

FORAGING BEHAVIOR OF THE EASTERN BLUEBIRD

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Avian foraging behavior is known to vary intraspecifically with habitat (Root 1967), weather (Lunk 1962:15), season (Ligon 1973), prey availability (Morton 1967), and from one population to another (Ligon 1968). Few studies, however, have examined the variety of factors influencing predatory behavior of a single species. I found the Eastern Bluebird (*Sialia sialis*) a good subject for such an investigation because this species forages in relatively open areas and is conspicuous from a distance. Moreover, bluebirds employ a variety of foraging tactics (Bent 1949:247) but typically use a lookout perch to locate prey on the ground (Preston and McCormick 1948, Krieg 1971); several parameters of the perch-feeding technique (perch height, predator-to-prey distance) can easily be quantified. In this paper I describe predatory behavior in the Eastern Bluebird and examine the effects of several environmental variables on bluebird foraging.

METHODS

Study area.—Observations were made in Macomb Co., southeastern Michigan (42°48'N, 82°59'W) during 1972 and 1973. The bluebird nesting period extended from late March to early August (Pinkowski 1975a) and most observations were made during the nesting season. Fifty nest boxes were available in the study area and bluebirds nested in these as well as in natural cavities (Pinkowski 1976a). In Michigan most bluebirds migrate south in winter; spring migrants first appear in early March with a peak arrival period occurring between 20 March and 20 April.

Six pairs of bluebirds were randomly observed at all times of the day, under all types of weather conditions, and in various stages of the nesting cycle. The bluebirds foraged in old fields (Fig. 1) characterized by hawkweed (*Hieracium* sp.), vetch (*Vicia* sp.), sheep sorrel (*Rumex acetosella*), goats-beard (*Tragopogon major*), cinquefoil (*Potentilla* sp.), daisy fleabane (*Erigeron philadelphicus*), oxeye daisy (*Chrysanthemum leucanthemum*), and various grasses. This is a low-growing, perennial sere that appears late in field succession in Michigan (Beckwith 1954). Common foraging perches were tree limbs and branches (especially if dead or defoliated, with oaks, *Quercus* sp., commonly employed), fence posts, boulders, and coarse weed stalks such as mullein (*Verbascum* sp.) and evening-primrose (*Oenothera* sp.). Foraging bluebirds were watched from a distance without disturbance and the presence of an observer did not alter their behavior in any way (cf. Krieg 1971:5).

Measurements.—Several parameters were measured on a foraging sequence, including the type of foraging tactic employed. A short "drop" to the ground (the "flydown" described for *S. sialis* by Goldman 1975) was most common. Measurements made on feeding drops were: perch height (vertical distance of the bird above the ground), drop base (ground level distance from a point immediately below the take-off perch to the landing location), hypotenuse of the resulting triangle (predator-to-prey distance), and



FIG. 1. View showing the old field flora with scattered trees and shrubs in the south-eastern Michigan study area.

distance between consecutive feeding perches (measured for birds moving along fence-rows having predetermined distances between fence posts). Not all perches resulted in the bird locating prey and not all drops resulted in prey capture. A perch was considered successful if a drop was made from it (prey was sighted but not necessarily captured) and a drop was considered successful if food was obtained. The latter was often impossible to determine with certainty, especially if small prey were pursued.

Each observation period lasted 1–2 h. Temperature was recorded in the field at the beginning and end of each observation period and the average value was assumed for all observations made during the period. Percentage of sunshine was obtained for each observation period by noting the proportion of time that shadows were cast. Wind speed could not be measured by instrument because the birds often foraged in valleys or behind wind breaks where wind speed was quite different than elsewhere. I estimated wind speed at a foraging site according to the effect of wind on feeding perches and foraging bluebirds. Light winds were those not causing noticeable movement of perches (tree limbs and weed stalks) and approximated actual speeds up to 5 km/h. Moderate winds (5 to 20–30 km/h) caused perch movement but did not interfere with foraging. Strong winds (over 20–30 km/h) caused at least some perches to move rapidly and be unacceptable as lookout posts.

Statistical procedures.—Percentages were examined for significant differences by a

t-test for the equality of percentages (Sokal and Rohlf 1969:607). I follow Verbeek (1975) in defining feeding tactic diversity (FTD) by the formula $FTD = -\sum_i p_i \ln p_i$, where p_i is the proportion of feeding involving the i^{th} feeding tactic. Unless otherwise stated, Chi-square tests on contingency tables employ Yates correction for continuity with d.f. = 1.

