noted a bird building on April 20, 1938, and incubating four eggs on May 7, so that in this instance the date for the laying of the first egg would have been not later than May 4. In 1957, the earliest date was May 8 at two nests, and in 1962, May 7. The latest known date for the laying of the first egg of the second clutch was June 24, 1956 and 1957. Karlstrom found a nest containing three eggs on July 7, 1952. The female was still incubating on July 18, when his observations ceased. This suggests that the laying of the first egg had taken place about July 1.

At one nest, the first egg was laid on the day after the completion of the nest. At four nests, first eggs were laid within two days, at most, after completion of the nest, and possibly on the day following completion. Most eggs were laid in the morning, although this was not invariable. One female was observed on the nest during the laying of an egg. She was on the nest at 11:45 a.m. and did not leave until 12:20 p.m. The egg was probably laid during two periods of violent straining totaling five minutes between 11:58 and 12:03.

The laying programs of most females were marked by irregularity in that the eggs of a clutch were not laid daily. Table 1 shows the programs at nine nests at the Reservation at which laying was followed accurately. In seven, one day was skipped within the limits of the entire laying period. At three nests at Carmel Highlands, according to data supplied by Laidlaw Williams, one clutch of four was laid on successive days. In the other two, laying was skipped on at least one day, two eggs of each clutch of four being laid in a three-day period.

TABLE 1

SEQUENCE OF LAYING OF INDIVIDUAL CLUTCHES

Date of first egg	Day of laying				
	1	2	3	4	5
May 7	X		X	X	X
May 8	X	X		X	X
May 16	X	X		X	
May 21	X	X	X		X
June 11	X	X	X		X
June 23	X		X	X	
June 23	X		X	X	X
May 8	X	X	X	X	
June 24	X	X	X		

The dates for the beginning of laying suggest that four of the nests in table 1 were first nests; at three, laying was irregular. Two were probably second nests; laying at each was irregular. One was a known second nest at which laying was regular. Two nests of intermediate date may have been replacement nests. Laying at each was irregular. The data from the small sample of nine nests indicate that most laying schedules are interrupted, whether at first or second nests.

Laying in this species varies from rhythmic, with egg deposition at approximate one-day intervals, to arhythmic. In the seven clutches which were laid irregularly, the second day was skipped in three, the third day in two, and the fourth day in two. Thus, it is impossible to suggest any standard interval between eggs that would account for the schedules at all nests. Since no two clutches were known definitely to be laid by the same bird, it is not possible to say whether or not a particular laying schedule is characteristic of the individual.

One incident suggests that laying may be rather rigidly timed to the schedule of nest construction and that, once started, it cannot be stopped. After the young of her first brood had left the nest on June 10, a female started construction of a new nest, some distance from the first, on June 13. On the afternoon of June 15, the nest had been pulled from its support, possibly by a Scrub Jay seen nearby; it was replaced on its support by the observer but by the morning of June 16 it had been pulled down again and it was not replaced. At noon on June 16 the much flattened first nest was checked; it contained one egg. On June 17, the female was found dead on territory. A brood patch was present and a fully formed egg lay at the entrance to her oviduct. In this female, the laying cycle was apparently closely integrated with, but not controlled by, the schedule of nest building and when the latter was interrupted, the laying cycle proceeded independently and the battered first nest was pressed into service to receive the eggs of the second clutch.

Two observations indicate that the Western Flycatcher is a determinate layer. The second egg of one first clutch was destroyed in marking but the female laid a total of only four, incubating the remaining three. The total laid agrees with the usual size of first clutches. In a second nesting, one of the first two eggs was found punctured and at some distance from the nest. This female laid one more egg for a total of three and incubated the remaining two. The total of three agrees with the usual size of second clutches.

The eggs.—Descriptions and measurements of the eggs of the Western Flycatcher are given by Bent (1942:249).

Incubation period.—We have nine definite records for the incubation period of the Western Flycatcher at the Reservation, calculating the incubation period from the laying of the last egg to the hatching of that egg. These records pertain to nests at which eggs were marked or at which all eggs hatched. At one nest three eggs were laid but only two were incubated; one of the first two was found destroyed and removed from the nest. The incubation period at this nest was 15 days. At seven other nests, each with four eggs, the incubation period was 14 days at two and 15 days at five. At a ninth nest, with four eggs, the incubation period was 15.5 days. At this nest the female, for some reason unknown to us, was absent on the sixth night of the incubation period. The temperature reached a low of 57°F. in her absence and this may have delayed hatching by a few hours. On behavioral evidence, incubation at a nest containing at least five eggs lasted 15 days. At another nest containing at least three eggs, behavioral evidence suggested an incubation period between 13.5 and 14 days. The incubation period at the Reservation is thus 14 or 15 days, with 15 days the usual period. This agrees with the figure of 15 days given by Williams (1942:239) for a nest at Monterey, California.

Incubation.—Incubation is performed by one bird, assumed to be the female. Heavy incubation starts with the completion of the clutch, although the female may spend an appreciable amount of time on the nest prior to this. The onset of roosting on the nest is variable. At three nests, the females started to spend the night on the nest after laying the first egg of a four egg clutch, the second egg of a three egg clutch, and the third egg of a four egg clutch.

The male remains near the nest site much of the time; he calls frequently and is often answered by the incubating bird. He does not appear to guard the nest, whether the female is present or not. Feeding of the incubating female by the male occurs occasionally. At Stub Nest 1, such feeding was observed once on the sixth day and once on the tenth day of the incubation period. It was noted three times at Stub Nest 2, on the second, fourth, and fifth days of incubation. At Barn Nest 2, the male fed the female on the sixth day of incubation. He also came to the nest on the tenth and fourteenth days, but it could not be seen whether or not he fed the female at these times.

Data for the attendance of the incubating bird are extensive for Stub nests 1 and 2 and for Barn Nest 2. The records cover the entire incubation period for each nest, from egg laying through hatching. Attendance of the female is given in figure 3. The percentages of time on the nest for the entire incubation period vary only 3.5 per cent for the three nests, ranging from 77.1 per cent of 94.1 hours of observation at Barn Nest 2 to 80.6 per cent of 70 hours of observation at Stub Nest 2. Figures for attendance from day to day vary, but not greatly. Attendance decreased markedly on the fourteenth day at Barn Nest 2, but this was probably because of the hatching of the first egg during the afternoon, when attendance was only 59.8 per cent. The attendance at Barn Nest 1 during hatching was also low (59.4 per cent).

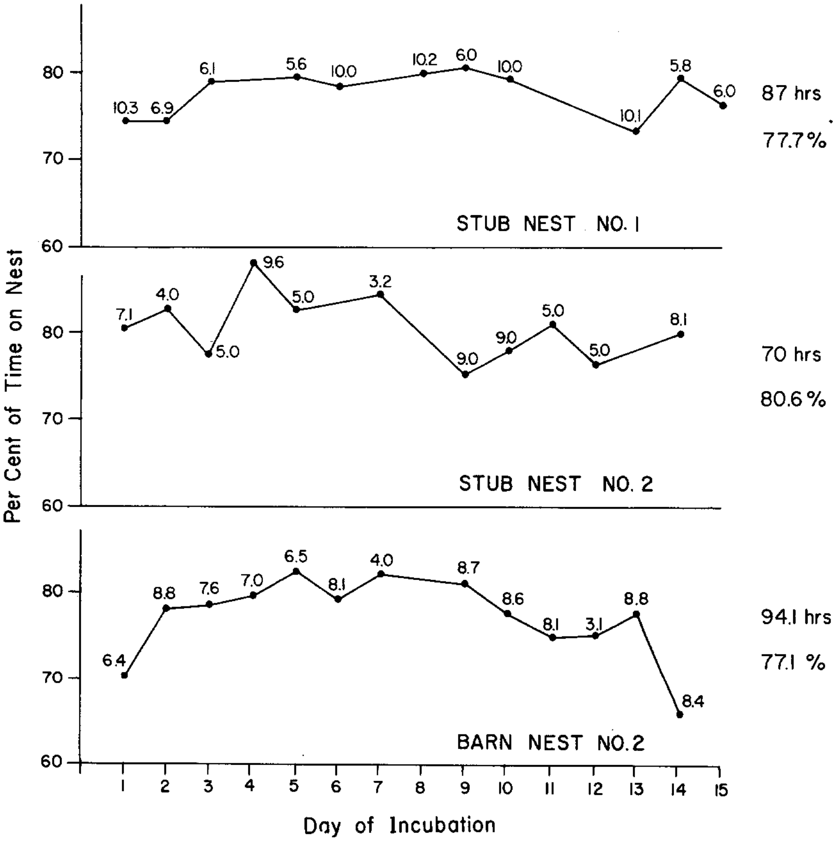

Fig. 3. Daily attendance at the nest during incubation at Stub nests 1 and 2 and Barn Nest 2. Numbers given for each day of observation indicate length of observation period in hours.

There is no correlation of attendance with mean daily temperature as regards total time spent on and off the nest during the entire incubation period. At Stub Nest 1, the entire incubation period fell on days averaging less than 58°F., and the attendance was 77.7 per cent. Incubation at Stub Nest 2 and Barn Nest 2 was carried out at daily mean temperatures ranging from 60° to 85°F. Attendance at these two nests was 80.6 per cent and 77.1 per cent, respectively. However, on a daily basis there was a slight correlation with the mean daily temperature at two nests. At Barn Nest 2, the average daily attendance figures ranged from 78.1 to 82.7 per cent at mean daily temperatures between 60° and 65°F., whereas these averages were 75.1 and 77.6 per cent for two days when the mean daily temperatures were 81° and 83°F., respectively. At Stub Nest 2, attendance on days averaging 60° to 65°F. was 80.1 to 82.8 per cent, but it was only 75.5 and 78.1 per cent on two days averaging 79° and 78°F., respectively. No such correlation existed at Stub Nest 1, perhaps because the entire incubation period was cool, with daily mean temperatures below 58°F.

Comparison of incubating attendance during the morning and during the afternoon does not show a clear and constant relationship to the temperatures at these times but suggests that incubation is heavier in the morning when temperatures are lower. However, comparison of the attendance rates on cool mornings with those on warm afternoons shows that on only 15 of 24 days was the attendance higher in the morning than in the afternoon.

