NORTHERN WINTERING OF FLYCATCHERS AND RESIDENCY OF BLACK PHOEBES IN CALIFORNIA

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WITH the advance of fall and winter in northern latitudes, such environmental changes as dwindling food supplies and the drop in temperature force many bird species to migrate. Those that stay behind, the residents, survive by various behavioral, morphological, and physiological adjustments. Flycatching is a very specialized way of feeding. Success in obtaining insects in this manner depends to a large extent on the movement of invertebrates through the air. During cold weather, insects do not move readily and in winter the insect biomass is strongly reduced. Thus one would not expect flycatchers to overwinter in northern latitudes. Species that do so are likely to show special ways of coping with the unfavorable winter conditions.

At the Hastings Reservation, Monterey County, California, Black Phoebes (*Sayornis nigricans*) occur in riparian woodland, around buildings, and along fences. The species is present year-round, except in December and January of some cold and wet years. In addition to the phoebe, two other small flycatchers, the Western Wood Pewee (*Contopus sordidulus*) and the Western Flycatcher (*Empidonax difficilis*), occur on the reservation and coexist. These latter two species are migratory. Comparative feeding behavior and habitat selection of the three species are presented elsewhere (Verbeek 1975).

The object of this study was twofold: (1) to find out what aspects of the feeding habits and ecology of the Black Phoebe enable it to stay on the reservation during the winter, and (2) to see how these help explain why only the phoebe stays and not the other two species.

METHODS

In early August 1967 I began to follow a particular Black Phoebe, recording its activities for several hours continuously at various times during the day. The following day I attempted to record data for those hours not covered on previous days, preferably on the same bird, but this was not always possible. Data thus gathered over several days give a good indication of activity during an average day (Verbeek 1972), provided the weather is about the same during the period. A deliberate attempt was made to collect data at all times of the day from 2–5 August, 5–9 September, and 26–28 October 1967, and from 25–28 February and 1–3 June 1968.

For each feeding sortie I recorded the estimated height of the perch, and the distance flown between the perch and the prey. I also noted whether a flight was ascending, horizontal, or descending. I distinguished between hawking and gleaning flights. Hawking is defined as the capture of a flying insect. Gleaning, which includes hovering, is the capture of a sitting insect. Gleaning from the ground occurred after

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a bird landed, or in a passing flight. Feeding maneuver diversity (FMD) values were calculated using the Shannon-Wiener information function

$$\text{FMD} = - P_i \ln P_i$$

where P_i is the proportion of the species in question using the i^{th} feeding maneuver. The same formula was used to calculate perch diversity (PD). Chi-square was used throughout except where mentioned otherwise.

RESULTS

I was never able to collect data for a whole "phoebe day." At the beginning of an observation period it was sometimes difficult to find a phoebe. Additional time was lost when a bird I watched flew to another feeding ground leaving me behind to catch up. As the gaps in my data occurred throughout the day, the overall effect is considered minimal.

Selection of perches.—The Black Phoebe makes its feeding sorties from a variety of perches. Table 1 shows the seasonal differences in the percentage use of these perches. The birds preferred fences. From September to February this preference was significantly higher ($P < 0.001$) than in the other 2 months. Their use of trees was significantly different ($P < 0.001$) comparing any 2 months, except February versus June. The frequent use of trees in August was partly because of the shade they provided, which presumably attracted insects as well. The increased use of insects on buildings as a source of food in June is associated with the fact that the birds stayed close to their nests. All months differed significantly ($P < 0.001$) from each other in the frequency of the various perches. Although the birds used the largest variety of perches in February and June (Table 1), the perch diversity index was highest in August. Many types of perches in February and June were used infrequently.

The frequency distributions of perch height and flight distance were positively skewed. For this reason, median values rather than means are shown in Table 2. Perches were lowest in August and September and highest in June. All months differed significantly ($P < 0.001$) from each other in median perch height, except August versus September, and October versus February.

On leaving their roosts in the summer, phoebes went to those parts of their territories where the sun shone. Presumably the insects were more active there than in shady places, and the sun warmed the birds. By about 0900 (in one case in August) the birds moved to more shady places and stayed there, with minor short excursions into the sun, until about 1700. In winter phoebes sought sunny perches throughout the day.