RESULTS AND DISCUSSION

Description of foraging tactics.—*Dropping* is the principal feeding mode of the bluebird. The ground is searched from a conspicuous perch and after locating prey, the bird sallies onto the ground and seizes its prey with the bill. Rarely is more than one food item obtained on a single drop to the ground. The food may be swallowed on the ground or brought to a perch for preparation and ingestion, but it is never held with the feet during capture and preparation. Only 21.7% of 189 small (< 1 cm long) food items were taken to a perch before ingestion compared to 88.5% of 43 large (> 2 cm long) food items. These percentages differ significantly ($t = 10.3$, $P < 0.001$).

Hunting bluebirds normally search the ground while perched upright. During inclement weather and more intensive feeding the head is lowered and the tail elevated. If low perches are not available bluebirds may perch horizontally part way up tree trunks or weed stalks to view the ground. When close to the ground bluebirds often turn the head and use monocular vision to search the ground. Binocular vision is frequently employed at relatively great heights. By changing perches when no food source is found, the bird is able to encounter a large number of possible foraging situations.

Flycatching involves capturing aerial insects by short flights into the air from a perch (usually the “new perch-short flight” pattern; Leck 1971), by more extended flights (“new perch-long flight”), or by seizing aerial prey without taking flight. I found that more than one item may be obtained per flight, and several aerial insects were fed to nestlings after a single flight, but Marshall (1957) and Krieg (1971) reported that only one item was captured per flight. Flycatching may temporarily become the only foraging tactic, as on summer evenings when aerial insects are highly visible in the long-angled sunlight (Morton 1967), after a rain, or at other times when certain prey species (e.g., swarming carpenter ants, *Camponotus* sp.) are abundant.

Gleaning occurs when the bird lands on and removes prey from the foliage and branches of trees or shrubs, or the main trunks of trees. Verbeek (1975), working with tyrannid flycatchers, defined gleaning as “capture of an insect sitting on any kind of substrate”; here, “gleaning” excludes prey capture on the ground. In early summer bluebirds glean small caterpillars (e.g., geometrids and pierids) from the leaves of trees. Many hymenopterans,

dipterans, coleopterans, and plecopterans (see Pinkowski 1976b) are obtained from tree trunks by gleaning.

Flight-gleaning is a modification of the dropping tactic and has been described for kingbirds (*Tyrannus* sp.) by Smith (1966:219). The bird descends toward the ground after locating prey, but remains in flight while plucking prey from vegetation. It may flutter briefly while inspecting the prey, but it never does so before locating an item; this sets flight-gleaning apart from *hovering*, a search method observed in Mountain Bluebirds (*S. currucoides*) by Criddle (1927), Power (1966), and Pinkowski (1975b) but not observed in Eastern Bluebirds during this study. Flight-gleaning is employed in areas of tall weeds and therefore becomes more common as the season advances and vegetation height increases.

Hopping is not a common feeding mode. Except for flycatching (new perch-long flight), it is the only foraging tactic wherein the prey is not located from a conspicuous perch. When feeding by this method a bluebird moves along the ground and feeds upon prey that is encountered after it lands on the ground. Hopping is limited to roadways, recently plowed farmlands, lawns, burnt areas, and other disturbed habitats that have few perches and sparse ground cover.

Of 2638 foraging sequences observed during March through June, 78.8% were accomplished by the dropping mode, a slightly lower percentage than that (87.4%) observed by Goldman (1975) for bluebirds feeding on lawns in Ohio. Flycatching and gleaning were more common foraging tactics (10.7% and 6.8%, respectively) than hopping (2.6%) and drop-gleaning (1.1%).

Feeding on fruit.—Beal (1915) found that up to 57.6% of the diet of *S. sialis* may consist of fruit during winter. I noted that bluebirds rely heavily on fruit sources in late summer and immediately after their arrival in early spring. Staghorn sumac (*Rhus typhina*) and multiflora rose (*Rosa multiflora*) are the common fruits eaten in spring. Honeysuckle (*Lonicera* sp.), cherry (*Prunus* sp.), and mulberry (*Morus* sp.) are eaten in summer.

Three distinct methods of obtaining fruit are employed; a bluebird may (1) hover in the air while ingesting berries (analogous to and employing the same motor patterns as flight-gleaning); (2) perch on a limb and pluck berries from an adjacent limb (similar to gleaning); or (3) perch on a fruit head (e.g., staghorn sumac) and pluck fruit from directly beneath its feet (not unlike securing animal prey on the ground after a drop).