TABLE 2

MEAN LENGTH IN MINUTES OF ON AND OFF PERIODS AT THREE NESTS DURING INCUBATION (N IN PARENTHESES)

a.m. on	a.m. off	p.m. on	p.m. off	Daily on	Daily off
		Stub Nest 1			
21.7 (120)	5.9 (130)	27.5 (34)	8.5 (37)	23.0 (154)	6.4 (167)
		Stub Nest 2			
31.4 (69)	7.6 (74)	36.8 (15)	12.2 (18)	32.4 (84)	8.5 (92)
		Barn Nest 2			
35.5 (50)	8.5 (58)	32.3 (52)	10.0 (60)	33.8 (102)	9.3 (118)

Incubation at the two Stub nests was undoubtedly performed by the same bird, and the same was true of the two Barn nests. Slightly higher attendance during the second nestings of both pairs of birds is evident. Attendance at Stub Nest 1 was 77.6 per cent whereas at Stub Nest 2 it was 80.6 per cent. Attendance at Barn Nest 1, with the records covering only the first and seventh full days of incubation (12.2 hours of observation), was 72.6 per cent whereas attendance at Barn Nest 2 rose to 77.1 per cent. There was a corresponding shortening of the incubation periods at these second nests, Stub Nest 2 taking one day less than Stub Nest 1, and Barn Nest 2 taking one-half day less than Barn Nest 1. There is no direct correlation of this change in attendance with temperature, as the incubation periods for the earlier, less attended nests came during periods of lower daily mean temperatures. The reason for the increased attendance at second nests is not clear. It is possible that a shortened incubation period during the second nesting may be advantageous in shortening the entire second nesting cycle, perhaps a necessity to insure sufficient time for proper development of the young before migration. Considering the length of time spent in the area after fledging of these second broods, however, it seems dubious that a shortening of the nesting period by one-half or one day would be of any real significance.

Sessions on and off the nest.—On the average, the incubating bird at Stub Nest 1 spent 23 minutes on the nest and 6.4 minutes off. However, at Stub Nest 2 the same bird was on the nest an average of 32.4 minutes and off for 8.5 minutes. At Barn Nest 2 the incubating bird averaged 33.8 minutes on the nest and 9.3 minutes off (table 2). The longest complete session on any nest was 178 minutes at Barn Nest 2. This occurred on the ninth day of incubation, a very hot day. Another session, incomplete, at Stub Nest 2 lasted 185 minutes and occurred on the fourth day of incubation, again a very hot day.

TABLE 3

FREQUENCY DISTRIBUTION OF THE LENGTH IN MINUTES OF THE ON AND OFF PERIODS DURING INCUBATION

Distribution limits	Stub 1		Stub 2		Barn 2	
	N	Per cent	N	Per cent	N	Per cent
			ON PERIODS			
0.5–5	0	0.0	0	0.0	1	1.0
5.5–10	11	7.1	2	2.4	0	0.0
10.5–15	16	10.4	6	7.1	9	8.8
15.5–20	41	26.6	12	14.3	9	8.8
20.5–25	33	21.4	9	10.7	22	21.6
25.5–30	28	18.2	17	20.2	13	12.7
30.5–35	10	6.5	10	11.9	13	12.7
35.5–40	10	6.5	5	6.0	6	5.9
40.5–45	2	1.3	6	7.1	9	8.8
45.5–50	1	0.6	5	6.0	3	2.9
50.5–55	0	0.0	6	7.1	7	6.9
55.5–60	1	0.6	2	2.4	4	3.9
60.5–65	0	0.0	1	1.2	3	2.9
65.5–70	0	0.0	1	1.2	1	1.0
70.5–	1	0.6	2	2.4	2	2.0
Totals	154	99.8	84	100.0	102	99.9
			OFF PERIODS			
0.5–3	4	2.4	9	9.8	2	1.7
3.5–6	93	55.7	27	29.3	12	10.2
6.5–9	50	29.9	28	30.4	52	44.1
9.5–12	12	7.2	10	10.9	36	30.5
12.5–15	7	4.2	7	7.6	10	8.5
15.5–18	0	0.0	5	5.4	6	5.1
18.5–21	0	0.0	1	1.1	0	0.0
21.5–24	0	0.0	3	3.3	0	0.0
24.5–	1	0.6	2	2.2	0	0.0
Totals	167	100.0	92	100.0	118	100.1

At the Stub nests, the average on and off periods were shorter in the morning than in the afternoon (table 2). At Barn Nest 2, the morning off periods averaged shorter, but the morning on periods were longer than those of the afternoon. In general, the on and off periods seem to be shorter during periods of lower temperature. This is further illustrated by the different patterns for Stub nests 1 and 2, at which the same female was involved. All daily mean temperatures at Stub Nest 1 were below 58°F., whereas at Stub Nest 2 all daily mean temperatures were 60°F. or above. The on and off periods were considerably shorter at Stub Nest 1. Nice (1937:125) has shown that the on and off periods for the Song Sparrow were shorter during lower temperatures. She offered the possible explanation that the incubating bird may become hungry more often and therefore leave the nest more frequently, but that the lower temperatures may stimulate her to return to the eggs sooner than when temperatures are higher. The same explanation may hold true for the Western Flycatcher.

Frequency distributions of all the on and off periods for the three nests studied in detail are given in table 3. The data show that the on periods at Stub Nest 1 were concentrated mainly between 15.5 and 30 minutes and the off periods between 3.5 and 9 minutes. The percentage distribution of the periods in the other two nests is spread out over a much wider range, again demonstrating the direct correlation between low temperatures and shorter on and off periods. During the warmer days, the on and off periods are not only longer, on the average, but they are also more variable. Again, at Stub Nest 1 only five on periods, or 3.1 per cent of the total, exceeded 40 minutes, in contrast to Stub Nest 2 and Barn Nest 2, for which the figures were 23 and 29 periods, and 27.4 and 28.4 per cent, respectively. This again emphasizes the shortness of the on periods in cool weather.

J. Davis (1960*b*:440) showed that the off periods of the Rufous-sided Towhee were nearly constant and did not vary with the length of the preceding on period. He suggested that the desire to return to the nest was a stronger stimulus than was hunger or whatever factor or factors compel the female to leave the nest. The off periods of the Western Flycatcher are not as consistent as were those of the towhee and there is a suggestion that the longer on periods are followed by longer off periods (table 4). This is especially pronounced at Stub Nest 2.

TABLE 4

RELATIONSHIP OF OFF PERIOD TO THE PRECEDING ON PERIOD DURING INCUBATION[1]

	Range of on period	0.5–15	15.5–25	25.5–40	40.5–
Stub Nest 1	Mean off period	6.2(27)	6.3(74)	6.9(48)	7.4(4)
	Standard error	0.51	0.35	0.38	....
	Range	3.0–14.0	2.0–24.5	3.5–15.0	5.5–10.5
	Coefficient of var.	43.1	48.1	38.4	....
Stub Nest 2	Mean off period	5.4(8)	5.4(21)	8.3(32)	12.0(19)
	Standard error	1.14	0.52	0.61	1.88
	Range	1.5–11.5	2.0–10.5	4.0–17.0	0.5–30.5
	Coefficient of var.	59.2	44.0	41.6	68.1
Barn Nest 2	Mean off period	8.8(10)	7.9(30)	9.6(31)	10.1(28)
	Standard error	1.26	0.49	0.56	0.55
	Range	2.0–16.5	0.5–13.0	4.0–18.0	6.0–17.0
	Coefficient of var.	45.5	33.9	32.5	28.8

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[1] Data expressed in minutes; N in parentheses.

Our data on attendance during the incubation period were gathered during long, almost daily, periods of observation. As a result, an observer could follow only one nest at a time. D. Davis (1954*b*) has suggested a method which would make it possible for a single observer to obtain the percentage of daytime incubation attendance at several nests simultaneously. According to this method, the observer makes periodic visits to a nest and the percentage of visits on which the incubating bird is present would yield a close approximation to the actual per cent of time spent in incubation. Davis cautioned against alarming the sitting bird, and he noted that an observer using this method must visit the nest at various times of the day in order to make an accurate study. To test the method, he reanalyzed various records of incubation attendance gathered by the actual watching of nests by making "pretend visits" to the nest at 15 minute intervals during the periods of actual observation. His data for the Hammond Flycatcher, for which actual attendance was 77 per cent, was 73.2 per cent on the basis of "pretend visits." He also reanalyzed original records made by S. C. Kendeigh for one female each of the Eastern Bluebird (*Sialia sialis*), Catbird (*Dumetella carolinensis*), and House Wren, and the results from these much larger samples showed a striking similarity between the actual per cent of time spent on the nest and the percentage of times the female was on the nest at the "pretend visits" (*op. cit.*:332).

Applying this method to our data, one finds a striking correspondence between the actual percentage of incubation attendance and the percentage derived from the "pretend visit" method. The percentages for Barn Nest 2, Stub Nest 1, and Stub Nest 2, with the actual percentages given first, are 77.1 and 76.9, 77.7 and 79.6, and 80.6 and 80.4, respectively. Only at Stub Nest 1 did the percentages differ by more than 0.2 per cent. The data computed for morning and afternoon attendance were usually quite close to the actual figures derived from actual observation, but there were enough exceptions to verify Davis's statement that visits should be made to the nest at all times of day. Daily percentages, figured for Barn Nest 2 on the basis of "pretend visits," deviated from actual percentages with such frequency and to such a degree (as much as 17 per cent) that the records for any one day could not be considered reliable. It would be necessary to make periodic visits to the nest not only at different times of the day, but also on most days in the incubation period.

This method provides only an estimate of the percentage of time spent in incubation and it provides no data on rhythm and length of the on and off periods and on the various facets of behavior at the nest which can be recorded only by patient watching. One could miss, by using this method, participation by both sexes in incubation. However, the simplicity of the method, its apparent high degree of accuracy, and its applicability to several nests within a short span of time, all recommend it to future testing and use in situations in which the only point of interest is the percentage of daytime incubation attendance.