Feeding maneuvers.—The total percent hawking and gleaning flights remained stable in all months except in June (Table 3). In comparing

TABLE 1

SEASONAL DIFFERENCES IN THE PERCENTAGE USE OF VARIOUS PERCHES FROM WHICH THE BLACK PHOEBE MAKES ITS FEEDING SORTIES

	1967			1968	
Location of perch	Aug.	Sep.	Oct.	Feb.	June
Canopy					
Bottom, outside	30.9	8.1	15.6	21.2	26.1
Bottom, inside	16.4		0.3	0.6	0.9
Middle, outside			0.8	4.1	2.0
Middle, inside	0.3			0.9	0.3
Top, outside		0.1		0.6	0.2
Top			0.5	0.6	0.2
TOTAL (tree)	47.6	8.2	17.2	28.0	29.7
Fence	31.4	78.4	56.6	66.3	37.5
Building	0.8	12.6	10.3	4.5	29.8
Ground		0.4	3.5	0.2	2.8
Utility wires	4.4	0.4	12.4	0.5	
Downed trees	15.8			0.5	
TOTAL (nontree)	52.4	91.8	82.8	72.0	70.3
N	416	507	371	816	648
Diversity index	1.52	0.70	1.31	1.07	1.34

the total number of hawking and gleaning flights between any 2 months only June differs significantly ($P < 0.001$) from all the others. The increase in hawking flights over the ground in September as compared to August was associated with a switch from tree perches to fences (Table 1). September had significantly more ($P < 0.001$) hawking flights over ground and grass combined than any other month. February differed significantly ($P < 0.02$) in this respect from August and June. The other 3 months did not differ significantly from each other on this point. Hawking in the open air, i.e. away from vegetation, water, or the

TABLE 2

SEASONAL DIFFERENCE IN HEIGHT OF PERCH AND DISTANCE OF FLIGHT TO CAPTURE PREY IN THE BLACK PHOEBE

		Height of perch (m)			Distance of flight[1] (m)		
Period	N	Median	Interquartile distance	Range	Median	Interquartile distance	Range
June	648	1.22	0.91–3.03	0.0–15	2.57	1.13–4.90	0.5–30
Aug.	416	0.91	0.69–1.04	0.5–12	3.00	1.56–5.13	0.2–40
Sep.	507	0.93	0.70–1.05	0.0– 8	4.10	2.13–6.45	0.3–30
Oct.	371	1.00	0.89–1.12	0.0–12	3.51	1.96–5.98	0.5–20
Feb.	816	1.04	0.87–1.21	0.0–25	3.11	1.65–5.73	0.5–25

[1] Distance between the perch and the prey.

TABLE 3

SEASONAL DIFFERENCES IN THE FORAGING MANEUVERS OF THE BLACK PHOEBE EXPRESSED IN PERCENTAGES

Foraging maneuvers	1967			1968	
	Aug.	Sep.	Oct.	Feb.	June
Hawking					
In tree	0.5			3.4	
Under tree	6.7	1.8	2.4		
Among tree leaves	1.2	0.2			4.8
Over grass	18.4 (0.7)[1]	21.5	8.4	15.2 (0.4)	10.0 (0.5)
Over ground	3.2 (0.2)	33.9 (1.2)	11.9 (1.6)	14.7 (1.7)	11.6 (6.9)
Over water	1.9	1.4	6.7	0.3	0.6
In open air[2]	63.1	37.9	64.7	59.8	55.3
TOTAL	95.0 (0.9)	96.7 (1.2)	94.1 (1.6)	93.4 (2.1)	82.3 (7.4)
Gleaning					
Off tree trunk			0.5	0.1	1.5
Off stems, branches		0.2	0.3	1.4	
Off tree leaves	0.7	0.2			1.1
Off ground	0.2 (0.2)[3]	1.0 (0.6)	1.4 (0.3)	0.2 (0.1)	0.5
Off grass	3.6 (1.2)	0.2	0.5 (0.3)	1.1	0.8 (0.2)
Off buildings	0.5	1.8	3.2	3.8	13.9
TOTAL	5.0 (1.4)	3.4 (0.6)	5.9 (0.6)	6.6 (0.1)	17.8 (0.2)
N	416	507	371	816	648
Index of diversity	1.35	1.34	1.25	1.26	1.21

[1] The figures in parentheses under Hawking indicates the percent of times the birds landed on the ground following a hawking flight.
[2] Hawking flights away from the ground, water, or vegetation.
[3] The figures in parentheses under Gleaning indicate the percent of times the birds landed on the ground while taking prey off the ground or grass.

ground, was the most important feeding maneuver at all times, but it reached a low point in September.