Feeding tactics and season.—Although the relative frequencies of feeding tactics used by Eastern Bluebirds vary during the nesting period, dropping is the principal tactic employed in all seasons (Table 1). Frequency of the

TABLE 1
SEASONAL VARIATION IN FEEDING TACTICS OF EASTERN BLUEBIRDS IN
SOUTHEASTERN MICHIGAN, 1972-1973^a

	Percentage Occurrence			
	March (N=584)	April (N=595)	May (N=770)	June (N=689)
Dropping	99.5	86.6	88.6	43.8
Flycatching	0.4	9.4 ^b	5.6	26.3
Gleaning	0.1	0.4	1.2	24.2
Hopping	0.0	3.7	3.9	2.4
Drop-gleaning	0.0	0.0	0.8	3.4

^a Based on 12 birds.

^b Most records (35 of 56) obtained during one observation.

dropping tactic decreases in summer as vegetation height increases. A sparse ground cover is required for effective feeding by bluebirds using the dropping mode. After the breeding period bluebirds regularly hunted on mowed lawns around residences adjacent to the study area and evidently preferred such places to undisturbed areas containing tall vegetation.

Feeding tactic diversity is lowest in March (FTD = 0.034), is higher in April and May (0.491 and 0.487, respectively), and increases markedly in June (1.261). The increase in diversity is the result of more aerial feeding late in the season as food resources are increasingly exploited in a third (vertical) dimension. Willson (1974) characterized the Eastern Bluebird as an insectivore that feeds by sallying in the low vegetation stratum (a member of the "insectivore, low, sally" guild; see Root 1967). In spring "insectivore, ground, ground glean" adequately describes the species, but by the end of summer much fruit is consumed and "omnivore, low, sally" is probably more accurate.

Feeding modes and weather.—Feeding tactics were found to vary in frequency according to weather conditions. Of 89 feedings recorded in May and June during exceptionally cold (0-10°C), cloudy, and rainy or damp weather, 64 (71.9%) were accomplished by the dropping mode. A nearly identical percentage of dropping mode sequences was observed for the same period during warm (15-25°C), sunny, favorable weather (72.2%, N = 251). Flycatching was more common during favorable weather (14.7%) than during inclement weather (1.2%, $t = 2.2$, $P < 0.05$) whereas the reverse was true for gleaning (20.2% and 7.9% for inclement and favorable weather, respectively; $t = 2.0$, $P < 0.05$).

Flycatching is not a common feeding mode during excessively windy conditions, probably because aerial insects are reduced in number at these

TABLE 2
SEASONAL VARIATION IN FORAGING MEASUREMENTS OF EASTERN BLUEBIRDS
IN SOUTHEASTERN MICHIGAN, 1972-1973^a

	Spring Mean \pm SD	Summer Mean \pm SD
Base (m)	3.22 \pm 1.85	7.04 \pm 5.71
Height (m)	2.02 \pm 1.09	3.76 \pm 2.43
Predator-prey Distance (m)	3.97 \pm 1.88	8.26 \pm 5.81

^a Values obtained by triangulations on the dropping tactic based on 12 birds with N = 100 for each period. The means of each measurement are significantly different ($P < 0.001$, Mann-Whitney U-test).

times (Freeman 1945). In May and June flycatching accounted for only 2.0% (N = 99) of all foraging sequences during strong winds, a significantly smaller percentage ($t = 2.2$, $P < 0.05$) than that observed during moderate or light winds (13.6%, N = 1360). Thus seasonal changes in foraging tactics are similar to weather-mediated responses in that flycatching is employed more often during favorable (warm, sunny, and calm) weather and as the season advances. Presumably more aerial insects are available in favorable weather and later in the season.

Factors influencing foraging height.—Measurements were made on 100 bluebird drops randomly observed in the early spring (15 March to 15 April) and 100 in the early summer (15 May to 15 June) to examine factors influencing foraging height and predator-to-prey distances. Each sample was evenly divided between males and females.

Bluebirds forage closer to the ground and consume prey located nearer to their perches in spring than in summer (Table 2). Seasonal variation in foraging height may be attributable to smaller, fewer, or less active vernal insects that are more difficult to detect at greater heights. Also, as noted above, more aerial feeding occurs in summer and the birds may adjust their foraging heights accordingly. As a consequence of the greater foraging area that each perch affords in summer, fewer perches are required later in the season. Bluebirds inhabit more open habitats during summer than spring, perhaps because of a reduced dependence on perches as the season progresses.