TABLE 5

ATTENDANCE AT THREE NESTS DURING THE HATCHING PERIOD

Observation period (min.)	Per cent on	On periods N	On periods Mean	Off periods N	Off periods Mean
		Stub Nest 1			
362	76.7	24	11.5	24	3.5
		Barn Nest 1			
180	59.4	10	9.7	10	7.1
		Barn Nest 2			
504	66.2	27	12.0	27	6.1

Hatching period.—Attendance at the nest and the length of the on and off periods changed considerably during the hatching period (table 5). Of the three nests for which sufficient data were available, only at Stub Nest 1 did the attendance percentage remain as before hatching. At the other two nests, attendance figures were reduced by as much as 11 per cent. At all three nests, the average length of the on periods was reduced appreciably, whereas the average length of the off periods was shortened to a lesser degree. It is possible that the sitting bird may have actually made feeding trips during the hatching period, although no food was observed in its bill on any of its return trips to the nest. The pecking and chewing motions seen during this period may actually have been attempts to feed the newly-hatched young rather than attempts at helping the young bird out of the egg or any of the other possibilities mentioned in the next section.

Hatching.—Hatching occurred over a period of two days, as a rule. However, there was one record of hatching occurring on three successive days. Observations of actual hatching are virtually impossible to obtain, but there are two records of the actions of the sitting bird during the process. Both instances were at the barn where the nests were more readily observed.

By the evening of May 27, three of the four eggs of Barn Nest 1 had hatched. At 1:56 p.m. of the following day, one egg still remained unhatched. Several times during the ensuing two hours the sitting bird probed into the nest with its bill. At 2:13, when it pulled its bill out, it made smacking motions. Again, about 2:46, this probing and smacking, followed by swallowing, was repeated several times. At 3:56 the sitting bird removed a piece of egg shell from the nest and carried it out through the barn door. The nest was checked at 4:40 and the hatching of the last egg was verified. A flattened piece of the egg shell remained in the nest. This had been removed from the nest by 3:33 p.m. of the following day.

On July 10, there were two eggs in Barn Nest 2 at 11:27 a.m. At 11:40, the sitting bird probed into the nest and appeared to be eating something. At 11:43, the process was repeated for 30 seconds, and again at 11:47 for 45 seconds. Finally, at 11:49.5, the sitting bird left the nest with a piece of egg shell, the larger end of the egg. At this time, the newly hatched young bird lay partly in the smaller end of the shell. At 12:00.5 p.m., the same parent was seen probing into and "eating" from the nest. At 12:02, this parent removed the other piece of the hatched egg. The young bird was red in color and lay huddled next to the unhatched egg.

On investigation, the larger end of the hatched egg was found outside of the barn about 30 feet from the nest. The nest was visible from the point at which the adult had dropped the egg shell. The smaller end of the shell, the second piece removed, was found about 12 feet northwest of the first piece, outside the barn, and out of sight of the nest. The second egg in this nest had hatched by 7:37 a.m. of the following day.

The maximum time required for the hatching of these two eggs was about two hours for the egg in Barn Nest 1 and about 23 minutes for the egg in Barn Nest 2. It was not known when the eggs pipped. The role of the adult in hatching is conjectural. The probing and apparent eating of objects within the nest at the time of hatching may indicate that the adult was actually extricating the young from the egg or it may have been a more passive activity, such as the cleaning up of bits of egg shell and membrane. The incubating bird is certainly aware of the impending hatching as judged from its increased restlessness on the nest at that time. The cues are probably through the movement and/or peeping of the young bird within the egg.

First feeding of the young.—The first feeding of the newly hatched young was not always easily seen and our data on this activity are fragmentary. At Stub Nest 1, pieces of egg shell were removed at 8:28 and 10:02 a.m. No feeding was observed up to 11:46, when the observer left the area. At 2:27 p.m., the observer had returned, but it was not until 3:24 p.m. that the male fed the young. The female fed at 3:25. These were the first observed feedings at this nest, although feeding may well have occurred between 11:46 a.m. and 2:27 p.m.

At Stub Nest 2, the young probably hatched on the morning of June 29, as judged from the behavior of the sitting bird. No feeding was observed until 5:01 p.m. when the female fed the young. Observations were continued until 5:58 but no further feeding occurred. On the next day, observations were made from 8:40 a.m. to 12:40 p.m. and from 3:05 to 6:30 p.m. During these periods, the female fed the young 26 times. The first feeding by what was probably, but not certainly, the male occurred at 5:34 p.m. Later, two feedings presumed to be made by the male occurred at 5:37.5 and 5:48.5.

A nest observed in July, 1961, contained three eggs. At 8:40 a.m. one egg had recently hatched, as part of the egg shell was still attached by partly dried membranes to the head of the young bird. At 10:35, an adult, probably the male, apparently fed this young bird. The female was soon brooding after this and she was then fed by the male at 10:42, 10:48, and 10:55. She did not feed the nestling. After the female left, the observer tapped the side of the nest and the young bird gaped at once, at 10:59. Six minutes later, the male fed the female who was by then back on the nest. She, in turn, apparently tried to feed the young bird but could not get a response. Then, two minutes later, she successfully fed the nestling. Subsequently, the male (?) fed at 12:05 p.m. After this, he fed the female at 12:07. She, in turn, tried to feed the nestling, unsuccessfully, and she tried three more times in the next three minutes, apparently with no success. It would seem that the adults will frequently try to feed a newly hatched nestling but that only occasionally will it eat. The parents probably continue to bring more food than is necessary at first. "Extra" food would probably be brought to the first hatched nestling only, as the first nestling would probably start taking food regularly by the time the second and later young hatched.

Feeding.—Observations of feeding were quite accurate at Barn Nests 1 and 2. The observer was a maximum of only 23 feet from the nest and only six feet below it. All approaches to the nest were easily visible and with the aid of binoculars it was relatively easy to ascertain whether or not the adults carried food. Observing at the Stub nests was more difficult because the observer was farther from the nest, light conditions were sometimes poor, and the nests were in more protected situations. Even at these nests, however, the number of trips to the nest could be counted accurately and feeding movements could be seen easily, although it was often impossible to see whether or not an incoming adult carried food or not. The data for all these nests were compiled on the basis of the day of nestling life and all begin with the first full day.

The general trend of feeding rates for the four nests may be seen in figure 4. As a rule, feeding is relatively light during the first four or five days of nestling life. These first few days are followed by a period of two to four days of increasingly heavy feeding after which a more or less maximal rate is reached and maintained until the young leave the nest. Thus, there is no steady increase in feeding rate throughout the entire nestling period; rather, a plateau is reached and maintained. The single exception was at Barn Nest 1, at which the feeding rate decreased prior to fledging.

The fact that feeding rates level off and do not increase steadily during the nestling period is of interest since one might assume that a steady increase would be required to support increase in weight of the young and to furnish sufficient energy for their increasing motor activities. Feeding activities of the parents at a nest watched by Chattin (see table 10) indicate that adult Western Flycatchers can vary their feeding rates considerably and it does not seem likely that the levels reached at the various nests represent the maximum feeding capabilities of the parents. Apparently, the young do not require steadily increasing amounts of food as the nestling period progresses. Relative daily increase in the weight of the young lessens as the nestling period wears on,

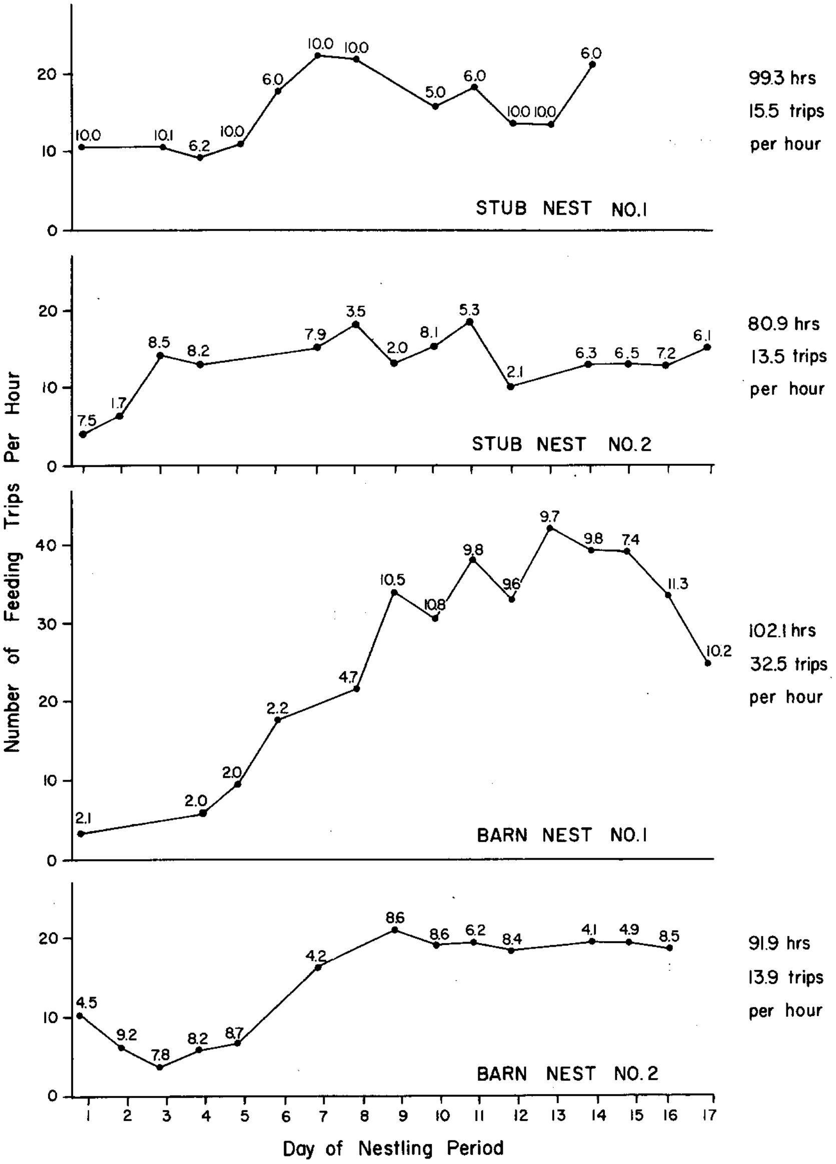

Fig. 4. Daily feeding rates. Numbers given for each day of observation indicate length of observation period in hours.

and this, together with the cessation of growth of some feathers, may provide the energy necessary for the development of motor faculties.