The median distance of flight between the perch and the prey was largest in September and smallest in February (Table 2). June's flight length differed significantly ($P < 0.01$) from those of September, October, and February. The median flight length of September was significantly longer ($P < 0.01$) than those of August and February.

Oberlander (1939) reported that in the evening upward flights predominated. I agree with this except in the September sample. In the evening the insects are more visible against the sky than against the dark background of the soil, so the birds then select low perches.

The percent horizontal flights was remarkably stable (Table 4). September and June had significantly more descending than ascending flights. The large percentage of descending flights in September was associated with the predominant use of fences as perches, and hawking flights over the ground and grass. In comparing the number of ascend-

TABLE 4

DIRECTIONS OF FEEDING FLIGHTS EXPRESSED AS PERCENTAGES OF ALL OBSERVATIONS FOR EACH MONTH

Period	N	Ascending	Horizontal	Descending	(χ^2)[1]
1– 3 June	648	40	14	46	2.74
2– 5 Aug.	416	45	16	39	1.80
5– 9 Sep.	507	19	15	66	132.54
26–28 Oct.	371	40	14	46	1.66
25–28 Feb.	816	36	18	44	6.48

[1] Chi-square values based on ascending and descending flights only ($\chi^2 \geqq 3.84$, $P \leqq 0.05$).

ing versus descending flights between any 2 months, September differed significantly ($P < 0.001$) from all the other months, and August differed significantly ($P < 0.02$) from February and June.

Territory.—Shortly after the independence of the second brood in July adults became intolerant of each other and one bird of each pair was chased off the territory. Such interactions between mates and/or wandering birds (this could not be established) might last into September. Provided the winter was not too cold or too wet, the remaining birds stayed on their territories until next year. They were joined by a mate in February. At that time intraspecific interactions between neighbors were again prominent.

One banded bird that had nested on territory B (Fig. 1) stayed there during the winter but took part of territory A as well, the owner of which had disappeared. The following spring the banded bird occupied territory A and nested there. This was not an unexpected switch because territory A appeared to be the better one, as the total area searched for food in September and October on B was much larger than on A.

Territory A was smallest in June, when two adults fed on it. This pair fledged two young on 8 May, but House Finches (*Carpodacus mexicanus*) then took over the nest. Because mud was very scarce, the building of a new nest progressed so slowly that a second clutch was never laid. The territory slowly expanded in size in September and October, with one bird in residence, and reached its largest size in February, when two birds fed on it.

The mean arrival date for the winter visitant Say's Phoebe (*Sayornis saya*), from 1967 to 1969, was 16 September (14 to 18). They did not leave again until at least the end of March. Only one or two Say's Phoebes were present each fall and winter. When the two phoebe species occasionally interacted, the larger Say's Phoebe was always dominant.

Feeding rate.—The number of feeding sorties per minute was highest in February and lowest in August (Table 5). Comparison between the