Pooled data for the spring and summer periods show positive regression when drop base (B) is plotted on foraging height (H) according to the relationship $B = 1.17 + 1.20H$ (measurements in m). The slope of the regression differs significantly from 0 ($F = 76.2$, $P < 0.001$, $r^2 = 0.28$), indicating that bluebirds search areas more distant from the perch when foraging at greater heights. Evidently the area searched (the "perceptual

field"; Holling 1966, Salt 1967) more closely approximates a narrow annulus rather than all of the area within a circle as might be expected, and increases in length (L) according to the relationship $L = 2\pi B = 7.4 + 7.5H$.

The significant relationship between foraging height and drop base also suggests that the search angle A, defined here as $A = \tan^{-1}B/H$, remains relatively constant. In spring and summer the search angle averages 58° ($\tan^{-1} 3.22/2.02$; Table 2) and 62° ($\tan^{-1} 7.04/3.76$), respectively. Over the normal range of foraging heights (1–10 m) the search angle varies from 67° ($\tan^{-1} 2.37/1$) to 53° ($\tan^{-1} 13.17/10$) and is surprisingly constant in view of the wide range of foraging heights and bases. Deviations from the mean search angle may occur because of the deviations from the upright posture normally assumed by perch-feeding bluebirds, different head positions relative to the body (particularly as related to monocular or binocular viewing of the ground), or different perch inclinations relative to the ground.

Positive correlations exist between foraging height and temperature ($r = 0.42$, $P < 0.01$) and between height and sunshine percentage ($r = 0.17$, $P < 0.05$). Lunk (1962:15) found that Rough-winged Swallows (*Stelgidopteryx ruficollis*) feed close to the ground in cool, cloudy weather, and attributed this to prey response to these weather conditions. Increased sunshine increases insect movement (Gangwere 1966), but also may enhance the visual ability of avian predators because of greater illumination. Low temperatures often occur on cloudy days, however, and it is difficult to separate the effects of sunshine and temperature on foraging behavior.

No relationship was found when mean foraging heights were compared for the various wind speed categories (single factor ANOVA test, $F = 1.1$, $d.f. = 2/197$, $P > 0.5$).

Males and females of the same species are known to partition the feeding niche by foraging at different heights (Jackson 1970). A *t*-test, however, revealed no significant differences in the foraging heights ($t = 0.8$, $P > 0.5$) and drop bases ($t = 0.4$, $P > 0.5$) of male and female bluebirds.

Predator-to-prey distances were great for both males and females. Among males the maximum height recorded was 14.6 m, the maximum base was 28.3 m, and the maximum predator-to-prey distance was 29.0 m (measurements from 2 drops). A female dropped from a height of 10.7 m onto a 48.8 m base to obtain prey 50.0 m away. The distances from which prey were sighted were remarkable considering the small size of many of the insects involved.

Perch use.—Early in the season prey are not always encountered when the ground is searched and uninterrupted bouts of continuous feeding are frequent. Observations during March and April 1972 indicated that "perch

success" (the ratio of the number of perches from which a drop is executed to the total number of different perches used) was significantly lower during March (76 of 140 perches successful, 54.2%) than April (502 of 702 perches successful, 71.5%; $\chi^2 = 15.3$, $P < 0.01$). In only 3 of 28 observation periods was perch success lower than 50.0%; all occurred in March and the lowest figure observed was 31.9%. After early May bluebirds rarely failed to locate prey from a perch and alternated feeding with other activities except when feeding nestlings.

Bluebirds foraging during March and April returned to the same perch after a drop on 83 of 568 occasions (14.6%). After hunting from an unsuccessful perch, bluebirds moved to a higher perch (as opposed to one distinctly lower) 50.0% of the time during March ($N = 34$), 68.3% during early April ($N = 41$), and 76.9% of the time during late April ($N = 26$). The trend to move to a higher perch later in spring is significant according to a test for a linear trend in proportions (Snedecor and Cochran 1967:246, $z = 2.2$, $P < 0.05$) and may occur because of increased availability of aerial prey that are searched for if prey is not located on the ground. In late spring, however, insects are more active and prey movement is less critical in the birds' ability to locate prey. Also, by late April most bluebirds are nesting and may exhibit greater selectivity in prey consumed. Possibly a greater variety of insects can be searched for at greater heights.