King (1955:162, fig. 2) presented a figure for the Traill Flycatcher in southeastern Washington which depicted a steady increase in weight of the young during the first 11.5 days of the nestling period, when maximum weight was reached, followed by a steady decrease in weight during the last two days of nestling life. He presented no data on feeding rates and no correlations can be made between feeding rates and the pattern of weight increase and decrease. It is of interest to note that the median weight of 15.0 gm. for five nestlings on day 11.5 of the nestling period is considerably above the weight of adults. Sixteen male *E. traillii* taken in Oregon in May and June (Mus. Vert. Zool.) averaged 12.6 gm. Four males and three females taken in Baja California in May and June (MVZ) averaged 12.6 and 10.4 gm., respectively. Although we are comparing samples of different origin, the differences between the weights of King's sample of nestlings and the samples of adult specimens are large enough to suggest biological significance and probable statistical significance.

King (*op. cit.*: 164) observed that "The decline in weight [of *E. traillii*] after day 11.5 is probably correlated with the increased activity of the young in the nest." This accumulation of additional weight above the adult weight may occur prior to the expenditure of this greater amount of energy for motor activity but after certain feather growth has essentially ceased. This extra weight may also serve to sustain the young temporarily if they should be forced to leave the nest prematurely.

TABLE 6

WEIGHTS IN GRAMS OF NESTLING WESTERN FLYCATCHERS

Day of nest life	N	Mean weight	Range	Mean change in weight
1	4	1.5	1.4–1.5	......
2	4	2.1	2.0–2.2	+0.6
3	3	2.8	2.8–2.9	+0.7
4	3	3.6	3.6–3.7	+0.8
5	3	5.0	4.9–5.0	+1.4
6	3	6.4	6.2–6.6	+1.4
7	3	7.3	7.1–7.7	+0.9
8	3	8.8	8.7–8.9	+1.5
9	3	9.4	9.2–9.6	+0.6
10	3	9.8	9.6–10.0	+0.4
11	3	10.2	10.1–10.3	+0.4
12	3	10.8	10.7–10.8	+0.6
13	3	11.0	10.8–11.2	+0.2
14	3	11.0	10.0–11.7	0.0
15	2	10.0	10.0	—1.0
16	1	10.0	......	0.0

We have data on nestling weights for one nest containing four young, later reduced to three, then two. It should be noted that one of the young hatched one day later than the other three. In the mean and range columns of table 6, in which the weights of these young are presented, we have adjusted the data for the late-hatched individual so that the data for all four are presented on the basis of actual day of nest life. The weight of the late individual was close to the mean weight of its sibs on all days of equal age, although it tended to gain at a slightly accelerated rate so that on the eleventh day after the first young had hatched, the weight of the late-hatched bird was the same as the weight of the other nestlings, although it was a day younger. This equality was nullified when it lost weight on the fourteenth day. The remaining sibling also lost weight on its fifteenth day of nest life so that the weights were equalized again. The drop in weight, of course, occurred on the same calendar day for both nestlings. At this time a heavy infestation of lice was noted which may have accounted for the weight loss, or at least a part of it, although both birds remained in excellent condition up to the time of fledging.

Assuming that most, if not all, of the weight loss was normal, the data agree with those of King for *E. traillii* in that weight loss occurred prior to fledging. However, the maximum weight of the young *E. difficilis* did not appreciably exceed the adult weight. Thirteen adults in the Museum of Vertebrate Zoology collected in California in April and May averaged 11.1 gm. (8 males, 11.2 gm.; 5 females, 10.9 gm.). The greatest weights reached by the nestlings were 10.8, 11.3, and 11.7 gm. The latter bird disappeared before the weight loss occurred in the other two.

Two recently fledged Western Flycatchers weighed 10.5 gm. each at the ages of 15 and 16 days. Comparison with the weights of the nestlings previously discussed suggests that a weight loss may have occurred before fledging. Although our data are few, they suggest that the pattern of increase and decrease in weight of nestlings of *E. difficilis* is similar to that described for *E. traillii* by King.

The average feeding rates per hour for the Western Flycatcher over the entire nestling period were nearly similar for three nests, but the rate at the fourth, Barn Nest 1, was more than twice that of the others (fig. 4). However, when calculated on the basis of trips made to the nest per young per hour, the rates for Barn nests 1 and 2 are nearly similar (8.1 and 7.0) and are well above the rates for Stub nests 1 and 2 (3.1 and 4.5, respectively). The higher rates of feeding at the Barn nests did not result in more rapid development and growth of the young, as the brood at Barn Nest 1 remained in the nest longer than any other, 17.5 days. One possible explanation for the greatly increased feeding rate is that the adults may have been exploiting an abundant, but low grade, food source and more frequent feeding may have been necessary to sustain the growing young.

Since only the female broods the nestlings, some difference between the early feeding rates of the male and female, and subsequently between the early and later rates of the female, might be expected. At only one nest, Stub Nest 1, did the male feed

TABLE 7

FEEDING RATES OF MALE AND FEMALE AT THREE NESTS IN RELATION TO BROODING ATTENDANCE

Day nestling period	Per cent of ♀ attendance	♂ trips per hr.	♀ trips per hr.	Day nestling period	Per cent of ♀ attendance	♂ trips per hr.	♀ trips per hr.
	Stub Nest 1				Barn Nest 2		
1	64.9	7.2	3.6	1[1]	66.3	2.0	8.7
3	51.6	6.5	4.2	2	52.0	2.9	3.3
4[1]	52.9	5.6	3.7	3	52.3	1.8	2.0
5	19.5	6.8	4.3	4	47.2	3.6	2.4
6[1]	21.0	9.8	8.2	5	21.5	2.8	4.0
7	0.8	12.9	9.7	7[1]	2.2	7.6	9.0
8	0.3	13.0	9.2	9	12.3	9.7	11.3
	Barn Nest 1			10	8.7	10.0	9.3
1[2]	59.6	0.0	3.4	11	4.7	8.5	11.3
5[1]	25.0	3.0	6.9	12	1.3	7.9	10.8
6[2]	0.0	4.7	13.5	14[1]	1.4	11.4	8.2
8	3.7	6.6	15.2	15[2]	0.3	10.3	9.6
9	1.7	15.1	19.1	16	1.8	9.3	9.6

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[1] Observations in a.m. only.

[2] Observations in p.m. only.

more than the female in the first few days of nestling life. In addition to performing her duty of brooding, the female still fed the young more than did the male at this stage of the nesting cycle. As brooding declined, the rate of feeding by the female increased correspondingly. However, the feeding rate of the male also rose at about this time and at six to nine days the rates leveled off and varied within narrow limits for both parents for the remainder of the nestling period. Therefore, the apparent correlation between the decline of brooding and the increase in feeding by the female was not primarily because she had more time for feeding but seemed to be geared to the increasing demands of the young, since the male, who did not brood, also increased his feeding rate in similar fashion (table 7).

The feeding roles of the males and females at the Stub and Barn nests are outlined in tables 8 and 9. At Stub Nest 1, the male fed more frequently than did the female on all but the twelfth and thirteenth days of the nestling period and the difference between the numbers of trips made by the male and female is significant (chi-square = 33.8, d. f. 1). At Stub Nest 2, the feeding trips were shared almost equally between the parents and the difference between the number of trips made by each is not sig-

TABLE 8

NUMBERS OF FEEDING TRIPS MADE BY MALE AND FEMALE AT STUB NESTS

Day nestling period	♂ trips	♀ trips	Sex ? trips	Total	♂ per cent	♀ per cent
			Stub Nest 1			
1	72	36	0	108	66.7	33.3
3	65	42	0	107	60.7	39.3
4	35	23	0	58	60.3	39.7
5	68	43	0	111	61.3	38.7
6	59	49	0	108	54.6	45.4
7	129	97	0	226	57.1	42.9
8	130	92	0	222	58.6	41.4
10	44	37	0	81	54.3	45.7
11	74	38	0	112	66.1	33.9
12	67	71	0	138	48.6	51.4
13	67	71	0	138	48.6	51.4
14	73	56	0	129	56.6	43.4
Totals	883	655	0	1538	57.4	42.6
			Stub Nest 2			
1	0	26	3	29	0.0	100.0
2	0	11	0	11	0.0	100.0
3	50	63	7	120	44.2	55.8
4	40	38	28	106	51.3	48.7
7	58	54	12	124	51.8	48.2
8	34	29	0	63	54.0	46.0
9	12	15	0	27	44.4	55.6
10	64	40	22	126	61.5	38.5
11	34	17	48	99	66.7	33.3
12	10	8	4	22	55.6	44.4
14	36	16	32	84	69.2	30.8
15	49	23	16	88	68.1	31.9
16	47	39	10	96	54.7	45.3
17	24	72	1	97	25.0	75.0
Totals	458	451	183	1092	50.4	49.6

nificant (chi-square = 0.27, d. f. 1) despite the fact that the male made more trips on every day of the nestling period except the first three, ninth, and seventeenth. At the Barn nests, the female fed more frequently in both nestings, and the differences between the number of trips made by each were significant at the first (chi-square = 39.0, d. f. 1) and second (chi-square = 4.8, d. f. 1) nestings. At no time did the male feed more frequently than the female at the first nestings, and he fed more frequently than the female on only four of the 13 days at the second nesting. As at the Stub nests, the adult that did less feeding at the first nesting increased its share at the second nesting. On the basis of our small samples, there appears to be a tendency for the members of a pair to retain their respective roles in feeding from one nesting to another, or at least there appears to be no significant reversal of roles in successive nests. The roles of the parents in feeding the young undoubtedly vary from pair to pair, but neither parent really dominates this activity and the duties of feeding are shared relatively equally.