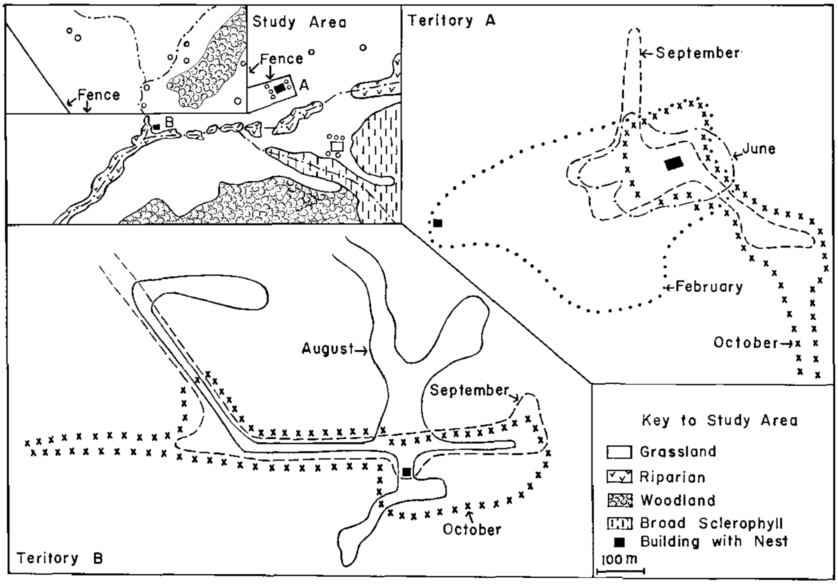

Fig. 1. The study area with two nest sites of the Black Phoebe (A and B). The seasonal change in the location and size of the territories are shown on the two enlarged maps. Note that in February, territory A encompassed both nest sites.

feeding rates of any two months shows February to differ significantly (t-test, $P < 0.05$) from all other months, and June from August. All other combinations are not significantly different. Although the feeding rates in September and October were equal, the calculated total number of invertebrates caught per day was less in October than in September, assuming that each sally resulted in the capture of an insect. The total distance flown per day was greatest in February (Table 5).

Discussion

Throughout the year the Black Phoebe makes continuous adjustments in its foraging habits and in the spatial aspects of its niche. These adjustments are dictated by the seasonal changes in the phoebe's environment that influence the availability and behavior of its food supply.

A pair of birds holds a territory from early March to late July. Then one member of each pair is chased off and the remaining bird defends the territory against all other Black Phoebes. The ousted birds must find a territory elsewhere. During the fall and winter the territory expands in size (Fig. 1). This expansion is possible because of the reduced phoebe population, and because the birds feed in places not used in times of food abundance. Maintaining a territory in winter is advantageous because it provides food, a roosting site, and, perhaps more importantly, an

TABLE 5

DAILY FEEDING RATE AND FLIGHT DISTANCE OF THE BLACK PHOEBE

Period	Total time observed (min)	Number of feedings	Feeding sorties per min	Length of day[1] (min)	Feedings per day[2]	Distance flown[3] (m)
1– 3 June	630	673	1.07 ± 0.18	918	982	6,874
2– 5 Aug.	605	440	0.73 ± 0.20	863	630	5,040
5– 9 Sep.	670	591	0.88 ± 0.12	786	692	6,685
26–28 Oct.	496	440	0.89 ± 0.20	635	559	4,863
25–28 Feb.	501	925	1.85 ± 0.34	700	1288	10,561

[1] Active period of the Black Phoebe from the time it leaves until it reenters the roost.
[2] It is assumed that with each sortie one invertebrate is caught.
[3] Distance flown is the sum of the length of each sortie times two.

old nest that usually needs but little repair. Building a new nest causes delay so that usually only one clutch is raised, instead of two when an old nest can be reused.

Aside from ranging further horizontally, the Black Phoebe in winter also adds a greater vertical dimension to its niche than in summer. It perches significantly higher in February than in August and September and it uses a greater range of perches as well, although many are used infrequently (Tables 1 and 2). This greater range is not because of the absence of the Western Wood Pewee and the Western Flycatcher, both of which have a greater median perch height (Verbeek 1975). The Western Flycatcher on the study area is strictly a canopy species, preferring the inner parts of trees. The Western Wood Pewee prefers the upper and outer parts of trees. In June, when both species coexist with the Black Phoebe, the phoebe's perches in trees do not differ significantly ($P > 0.05$) from those in February (Table 1).

Additionally, in winter the Black Phoebe is found more in the open where sunshine warms the bird, thereby lowering its energy requirements. Sunshine also makes the insects more active and thus more visible. This choice of and need for sunny sites is very evident on the reservation. The entire Black Phoebe population that nests under bridges in the deep shady canyon of Finch Creek disappears from that habitat in winter. Significantly, the phoebe is black. Absorption of radiant energy in the solar spectrum is greatly increased because of this as shown in some recent studies (Lustick 1969, Ohmart and Lasiewski 1971).