Time between drops during bouts of continuous feeding averaged 46.7 sec during March and April ($N = 61$), with a maximum of 186 sec. Time spent on a successful perch before a drop was made averaged 23.3 sec ($N = 291$) and was less during inclement weather conditions ($\bar{x} = 20.0$ sec, $N = 103$) than during favorable conditions ($\bar{x} = 25.2$ sec, $N = 188$); the means differ significantly ($t = 2.2$, $P < 0.05$). Time spent on unsuccessful perches before the bird moved to a new perch averaged 27.2 sec but was significantly less during inclement weather (22.7 sec, $N = 162$) than during favorable weather (34.5 sec, $N = 102$; $t = 4.6$, $P < 0.01$). Thus inclement weather imposes greater energy demands on the bird by necessitating more frequent movements (more perch changes and more drop attempts). Fewer insects are active during inclement conditions and reduced prey availability and activity evidently cause the birds to forage closer to the ground, thereby reducing the perceptual field because of the relatively constant search angle. A smaller area can presumably be searched more rapidly than a larger area.

Distances traveled by birds moving from an unsuccessful perch to a new perch averaged 7.6 m ($SD = 7.9$ m, $N = 132$) and were significantly greater (Mann-Whitney U-test, $P < 0.001$) than the average distance of 4.1 m ($SD = 5.5$, $N = 211$) traveled by birds foraging from a successful perch, based

on observations made during March and April. The mean distance traveled when moving from an unsuccessful perch is 18.0% greater than twice the average drop base observed in the spring period (Table 2), indicating that the birds move only slightly more than the minimum distance required to afford them a completely new perceptual field. By contrast, birds leaving successful perches move only 63.7% of twice the average drop base and thus search successive areas that overlap. The tendencies for bluebirds to move shorter distances and search successively overlapping areas after foraging from successful perches are similar to the findings of Smith and Sweatman (1974), who noted that Great and Blue tits (*Parus major* and *P. caeruleus*) were more likely to return to previous capture sites when food was encountered.

No differences were found when distances traveled in leaving successful and unsuccessful perches were compared for males and females ($P > 0.3$ in each case).

I found that pairs of bluebirds exhibited great differences in the relative sizes of areas used for foraging during the nestling period. Ten foraging ranges were examined in spring 1972 to determine the effect of perch abundance on the size of the foraging area. Although the size range of an entire foraging area was surprisingly large (4.5–38.9 ha), the size of the area containing perches was relatively constant (3.9–8.4 ha). The variances of the 2 sets of measurements (91.4 and 2.2, respectively) are significantly different ($F = 41.5$, $P < 0.01$), suggesting that perch distribution may influence territory size.

Factors limiting bluebird abundance.—Although the absence of nest cavities may limit the number of Eastern Bluebirds (Pinkowski 1976a), the availability of perches may also be an important limiting factor in some ecological situations. Habitats having few or no perches are rarely used by Eastern Bluebirds; these areas elevate the energy demands imposed on foraging birds by necessitating more prolonged flights as the birds move from one foraging situation to another.

Several aspects of this study suggested that the feeding requirements of bluebirds are stricter in spring than summer. The bluebirds I observed experienced little difficulty in obtaining food in summer and used a greater variety of habitats at that season. Of 39 nest boxes used by bluebirds at one time or another, 23 were used in spring compared to 37 in summer. The difference in use frequency for the 2 seasons is significant ($\chi^2 = 12.2$, $P < 0.001$) and appears related to the fact that foraging heights are less in spring and more perches are required at that season. In Michigan temperatures below

5–8°C are common until late May and, when accompanied by overcast conditions, inhibit bluebirds from feeding on insects. Interestingly, most records of severe bluebird mortality in “winter” (Musselman 1941, Kenaga 1958) actually refer to extensive mortality in early spring (late February to early April).

Optimum conditions for bluebirds occur in areas containing an abundance of dead trees and limbs that are used as nest cavities and as foraging perches. Poor soil and a sparse ground cover help create ideal feeding conditions.

SUMMARY

Eastern Bluebird foraging behavior was studied in southeastern Michigan during 1972 and 1973. Bluebirds seize most prey after a short flight (“drop”) to the ground from a conspicuous perch. Other foraging tactics that may be used are flycatching, gleaning, flight-gleaning, and hopping. Frequencies of various feeding modes depend on season and weather, although dropping comprised 78.8% of the foraging sequences observed under all conditions. The base of a feeding drop increases with foraging height, suggesting a relatively constant search angle.

Prey is usually located from a perch before it is pursued and habitats having a short, sparse ground cover are preferred by feeding bluebirds. Foraging height is greater in summer and during favorable, warm weather than in spring or cold, inclement weather. Bluebirds travel shorter distances to new perches if prey is sighted from the previous perch than if prey is not sighted. Males and females exhibit no differences in temporal and spatial use of perches. Perch abundance, however, influences the size of the area required by adults feeding nestlings and may be a factor limiting the distribution of bluebirds, especially in spring.

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