TABLE 9

NUMBERS OF FEEDING TRIPS MADE BY MALE AND FEMALE AT BARN NESTS

Day nestling period	♂ trips	♀ trips	Sex ? trips	Total	♂ per cent	♀ per cent
			Barn Nest 1			
1	0	7	0	7	0.0	100.0
4	1	3	8	12	25.0	75.0
5	6	14	0	20	30.0	70.0
6	10	29	0	39	25.6	74.4
8	31	72	0	103	30.1	69.9
9	158	200	0	358	44.1	55.9
10	160	174	0	334	47.9	52.1
11	155	224	0	379	40.9	59.1
12	149	173	0	322	46.3	53.7
13	198	213	0	411	48.2	51.8
14	182	207	0	389	46.8	53.2
15	134	160	0	294	45.6	54.4
16	175	213	0	388	45.1	54.9
17	115	144	0	259	44.4	55.6
Totals	1474	1833	8	3315	44.6	55.4
			Barn Nest 2			
1	9	39	0	48	18.8	81.2
2	27	30	0	57	47.4	52.6
3	14	16	0	30	46.7	53.3
4	30	20	0	50	60.0	40.0
5	24	35	0	59	40.7	59.3
7	32	38	0	70	45.7	54.3
9	83	97	0	180	46.1	53.9
10	86	80	0	166	51.8	48.2
11	53	70	0	123	43.1	56.9
12	66	91	0	157	42.0	58.0
14	47	34	0	81	58.0	42.0
15	50	47	0	97	51.5	48.5
16	79	81	0	160	49.4	50.6
Totals	600	678	0	1278	46.9	53.1

A most interesting situation developed at a nest watched by John E. Chattin from May 20 to 28, 1940. The observer was able to distinguish the male from the female on the basis of their call notes. The nest was placed in the space between the main trunk of a sycamore and a piece of partly shed bark 6 feet above ground. When observations started on May 20, four nestlings were present. At 10:57 a.m., May 22, the nest and the supporting bark flap suddenly fell to the ground and one nestling was killed. The observer placed the nest and the three remaining nestlings behind another flap of loose bark near the original site. The adults brought food to the original site several times but began feeding the young at the new site 18 minutes after the nest had been replaced. At midday, May 23, another nestling had disappeared. At 10:40 a.m., May 24, the nest again fell to the ground as an adult landed on the rim. One nestling remained in the fallen nest, and one on the ground near it. Both nestlings were fed regularly, the male parent feeding the one in the nest and the female the one on the ground. At 1:50 p.m., May 26, the young bird in the nest had disappeared. The sole survivor of the original brood was then fed by both parents until observations ceased at midday, May 28, with the surviving nestling apparently in good condition. The gradual reduction of the brood from four to one was accompanied by marked changes in the feeding rate (table 10).

TABLE 10

FEEDING TRIPS MADE BY ADULTS AT NEST WATCHED BY CHATTIN

Date	Observation period (in hrs.)	Number of young	Total number of trips	Trips per hour	Trips per young per hour
May 20	7.0	4	127	18.1	4.5
21	10.0	4	189	18.9	4.7
22[1]	5.0	4	102	20.4	5.1
22[2]	5.0	3	77	15.4	5.1
23[2]	4.0	2	60	15.0	7.5
24[1]	4.0	2	52	13.0	6.5
24[2]	2.0	2	54	27.0	13.5
25	10.0	2	257	25.7	12.9
26[1]	5.5	2	142	25.8	12.9
26[2]	4.5	1	55	12.2	12.2
27	10.0	1	128	12.8	12.8
28	5.0	1	58	11.6	11.6

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[1] a.m.
[2] p.m.

From the data in table 10, it is apparent that the distribution of the nestlings in space had a major influence on the feeding rate. On the afternoon of May 23 and on the morning of May 24, when there were two young in the nest, the numbers of trips to the nest per hour by the adults were similar. After the nest had fallen and the young birds had become separated late in the morning of May 24, the feeding rates at once doubled and remained at this high level until one nestling disappeared on the morning of May 26. Each adult concentrated on a different nestling and the net result, in terms of number of trips per hour, was the same as if each parent were feeding a single young in a nest of its own.

The feeding rate of each parent was profoundly influenced by the feeding rate of the other. When the two separated young were being fed, one by the male and one by the female, the combined rate ranged from 25.7 to 27.0 trips per hour, but when one of the young disappeared, the combined feeding rate ranged from 11.6 to 12.8 trips per hour, approximately half of the former rate.

The feeding rate when four young were in the nest, 18.1 to 20.4 trips per hour, was well within the limit of the parents' capabilities, as the rate rose to as high as 27.0 trips per hour when the nestlings became separated on May 24.

The feeding rate correlated only partly with the number of nestlings being fed. When the number of nestlings dropped from four to three, the number of trips per hour fell from 20.4 to 15.4. When the number of nestlings fell to two, the feeding rate did not fall appreciably. When the two surviving nestlings became separated, the feeding rate rose sharply, but the number of trips per hour made to each young was comparable to the number made per hour when only one nestling remained and was fed by both parents. The feeding program of this pair of flycatchers was similar to that described by Kendeigh (1952:63), for the House Wren. Kendeigh states: "If the willingness or ability of both parents were identical and the only factors involved, one would expect that the young would be fed twice as often when both sexes participated as when only one did. This, however, is not the case. With only one young in the brood there was no significant difference in number of trips per day whether both adults were feeding or only one."

At Stub Nest 1, a small branch stub was present a few inches from the nest and the male invariably landed on it before flying to the rim of the nest to feed the young. The female, on the other hand, always flew directly to the rim of the nest to feed. Interestingly, D. Davis (1954*a*:168) found precisely the same difference between the male and female of a pair of Hammond Flycatchers. At Stub Nest 2, no twig was present near the nest and both adults flew directly to the rim with food.

Nest sanitation.—At each nest, both parents disposed of the fecal sacs of the young, either eating them or carrying them well away from the nest. After feeding the young, an adult would pause briefly on the nest rim and, if a nestling raised its posterior toward the parent and started to defecate, the parent would seize the sac, either as it fell from the young bird's vent or, more often, grasping the sac as it first appeared at the vent and removing it when it was free. Several times, an adult which had just started its flight from the nest as a nestling started to get into position to defecate returned to the nest to carry off the sac. In nearly every case only one sac was removed at a time; rarely, two were removed. The faithful disposal of sacs by the adults and the nestlings' habit of thrusting their posteriors over the nest rim before defecating made for a high degree of sanitation. Since most nests were so located that the young had to thrust their rear ends over the front wall, this served to enhance nest sanitation, as sacs were nearly always extruded in the direction from which the parents came to the nest. The interiors of all nests examined by us were either entirely free of fouling or nearly so, and the outer front walls had only a few old sacs adhering to them. At Stub Nest 2, sacs adhering to the front wall when the observer left were gone the next day. It seems likely that the adults had removed them, in the light of the observation by Nice and Collias (1961:149) of an adult Least Flycatcher removing two sacs from an empty nest from which the last young had just fledged. Once the Western Flycatchers had fledged, the adults ignored their droppings, although the young sometimes defecated while perched only a foot or so above the ground.

Nice and Collias (*loc. cit.*) stated that the adult Least Flycatchers watched by them removed sacs after 28 per cent of feeding trips to the nest, although the figure is actually 26.5 per cent (43 sacs disposed of in the course of 162 feeding trips). They note that the figure is close to the median of 25 per cent given by Nice (1943:237) for 35 studies in 28 species. The rate of disposal was about half as high in the Western Flycatcher. In the course of 7223 feeding trips at the Stub and Barn nests, 1024 sacs were disposed of. Thus, sacs were taken by the adults after only 14.2 per cent of all feeding trips. It should be emphasized here that our observations, and those of Nice and Collias, were made throughout the entire nestling period. Thus, they are comparable, and maturation factors would be the same for the nestlings at all five nests.

The rates of sac disposal at the two Stub nests and the two Barn nests were remarkably similar when expressed in terms of percentage of feeding trips after which sacs were removed (table 11). Further, there is a significant correlation at the 1 per cent level between the feeding rates and the rates of sac production given in table 11 (r = .991, d. f. 2). This suggests that the amount of food presented to the nestlings, and not the quality of the food, is of primary importance in inducing defecation. The young Least Flycatcher, on the basis of the single nest for which data are presented in table 11, is considerably more prolific in its production of sacs than is the Western Flycatcher.

TABLE 11

RATES OF DISPOSAL AND PRODUCTION OF FECAL SACS

Young per nest	Total feeding trips	Total sacs removed	Per cent trips sacs removed	Trips per sac	Feeding rate per young per hour	Sacs produced per young per hour
			Stub Nest 1			
5	1538	222	14.4	6.9	3.1	0.45
			Stub Nest 2			
3	1092	143	13.1	7.6	4.5	0.59
			Barn Nest 1			
4	3315	486	14.7	6.8	8.1	1.19
			Barn Nest 2			
2	1278	173	13.5	7.4	7.0	0.95
			Least Flycatcher (Nice and Collias, 1961)			
2	162	43	26.5	3.8	3.5	1.09

Brooding.—Brooding was accomplished only by the female at all of the nests observed. The male occasionally paused at the nest while feeding the young but he never made any movement toward brooding them. If the female was on the nest when he came with food she usually left, either just before he had reached the nest or just as he landed on the rim or on a perch near it. Occasionally, the male would feed the brooding female and she would later transfer the food to the young. Only rarely would the female raise up and allow the male to feed the young directly.

Attendance patterns were similar at the four nests for which the most data are available (table 12). Brooding was moderately heavy for about the first four days and then diminished until it had virtually ceased by about the eighth day after hatching. However, at Barn Nest 2 brooding was heavier on the ninth through the twelfth days after hatching than at the other nests. Ambient temperatures were lower than usual on the ninth and tenth days at this nest, perhaps accounting in part for the increased amount of brooding on those days in comparison with the other nests. This same bird tended to do more brooding later in the nestling period at both of her nests than did the female at the Stub nests. The brooding rates at Stub Nest 1 and Barn

TABLE 12

BROODING ATTENDANCE AT FOUR NESTS

Day of nestling period	Observation period (min.)	Brooding attendance (per cent)			Mean temp. (°F.)
		a.m.	p.m.	Day	
		Stub Nest 1			
1	602	67.8	60.5	64.9	50
3	606	57.9	41.9	51.6	53
4	373	52.9	....	....	63
5	600	32.1	0.6	19.5	63
6	360	21.0	....	....	56
7	600	1.2	0.0	0.8	52
8	602	0.6	0.0	0.3	52
		Stub Nest 2			
1	451	62.2	59.5	56.2	59
2	102	56.4	....	....	60
3	511	57.2	33.7	47.8	61
4	494	25.0	0.0	14.4	67
7	475	0.0	0.0	0.0	83
		Barn Nest 1			
1	125	......	49.6	....	52
4	120	......	52.1	....	59
5	122	25.0	....	....	59
6	129	......	0.0	....	65
8	284	28.0[1]	0.0	3.7	57
9	628	6.6	0.0	3.3	53
		Barn Nest 2			
1	270	66.3	....	....	72
2	550	62.7	41.2	52.0	67
3	469	63.3	38.8	52.3	67
4	494	53.8	41.2	47.2	68
5	519	43.9	1.6	21.5	74
7	253	2.2	....	....	73
9	513	25.9	0.0	12.3	57
10	516	16.7	0.0	8.7	55
11	372	7.0	0.0	4.7	64
12	504	2.7	0.0	1.3	65
14	248	1.4	....	....	68
15	292	....	0.3	....	65
16	507	3.1	0.4	1.8	57

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[1] Morning observation period of 27 minutes only.

nests 1 and 2 for the first day or two are comparable to the attendance rates during the hatching period.