Finally, and perhaps most importantly, the ability to forage on the ground on cold and rainy days allows the Black Phoebe to bridge periods of bad weather. Cade and White (1973) came to a similar conclusion when they suggested that Say's Phoebe may have been able to establish itself in the arctic tundra because of its ability to forage on the ground.

Perching on the ground (Table 1) and feeding on the ground (Table

3) do not appear important in this study. There are two reasons for this. First, early in the morning when it was cool, phoebes fed on the ground, even in summer, but they were difficult to distinguish against the dark background and the details of their feeding activities went unrecorded. Some quotes from my field notes may be instructive here. On 4 August 1967 at 0558 "a phoebe comes from its roost and begins feeding right away. Feeding is done on or near the ground." At ca. 0700 on 5 August "I see a phoebe feeding along Finch Creek [heavily shaded], by hopping from one stone to the next," and on 2 December "the banded bird does a lot of feeding close to the ground and often sits on the ground." Secondly, my samples in August, September, and October, were collected on sunny days. To make the data comparable I selected a sunny period in February as well when collecting that month's sample.

The abundance of insects on the study area reaches a peak in May-early June and declines through the dry summer until the first rains in October, which results in a slight increase again (Root 1967, Verbeek 1973). This general trend in invertebrate abundance is reflected in the mean distance flown to capture prey (Table 2). The median flight distance per sally was longest in September when food was scarcest and shortest in June when food was most abundant. The greater proportion of downward flights (Table 4) and the selection of low perches (Table 2) in September as compared with the other months, indicates that the available food lived close to the ground.

Because of the shorter day, reduced intake in October is compensated for by the availability of a slightly higher insect abundance, allowing a shorter median flight distance than in September (Table 2). The total calculated distance (Table 5) is thus 1.82 km per bird less in October than in September. This is assumed to be a significant energetic saving. Greater food abundance in February than in September apparently reduces the flight distance. This combination of factors allows the phoebe to almost double its feeding effort in February, thus compensating for lower winter temperatures. Consequently the total distance flown per day per bird is greatest in the winter months.

The feeding maneuver diversity seemingly varies less between months than the perch diversity indexes. The phoebe apparently uses its varied foraging tactics most of the time, placing differing degrees of emphasis on particular ones depending on the circumstances. The phoebe uses a variety of perches as well, but their relative usefulness is more subject to seasonal changes in the availability and distribution of the insects that can be obtained from these perches.

Thus, two periods of stress occur annually on the Hastings Reservation. One of these falls in late summer when food is scarce, and several summer resident species leave in midsummer (Linsdale 1947, pers. obs.). In some other species, such as the Western Flycatcher (Davis et al. 1963) and the Western Wood Pewee, most of the population moves out in August, and specimens seen later are considered to be transients. This early departure is probably not in response to summer heat, as birds have means to cope with it, but to food scarcity. The other period of stress falls in the winter, when lower temperatures require a greater feeding effort (Verbeek 1972).

As stated earlier, a bird that lives by flycatching depends on moving prey, which may be flying or crawling. Movement is enhanced by temperature, and invertebrates that live where the sun can reach them tend to move more readily and earlier in the day than those living in shady places. Temperatures also tend to rise faster near the ground than at some distance above it. In short, one might expect a flycatcher that lives in the open, uses low perches, and feeds near the ground to be in a better position to overwinter than one that does not.

To see whether the importance of low perches, open habitat, and the ability to feed on the ground holds in general among flycatchers that stay in the United States during the winter, I searched the literature (Table 6). Included are all flycatchers that nest in North America, except those that are represented by small populations in the extreme south, such as the Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*). In preparing this table, I assumed that flycatchers, like other birds, feed in approximately the same way and at similar heights in their summer and winter ranges. In other words, a flycatcher that feeds in the tops of tall trees by long sallies in summer is likely to do the same on its winter ground. Several of the perch heights in Table 6 had to be guessed at from general statements in the literature. The species are arranged approximately in descending latitudinal order according to the northernmost limit of their winter ranges. The results, summarized in Table 7, are indeed suggestive. The northernmost wintering species mainly inhabit open country, use low perches, and feed in varying degrees on or from the ground. Those feeding high off the ground and/or in shady woods or thickets tend to winter farther south.

Considering the pattern of food availability specifically, and the apparent importance of ground foraging in influencing winter distribution in general, it pays to reexamine briefly the basic aspects of the niches of the three small flycatchers on the Hastings Reservation.

The Western Flycatcher lives in riparian woodland where it hunts at a median height of ca. 5 m, making quick sorties among the open spaces in the tree canopy. It also gleans much of its insect food off leaves and branches. In winter this habitat tends to be too cold, damp,

TABLE 6

SPECIES OF NORTH AMERICAN FLYCATCHERS, THEIR HABITATS, PERCH HEIGHTS, AND GROUND FEEDING HABITS[1]

Species	North and south extent of winter range	Habitat	Perch height	Feeding on ground	Source
Sayornis saya	N California to Puebla	Open country, arid	Low	Yes	
S. nigricans	California to Colima	Open country, riparian	Low*[2]	Yes*	Verbeek 1975
S. phoebe	Virginia along coast to Oaxaca	Open country, riparian	Low	Yes*	Todd 1940
Tyrannus vociferans	C California to C Guatemala	Open country, scattered trees	Low to high	Yes	
Empidonax wrightii	S California to Puebla	Sparsely covered ground among brush	Low	Yes*	Johnson 1963
Myiarchus cinerascens	SE California to El Salvador	Open brush, cactus country	Low to medium	Yes*	Gullion 1948
Tyrannus verticalis	S Carolina to Florida, and Guerrero to N Nicaragua	Open country	Low	Yes*	Dick and Rising 1965
Empidonax oberholseri	SE Arizona to Oaxaca	Brushy understory among tall trees	Medium	Yes*	Johnson 1963
E. hammondii	SE Arizona to N Nicaragua	Openings among tall conifers	Very high	No	
Pyrocephalus rubinus	Louisiana to Puebla	Edge of shrubs along streams	Low	Yes	
Muscivora forficata	S Florida, Chiapas to W Panama	Open country, scattered trees	Low	Yes	
Empidonax fulvifrons	SE Sonora to Morelos	Riparian to pine forest	Medium to high	No	
Contopus pertinax	S Sonora to Guatemala	Tall trees in pine forest	High	No	
Empidonax difficilis	S Baja to S Oaxaca	Shady woods along streams	Medium to high*	No*	Verbeek 1975
E. minimus	Sinaloa to Panama	Open country, scattered trees	High*	No*	Johnston 1971
E. flaviventris	Tamaulipas to E Panama	Dense forested swamps	Low	No?[3]	

TABLE 6 (continued)

Species	North and south extent of winter range	Habitat	Perch height	Feeding on ground	Source
Myiarchus crinitus	S Veracruz to NE Colombia	Open mature forest	Low to very high*	Yes	Johnston 1971
Empidonax traillii brewsteri	Guatemala to Bolivia	Clearings, open brushy places	Medium	No*	King 1955
E. t. traillii	El Salvador to N Argentina	Shrubby thickets in swamps	Medium to high	No	
Tyrannus dominicensis	Puerto Rico to N Venezuela	Mangrove tangles	Medium to high	No	
Empidonax virescens	Costa Rica to Ecuador	Dense mature woodlands	Medium	No	
Contopus virens	C Costa Rica to Peru	Mature woods, old orchards	High, very high*	No*	Johnston 1971
C. sordidulus	C Panama to Bolivia	Open mature woods	Medium to high*	No*	Verbeek 1975
Nuttallornis borealis	Colombia to Peru	Edge of openings in mature forest	Very high	No	
Tyrannus tyrannus	Peru and Bolivia	Open country	Low*	Yes*	Dick and Rising 1965

[1] Arranged approximately in descending latitudinal order according to the northern limit of their winter ranges. Data taken from A.O.U. Check-list (1957) winter ranges; Pough (1949, 1957) habitat; Bent (1942) perch height and ground foraging, unless otherwise indicated.
[2] The asterisk means that the information is derived from the source indicated.
[3] I have found no record of ground foraging in summer. Skutch (1969) reports yes in winter.