No strict correlation between brooding rates and mean daily temperature was noted. However, it is evident that the daily fluctuation of temperature has some correlation with brooding, as the rate in the cool of the morning is considerably higher than the rate in the afternoon, when temperatures are higher. Further, the brooding rate for the afternoon diminishes much more rapidly over the nestling period than does the morning brooding rate. It is evident, then, that lower temperatures induce more brooding during the daily cycle but a day which is generally cooler does not induce more brooding than a day which is warmer (table 12). Occasional brooding occurred after the initial period of decrease had essentially reached zero per cent (about the eighth day, except for Barn Nest 2), but these periods seldom exceeded two minutes and were apparently not correlated with temperature with two exceptions. Brooding periods of four, five, and eight minutes on the morning of the tenth day of nestling life were recorded at Barn Nest 1, a morning cooler than usual at that time of year. At Stub Nest 2, late in the afternoon of July 9, the tenth day of the nestling period, an adult, probably the female, twice forced its way into the extremely crowded nest cavity and sprawled on top of the large, active young, sheltering them from the direct rays of the sun which were falling on the nest. These periods of "brooding" lasted one and three minutes. It was undoubtedly very warm in the nest cavity, as the young had been panting for some time before the arrival of the adult. Although the sun shone on the nest cavity every afternoon and panting by the young had been noted at that time of day as soon as they had become active enough to be seen above the rim of the nest, the sheltering behavior of the adult was noted only on this one afternoon.

Because of the continued day to day changes in the length of the on and off sessions during the brooding period, it is misleading to calculate averages for the entire brooding period. Rather, this must be done on a daily basis, since only in this way can one record the changes taking place. The initial on and off sessions on the first full day of nestling life are more nearly similar to those recorded for the hatching period than to those recorded for the incubation period. At first, the on sessions are considerably longer than the off sessions, but by the fourth or fifth day, in the morning, and as early as the second day in the afternoon, the off sessions become longer and eventually the on sessions dwindle to infrequent periods of one to five minutes duration. The manner in which the length and frequency of the on sessions decrease once again points to the influence of temperature on these functions, since the afternoon off periods tend to be longer than the on periods almost from the first day of nestling life.

The general agreement of the brooding attendance at all four nests studied in detail is striking (table 12). Individual variation at other nests certainly must occur, but the general pattern for the Western Flycatcher at this locality is undoubtedly as reported here.

Fledging.—The most accurate data we obtained for duration of the nestling period were from Barn nests 1 and 2 and a nest at the Von Soosten Cabin in Anastasia Canyon. The nestling periods for these nests were 17.5, 16, and 14.5 days, respectively. At Stub Nest 2, although the nest contents could not be seen directly, as in the other three nests, the fledging period, with time of hatching determined on behavioral evidence, was 16.5 days.

Fledging of an entire brood was seen on three occasions, at Barn nests 1 and 2 and at Stub Nest 2. In each nest, the young were actively moving about and flapping their wings vigorously for four (Barn Nest 2) or five (Barn Nest 1, Stub Nest 2) days before flight. The first wing flapping was noted on the twelfth day at both Barn nests and on the tenth day at Stub Nest 2. In the Barn nest fledging was natural, but at Stub Nest 2 fledging was "accidental" in that one bird was shoved out of the nest, tried to climb back in, and pulled a second nestling out of the nest in so doing. Because of the scarcity in the literature of actual observations of fledging, and because the fledgings which we witnessed illustrate some of the hazards inherent in this process, these three fledgings will be described in some detail.

Barn Nest 1.—Four young were successfully raised in this nest. As much as five days before leaving the nest the young were flapping their wings vigorously. Occasionally they stepped onto a nearby board and walked as far as six or eight inches from the nest. One short "flight" of three inches back to the nest was seen on the day before fledging. Occasional jostling of one young by another would sometimes almost knock one from the nest or board, but each incident of this nature ended up with all young safely back in the nest. Finally, one morning, after only a little preliminary flapping, one young bird flew from the board near the nest at 10:11 a.m. It rose slowly and steadily, rather like a balloon, a distance of about 25 feet to within a few feet of the barn roof, and then it descended and landed near the nest. At 10:14, a second young bird flew from the same board straight out to a beam about 20 feet away, failed to land on the beam, and then glided to a lower rail about 10 feet below and to one side of the nest. Both young flipped their tails vigorously after landing, perhaps to gain their balance. At 10:23 the third sibling left the nest, flying on about a 30° angle down toward the barn gate. It acted as if it could not direct its flight, for it crashed headlong into the lowest slat of the gate and collapsed in a heap on its back with its feet held up toward the roof. Stunned, it lay at the base of the gate for a full minute. When it recovered it flew unsteadily up to a perch in the barn only ten feet off the ground. The fourth young left the nest at 10:25 and landed about six feet below and 30 feet to one side of the nest. After fledging, the young changed positions frequently. The female flew all about the barn uttering *pik-pik* notes after the last young had fledged. Finally, at 10:32, seven minutes after the last young had left the nest, all four had left the barn and were regrouped in a black locust tree just outside the barn gate. All appeared able to fly well after the few short, rather clumsy flights in the barn. The entire brood of four fledged voluntarily over a period of 14 minutes after 17.5 days in the nest.

Barn Nest 2.—Just prior to fledging, the two young in this nest were flapping vigorously on the nest rim for several minutes. Finally, after being fed at 7:40 a.m., one young bird flapped strongly and simply took off. It flew directly to a rail across the barn, a distance of about 20 feet, where it landed with such facility that it could have been mistaken for an adult, at least as far as its actions were concerned. The female then flew from outside the barn to the nest, gave several *pik-pik* notes, fed the remaining nestling, and left. The second sibling then flew heavily to a rail about 15 feet away and six feet below the nest, at 7:43. This second young could not fly as well as the first. After some 15 minutes of changing perches inside the barn, the young came together not far from the nest. During this period of shifting about, the female flew about inside the barn, uttering *pik-pik* notes, although she occasionally flew outside briefly only to return and feed the young. She did not appear to be as excited as during the fledging of her first brood. Further, the two siblings came together inside the barn, not outside in the locust trees, as the first brood had done.

It was apparent that the second young could not fly as well as the first to fledge. One of the young probably hatched about 18 hours after the first and this discrepancy may have been reflected in the different flying abilities of the two. These two young fledged within three minutes of each other after 16 days in the nest.

Stub Nest 2.—As in the Barn nests, much wing flapping and moving about in the nest preceded fledging, these activities starting about five days before the departure of the young. At this nest, which was placed within a small cavity in a dead stub, the young frequently perched on the front rim, at the cavity entrance. No more than two birds could occupy this perch at one time. Jostling was frequent, and any young perched on the front rim was in danger of being pushed outside the nest cavity by the sudden movements of the bird or birds behind it. Several times, on the day preceding fledging and on the day of fledging, a young bird was nearly knocked out of the cavity in this fashion and regained its balance only by vigorous flapping. Once, on the day before departure, one young was actually pushed from the front rim of the nest and fell four inches down the trunk of the stub before it managed to grasp some bark and arrest its fall. After three minutes of flapping and scrambling, the young bird managed to regain the nest rim, reach up, and pull itself back into the cavity, breathing heavily and obviously tired. It was evident that there was, right up to the moment of accidental fledging, a strong attachment of the young to the nest or to the sibs.

Finally, after 16.5 days in the nest, the unintentional fledging occurred. At 3:55 p.m., there was a great deal of shifting of position by the three young and one, perched on the front rim, was knocked out of the cavity. It succeeded in clinging to bark two inches below the nest cavity and started to toil back to the nest, flapping vigorously. Meanwhile, one of the other nestlings had taken its place on the front rim. The bird on the trunk finally came to within grasping distance of the rim of the nest and reached up to gain a foothold, but instead grasped the leg of the young perched on the front rim. It pulled, dislodging the bird on the rim, and both fell, fluttering down into heavy brush about six feet downhill from the base of the nest tree. An adult flew down to this area shortly after, and an adult fed the remaining nestling at 3:57. This young bird was quite restless, although it now had the entire nest to itself. Finally, it hopped to the front rim of the nest, then to the lip of the nest cavity, and at 4:11, just 16 minutes after the first two young had fallen, it gave several *peep* notes and few cross-slope, steadily descending until it disappeared under an oak 23 feet from the nest stub. The three young were not seen again on the afternoon of their departure and it is not known when they regrouped. They were next seen on the second day after fledging, huddled together on the lowest branch of a large coast live oak 160 feet cross-slope from the nest stub, attended by both adults.

Since the young bird remaining in the nest after the "accidental" fledging of the other sibs followed them voluntarily after 16 minutes, it seems probable that the attachment of young jostled outside the nest, or nearly so, preceding fledging was to the sibs and not to the nest.

Discussion.—At Barn Nest 1 and Stub Nest 2, considerable hovering before the nest was done by the adults a day or so before fledging. However, this undoubtedly had no influence on the actual time of fledging but rather represented a reaction of the adults to the lack of space on which to land in order to feed the large young. This suggestion is borne out by the fact that these two nests held four and three nestlings, respectively, whereas Barn Nest 2, at which very little hovering was noted, held only two nestlings. Presumably, there was sufficient room for the adults to land at this nest without hovering briefly while finding a landing place.

Both adults continued to feed the young during the fledging period. It took only a few moments for them to find the newly fledged young. After the last young bird had left the nest, the parents quickly adjusted to the new situation. At Barn Nest 2, it took three trips to the nest to show the female that she must look elsewhere for the young. At Barn Nest 1, no feeding trips to the nest were noted after the last young had fledged.