TABLE 7

GROUND FEEDING HABITS IN RELATION TO DISTRIBUTION OF FLYCATCHERS[1]

	Species of flycatchers				
	Breeding in			Wintering in	
Feeding habit includes	Canada and USA	USA only	Total	USA and farther south	Mexico and farther south
Ground foraging	5	7	12	10	2
No ground foraging	10	3	13	1	12
TOTAL	15	10	25	11	14

[1] Including two subspecies of *Empidonax traillii.*

and open to favor invertebrates. The Western Wood Pewee usually sits high (ca. 5.5 m) off the ground and dives on its prey in rapid long downward flights. In winter insects are not likely to be found high off the ground. Whereas the Black Phoebe in summer occupies a niche that is also favorable in winter, the Western Flycatcher and the Western Wood Pewee do not. These two apparently cannot make the behavioral adjustment of coming into the open, selecting lower perches, and feeding on the ground. With food scarcity in September and invertebrates occurring primarily near the ground, as judged by the Black Phoebe's downward directed sallies at that time, the other two species apparently find it increasingly difficult to obtain food and go elsewhere.

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SUMMARY

On the Hastings Reservation, California, the Black Phoebe is a permanent resident and remains during most winters. The behavioral adjustments of this flycatcher, allowing it to overwinter, include single occupancy of a territory, expansion of the summer territory, the addition of a vertical component to its feeding niche, increased use of ground foraging, selection of perches where the sun shines, and a wider choice of perch sites.

It is further suggested that flycatcher species that feed in the open, use low perches, and feed on insects on the ground, are favored in overwintering nearer to their summer range than those that feed among foliage and/or higher off the ground. This suggestion is strengthened by data collected in a survey of feeding habits of North American flycatchers.

Literature Cited

American Ornithologists' Union. 1957. Check-list of North American birds, fifth ed. Baltimore, Amer. Ornithol. Union.

Bent, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Natl. Mus. Bull. 179.

Cade, T. J., and C. M. White. 1973. Breeding of Say's Phoebe in arctic Alaska. Condor 75: 360–361.

Davis, J., G. F. Fisler, and B. S. Davis. 1963. The breeding biology of the Western Flycatcher. Condor 65: 337–382.

Dick, J. A., and J. D. Rising. 1965. A comparison of foods eaten by Eastern Kingbirds and Western Kingbirds in Kansas. Kansas Ornithol. Soc. Bull. 16: 23–24.

Gullion, G. W. 1948. An early record of the Western Kingbird in Lane County, Oregon. Condor 50: 46.

Johnson, N. K. 1963. Biosystematics of sibling species of flycatchers in the *Empidonax hammondii-oberholseri-wrightii* complex. Univ. California Publ. Zool. 66: 79–238.

Johnston, D. W. 1971. Niche relationships among some deciduous forest flycatchers. Auk 88: 796–804.

King, J. R. 1955. Notes on the life history of Traill's Flycatcher (*Empidonax traillii*) in southeastern Washington. Auk 72: 148–173.

Linsdale, J. M. 1947. A ten-year record of bird occurrences on the Hastings Reservation. Condor 49: 236–241.

Lustick, S. 1969. Bird energetics: Effects of artificial radiation. Science 163: 387–390.

Oberlander, G. 1939. The history of a family of Black Phoebes. Condor 41: 133–151.

Ohmart, R. D., and R. C. Lasiewski. 1971. Roadrunners: Energy conservation by hypothermia and absorption of sunlight. Science 172: 67–69.

Pough, R. H. 1949. Audubon bird guide. New York, Doubleday and Co.

Pough, R. H. 1957. Audubon western bird guide. New York, Doubleday and Co.

Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Monogr. 37: 317–350.

Skutch, A. F. 1969. Life histories of Central American birds, 2. Pacific Coast Avifauna No. 34.

Todd, W. E. C. 1940. Birds of western Pennsylvania. Pittsburgh, Univ. Pittsburgh Press.

Verbeek, N. A. M. 1972. Daily and annual time budget of the Yellow-billed Magpie. Auk 89: 567–582.

Verbeek, N. A. M. 1973. The exploitation system of the Yellow-billed Magpie. Univ. California Publ. Zool. 99: 1–58.

Verbeek, N. A. M. 1975. Comparative feeding behavior of three coexisting tyrannid flycatchers. Wilson Bull. 87: 231–240.

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