The reactions of the presumed female parents to the fledging of their young differed between the Barn nests and the more natural Stub Nest 2. Within the barn, the female flew about excitedly, uttering *pik-pik* notes. Most of this activity occurred after the last young had fledged. The female at the barn was apparently trying to gather the young, which were flying about in random fashion, into an integrated unit. As soon as the fledglings had come together, the female settled down and ceased her excited flights and *pik-pik* notes. Also, at this time the young stopped the nearly continuous peeping which they had been doing since fledging. This type of behavior was not shown by the female at Stub Nest 2. The difference in the actions of the two females probably depended on the fact that in the barn the young could not perch in areas of dense cover but were always out in the open. At the stub, after fledging, the young birds were at once in dense cover. At Barn Nest 2, the two fledglings actually regrouped for the first time only a few feet from the nest in an area which afforded about as much protection as did the nest site proper. This evidently satisfied the drive of the female to have her young together and, particularly, under cover. Later, when these two fledglings moved from the barn, about ten minutes apart, they peeped a great deal and the female flew about in an agitated manner giving repeated *pik-pik* notes.

The fledging of a brood is accomplished within a very short time. Once one young had left the nest, the others soon followed. This would seem to have survival value in that the parents, after the young have come together outside the nest, do not have to care for the young at two widely separated localities. Once fledged, the young do not return to the nest.

Dawson (1923:884) notes the readiness with which nestling Western Flycatchers "explode" from the nest when disturbed. This is true, but Dawson's assumption that young leaving the nest prematurely are doomed is wholly unsupported by our observations. In the course of our work, two broods "exploded" from the nest when disturbed by the observer in the latter stages of the nestling period. In each case, the parents soon established contact with the young and were caring for them. At Stub Nest 1, which contained five young, a snake raided the nest and ate or killed four. The fifth either jumped or was pushed out by the snake as it crawled about. Although this bird was unable to fly, it scrambled into cover, was later found by the adults, and was raised successfully. At the nest watched by Chattin in 1940, the adults fed the young faithfully on the ground. The strength of the drive to feed the nestlings, despite the difficulty involved, is suggested by an excerpt from Chattin's notes: "Young bird is now fairly well hidden beneath *Bromus rigidus* [ripgut grass] that is bent over. ♀ seems to have trouble feeding this young bird since it (♀) seems to be reluctant to light in the long grass and instead tries to hover above the bird finally alighting however to feed the young one." There is no doubt that young of this species leaving the nest prematurely are, in the great majority of cases, found and cared for by the parents.

Whether the young will leave the nest when disturbed apparently depends in large part on whether or not they can fly. In the nest visited by the snake, just referred to, since the sole survivor was unable to fly, it seems likely that none of the nestlings could fly. None of the young showed the slightest inclination to avoid the marauder; indeed, one perched comfortably on the snake's back while the snake ate a nestling, after which the predator reached over its shoulder, so to speak, and plucked the young bird from its back. It seems likely that the nestling which escaped from the nest had been pushed out by the snake.

Post-fledging.—Many of the activities of the young and their parents were difficult to follow after fledging. Usually, it was nearly impossible to count accurately the feeding trips made by the adults. The young gave begging notes at most, but not all, feedings, and at other times they gave such notes when an adult flew near but did not bring food. Frequently, the fledglings were completely hidden in dense foliage. The behavioral distinctions between the adult male and female were no longer as clear. During much of the day, the young were constantly changing positions so that it was impossible to follow any one fledgling for a long period. However, it was possible to record many of the changes in the life of the family groups by carefully observing the general activities of the family as a unit. The three families which were followed for appreciable periods of time were those from Stub Nest 2 and Barn nests 1 and 2.

Once the family had come together after fledging, a routine seemed to develop, the feeding of the young by the adults together with the slow but often steady and nearly constant movement of the young to new positions by "twig-hopping," seldom employing flights of any great length. When fed, the young made no movement other than to turn toward the adult, if this were necessary. Never were any "coaxing" movements of the wings seen, as reported by Wheelock (1904:438). The adults delivered food rapidly, either perching next to the young bird being fed or, less frequently, hovering before it. Accurate counts of feeding trips were made for the two young from Barn Nest 2 on the day of fledging. In one morning period of two hours and one minute, one fledgling was fed 27 times and the other 20 times. In the afternoon one young was fed eight times and the other seven times in one period of one hour and 59 minutes, and the two young together were fed 38 times in another period of one hour and 16 minutes. All told, in 5.3 hours of accurate counting the two young were fed by both parents at a rate of 19 trips per hour, essentially the same as that for the last eight days of the nestling period. Another accurate feeding count, at another nest, showed one parent feeding a total of 44 times in 52 minutes on the morning of the sixth full day after fledging. In two morning periods aggregating one hour and 57 minutes on the third full day after fledging, the three young from Stub Nest 2 were fed 47 times by both parents, a feeding rate of 24 trips per hour. This was well above the maximum level of feeding during the nestling period. A departure from the feeding routine in the nest was the failure of the parents to wait for the young to extrude fecal sacs at each feeding.

Young birds were seen to peck at bark, foliage, and apparently at the air, or perhaps at very small, flying insects, soon after fledging. This behavior continued for several days. It is unlikely that they obtain much food in this way. The young were seen to fly toward the parents as the latter brought food as early as the first full day after fledging, but such behavior became common only after the fourth or fifth days. The development of this behavior is undoubtedly correlated with the development of the power of flight.

Young were first seen to hawk for insects on the seventh day at Barn Nest 2, the eighth day at Stub Nest 2, and the ninth day at Barn Nest 1. By the ninth to twelfth day after fledging, hawking was frequent and effective. However, one parent continued to feed the young as long as the fourteenth day for the brood at Barn Nest 1, the fourteenth or fifteenth day for the brood at Barn Nest 2, and at least the twenty-second day for the brood at Stub Nest 2. At the latter nest, however, feeding was only occasional and the young were almost entirely independent.

In each brood, both parents fed initially but at Barn Nest 1, one parent, presumably the female, virtually stopped feeding the young after the fourth day. Undoubtedly, this was because of the renesting activities of this bird. After the fourteenth day the male also stopped feeding the young and spent his time near the barn and the second nest, which at that time had been under incubation for two days. At Barn Nest 2, both parents fed at least through the eleventh day, and possibly until the thirteenth day, after fledging. At Stub Nest 2, both parents fed at least through the ninth day after fledging.

Although some of the young appeared to be good fliers on fledging, on the basis of subsequent movements it appeared as if they were not capable of flights of long distance or duration. During the first few days of post-fledging life, most of the movements of the young are accomplished by "twig-hopping" or by very short flights. The young do not move very frequently from tree to tree unless trees are so close together that their branches meet. However, by the fifth to seventh days, longer flights are more frequent and twig-hopping is less common. As previously noted, hawking flights are proficient by the ninth to twelfth days. It may be that such flights, and others involving more complicated maneuvering, were contingent not only on the development of coordination and endurance, but also on the growth of the tail. At fledging, the tail is only about 20 to 25 per cent grown and it does not attain its full growth until the fourteenth to sixteenth day after fledging. At this time, or perhaps a little earlier, the young seemed as adept in flight as the parents.

The only notes heard from the fledglings for the first few days were the series of *eep* notes given as the adults came in with food, and the soft *peep* notes given when they were moving about, or when they became separated. Both of these notes decreased in frequency as the young matured but they were still heard as late as the twenty-fourth day after fledging at Stub Nest 2. The *peep* notes are comparable to the *tsit* location note of the adult female and, indeed, became strongly suggestive of that note as the young grew older. The adult *pee-ist* was never heard from the young at Barn Nest 2. However, it was definitely given by the fledglings from Barn Nest 1, first heard on the fifteenth day after fledging, and by the young from Stub Nest 2, first heard on the twentieth day. It was heard only infrequently.

The young tended to stay close together, even huddling, for the first few days after fledging. When one moved, all eventually moved, as a fairly closely knit unit. However, perhaps concurrent with the development of flying ability, the group became more and more dispersed, and by the seventh or eighth day the different young might be in different parts of the same tree, or even in different, though adjacent trees. Huddling together on one branch was infrequent at this stage. By the time they were 14 or 15 days out of the nest, the young birds seemed quite independent of their siblings and parents, although they were still fed occasionally by the parents. The young still tended to move as a group, but individual movements were often not coordinated with the movements of the other fledglings and the family group had lost most of its cohesion.

The range of movement of the different family groups varied considerably. Understandably, all three groups that were watched moved over restricted areas in the first few days after fledging. However, it was obvious that the two family groups from the Barn nests moved about less than did the family at Stub Nest 2. This difference was undoubtedly due to the scarcity of trees in the barn area. For the first four days the young raised in the barn stayed in the six black locusts immediately adjacent to it. It was only after this initial period that the young attempted the relatively long flight of 180 feet to the nearest group of trees. These trees were in turn separated from the more extensive oak woods beyond, and the families from the barn nests moved over only about two acres while under observation. In contrast, the group at Stub Nest 2 ranged so widely that it was difficult to locate them at the start of each period of observation. The area in which they moved was grown mainly to oaks, with few open spaces between the trees. After the young had been out of the nest about seven or eight days, the family roamed freely over this wooded area. Original territorial boundaries with other nesting pairs of flycatchers were transgressed without opposition, as these other pairs had disappeared.

There was no evidence that the male at the barn tried to drive the young away before the second nesting, nor was there any definite evidence that any adult tried to drive any of the young away at any other nest. The break-up of the family seemed to be more of a natural process as the young became more independent of the parents and of each other. Gradually they drifted apart and farther and farther away from the "home" area. At Barn Nest 1, the parents were not seen to feed after the fourteenth day. On the sixteenth day only one young bird was found in the area and on the seventeenth day after fledging none was seen. At Barn Nest 2, apparently only one parent was feeding the young on the thirteenth day and on the fifteenth and sixteenth days only one young and no adult could be found. In the family at Stub Nest 2, an adult was still present with the three young on the twenty-second day after fledging. On the twenty-fourth day only two of the three young were found, and no adult was seen. However, a series of begging notes was heard in the area, suggesting that one of the adults was still present. On the twenty-sixth day, two juveniles were present. By the twenty-ninth day no member of the family was seen in the entire area.

At the Chinchilla House Nest, the two young remaining of the original brood of three left the nest on June 10 and the female parent was found dead on June 17. The male remained with the young and cared for them until they were fully grown and able to forage for themselves. The last date on which the male was seen with the young was June 30, when the juveniles were hawking adeptly and obviously able to take care of themselves. Begging sounds were heard but no actual feeding of the young by the male was seen. The male remained in the area for some time after this date, but the young were not seen again.

Nesting success.—The difficulties encountered in presenting data on nesting success have been discussed recently by Mayfield (1960, 1961). He proposed a method of computing nesting successs on the basis of the observation of eggs or nests as they are exposed to the factors which might destroy them. The unit of exposure would be the egg-day or the nest-day. This method allows one to use fragmentary observations which are usually not considered in most nesting studies. The data for the Western Flycatcher (table 13) are compiled by the use of the formula given by Mayfield (1961), that is, the probability of survival (S^d) of a nest during either the incubation period or the nestling period is expressed as $(1—r)^d$ where r is the mortality rate and d is the number of days of exposure. The probability of survival from the beginning of incubation to fledging is the product of the two separate probabilities of survival during the incubation and nestling periods.

TABLE 13

SURVIVAL OF THE NEST DURING INCUBATION AND NESTLING PERIODS

	Nests	Nests lost	Nest days	S	Incubation period[1]	S^d
Western Flycatcher	23	2	304	0.99	15	0.86
Kirtland Warbler	154	35	878	0.96	14	0.56
	Nests	Nests lost	Nest days	S	Nestling period[1]	S^d
Western Flycatcher	20	4	220	0.98	16	0.75
Kirtland Warbler	144	22	735	0.97	9	0.76

[1] In days.

It is evident that the probability that a nest will survive the incubation period is considerably higher for the Western Flycatcher than it is for the Kirtland Warbler, *Dendroica kirtlandii* (table 13). Since the incubation periods of these two species are virtually the same, we may have here a mathematical expression of what has long been known, namely, that the nest mortality of ground-nesting species such as the Kirtland

Warbler is considerably higher than it is for tree-nesting species such as the Western Flycatcher. However, we also find that the probability of survival during the nestling period is essentially the same for the two species (table 13). This is due primarily to the considerably longer nestling period of the Western Flycatcher. The survival rate for the flycatcher is slightly higher than that for the warbler but the longer nestling period of the former negates this advantage. If the nestling period of the flycatcher were the same as that of the warbler, and if the survival rate remained the same, we would find that the probability of nest survival would be 0.85 rather than 0.75, a greatly increased probability.

Although the total time that an occupied nest is exposed to the hazards which may cause destruction is considerably longer in the flycatcher (31 days) than in the warbler (23 days), the probability that a nest will survive both the incubation and nestling periods is considerably higher in the former (0.65) than in the latter (0.43). This further illustrates the greater vulnerability of ground nests to destruction. The comparison must be slightly modified in this case, however, since the Western Flycatcher sometimes nests in tree cavities. Thus, tree nesting in this species does not indicate that nests are always placed in relatively exposed situations.

The pronounced changes in productivity that can occur in a limited number of pairs from year to year is illustrated by the difference in nesting success on the territories observed in 1957 and checked in 1958. The two Barn nests produced a total of six fledglings in 1957; in 1958, a single nest in the barn produced two fledglings. The Chinchilla House Nest produced three fledglings in 1957; in 1958, a male occupied the same territory but failed to attract a mate. In 1957, the Stub nests produced a total of four fledglings. In 1958, a pair occupied this territory and made several abortive attempts to nest between April 17 and June 20. Although the birds remained in the area until late July, no nesting was attempted after June 20. In 1957, a total of five nests produced 13 fledglings, an average of 2.6 per nest. In 1958, a single nest produced two fledglings.

SUMMARY

Studies involving 1238 hours of field observation of the Western Flycatcher (*Empidonax difficilis*) have yielded information on various aspects of the breeding biology of this common, but little known, bird. Flycatchers arrive at the Reservation in early March and usually leave by the end of August. Canyon bottoms and stream courses are their preferred habitats, but buildings, even if in marginal situations, are often used as nest sites.

The Western Flycatcher has an alert, aggressive, snappish nature and reacts to intruders with a swift chase, usually accompanied by threat notes and sometimes by squeaks and loud bill snapping as well. Hostile behavior between the members of pairs, ranging from simple displacement of one by the other to violent attacks, occurs often enough to be considered typical behavior. Interspecific intolerance is usually directed at small birds. A few attacks were directed at larger birds and at woodrats and lizards.

The vocal repertoire of adult Western Flycatchers consists of six principal vocalizations: song, in the male only; male position note; female position note; alarm note; *chrrip* note; and *pik-pik-pik* note. Mated males have only a dawn song. Unmated males sing at dawn and during much of the day as well. Song appears to function primarily in mate attraction. The *chrrip* and *pik-pik-pik* notes have certain functions which appear obscure, but the *chrrip* note is usually a threat and the *pik-pik-pik* note is usually used to notify the young of the approach of an adult with food.

The nesting cycle begins in late April or early May and second nestings may continue well into July. Natural nest sites averaged 10.9 feet above ground; nests were all in trees except for one on the ground, and over half were in riparian willows or sycamores. Nest sites in buildings were common and involved a supporting structure with shelter from above. The facts that individuals tended to use a particular type of nest site for successive nestings in a season and that certain nest sites are used year after year suggest that individual builders prefer a particular type of nest site although there is considerable variation in choice of nest sites in the whole population. The materials used in construction are highly varied. Birds apparently use whatever is readily available. The size and shape of the nest vary within narrow limits. The nest is built by one member of the pair, presumably the female, over a period of four or five days.

The first egg is laid on the first or second day after completion of the nest. Subsequent eggs are laid irregularly, with successive daily layings being the exception. The usual clutch size in this area is four in first nests and three in second nests. The Western Flycatcher is a determinate layer.

The incubation period is 14 or 15 days, with 15 days the usual period. Incubation is performed by one bird, evidently the female. She may spend appreciable amounts of time on the nest during the laying period but heavy incubation starts with the completion of the clutch. The onset of roosting on the nest is variable but occurs within the laying period. During incubation the male exchanges frequent calls with the sitting female and he feeds her on the nest infrequently. Attendance ranged from 77 to 80 per cent. There appears to be no over all correlation of attendance and mean daily temperature but incubation tends to be heavier in the morning when air temperatures are lower. In general, on and off periods are shorter during periods of low temperatures and abnormally long off periods occurred only on hot days.

Attendance falls to about 59 per cent during hatching. At this time the female is restless. She probes into the nest and gleans objects which she swallows and later carries off the pieces of egg shell. The adults often try to feed newly hatched young but with little success in the first few hours after hatching. Generally, feeding is relatively light in the first four or five days, increasingly heavier in the next two to four days, and it then reaches a maximal level which is maintained until the young fledge. As the nestling period progresses, the weight of the nestlings reaches a maximum which is slightly greater than the adult weight and then there is a slight weight loss just prior to fledging.

The feeding rates of the parents and their roles in this activity were studied in great detail. Although brooding is carried out by the same bird that performed all the incubation, evidently the female, in most instances she also feeds the young more than does the male in the first few days of the nestling period. As this period progresses, the feeding rates of both parents rise, apparently geared to the increasing demands of the young. The roles of the parents in feeding varies from pair to pair and there is a tendency for the members of a pair to retain their respective roles in feeding in successive nests. However, this activity is not dominated by either parent but is more or less shared. The feeding rate correlated in some nests with the number of young; in others, it did not. Perhaps in the latter, quality of available food may have had some influence.

Brooding attendance at all nests studied was remarkably similar. The presumed male sometimes paused at the nest after feeding the young but was never seen to brood them. Usually the female leaves the nest when the male arrives with food. Occasionally he feeds her and she transfers the food to the young. Only rarely does she move aside and allow him to feed the young directly. Brooding is moderately heavy in the first four days and then diminishes until it virtually ceases by the eighth day. Although there was no well-marked correlation between mean daily temperatures and brooding rates, it was evident that attendance was greater in the morning, when air temperatures were relatively low. Further, afternoon attendance decreased much more rapidly than morning attendance during the nestling period.

Nest sanitation was effective since both parents faithfully disposed of the fecal sacs of the young, and the latter always thrust their posteriors over the rim of the nest before defecating. The significant correlation between feeding rates and the rates of sac production suggests that amount, and not quality, of food presented to the nestlings is of primary importance in inducing defecation.

The duration of the nestling period ranged from 14.5 to 17.5 days. Four or five days prior to fledging the young move about in the nest actively and flap their wings vigorously. Natural fledging was observed at three nests. It was evident that some young were more proficient in flight than were their sibs, this possibly resulting from age differences; that fledging of a brood occurs rapidly after the first young has left the nest (within 3 to 16 minutes); and that the parents establish immediate contact with the young after fledging. Young force-fledged from two nests were soon found and cared for by their parents. During the early post-fledging period the young frequently move about by twig-hopping or short flights. They take food from both parents, begging vocally but not using any coaxing movements of the wings.

On the day of fledging, counts of feeding trips to two young at one nest averaged out the same as the feeding rate during the last eight days of the nestling period. As the post-fledging period progressed, the feeding rate exceeded the maximum level reached in the nestling period. For several days after fledging, the young peck at bark, foliage, and the air, but they probably do not obtain much food in this way. By the seventh day out of the nest they begin to hawk insects, and by the ninth to twelfth day after fledging hawking is frequent and effective. Although both parents fed the young initially, in one brood the female stopped feeding them after the fourth day and started her second nest; in two others both parents fed up to the eleventh and ninth days, after which one parent remained with the young until the fourteenth and twenty-second days, respectively.

The young, communicating by *peep* notes, tend to stay close together for the first few days after fledging. From the fifth to seventh day on, longer flights are performed, and thereafter hawking flights commence. The latter, which require more complicated maneuvers, may be dependent not only on the development of endurance and coordination but on the growth of the tail, which is only 20 to 25 per cent grown at fledging. By the fourteenth or fifteenth day the young have full-grown tails and fly almost as well as the adults. They are quite independent of other members of the family and although they are still fed occasionally by the remaining parent they move as a much less cohesive group. The final break-up of the family is the result of a gradual drifting apart as the young move farther and farther away from the original territory.

Data are presented on nesting success and on changes in productivity in a limited number of pairs on the same territories in successive years. In 1957, 13 young were fledged from five nests, an average of 2.6 fledglings per nest. In 1958, two young were fledged from a single nest.

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