DIETARY VARIATION AMONG NESTLING STARLINGS[1]

JANICE MOORE[2]
Department of Biology, University of New Mexico, Albuquerque, NM 87131
and
Department of Zoology, University of Texas, Austin, TX 78712

Abstract. I sampled diets of nestling European Starlings (*Sturnus vulgaris* L.) in central New Mexico for four consecutive years. The prevalence of prey in these diets varied within and between years, within days, and relative to nestling age and brood size. Dietary diversity was not significantly different between early and late broods. Young birds were fed more diverse diets than older nestlings, and among these young birds, large broods had more diverse diets than small broods. Different broods received different prey, despite similar conditions of location, time, weather, brood size and nestling age.

Key words: European Starling; Sturnus vulgaris; *nestlings; diets; dietary diversity; New Mexico.*

INTRODUCTION

The European Starling (*Sturnus vulgaris*) is a successful and widespread colonist whose feeding ecology has not gone unnoticed. As studies emerge from around the world, it has become apparent that starling foraging behavior can be highly variable. Prey brought to nestlings is known to vary with time of day (Dunnet 1955), weather (Kalmbach and Gabrielson 1921, Gromadzki 1969), brood size (Tinbergen and Drent 1980, Tinbergen 1981), nestling age (Kalmbach and Gabrielson 1921, Coleman 1977, Tinbergen 1981), and between and within years (Gromadzki 1969, Coleman 1977, Tinbergen and Drent 1980).

From the variation that has been recorded in starling diets, it is clear that extrapolations from other data sets may be of limited utility in describing its food in a new habitat. The starling was first sighted in New Mexico in 1935, was found nesting there in 1954 (Ligon 1961), and is now a resident in central New Mexico (Hubbard 1970). The dietary habits of this newcomer are important not only because of its importance as an agricultural pest (Wright et al. 1980), but also because such baseline information will enhance its considerable value as a readily available and unrestricted subject for field study. In addition, this study may provide useful data for future ornithologists who wish to assess historical changes in the diet of starlings. Is the bird inevitably an opportunist, or do resident populations refine dietary choices over time? In an effort to examine starling dietary variation in a new habitat, I studied the food of nestling starlings in central New Mexico for four years. I asked the following questions:

1. What are these nestling starlings fed in urban and in rural settings?
2. How do diets vary relative to space, time, brood size, and age?
3. If such factors do not vary, are diets similar among broods?

MATERIALS AND METHODS

I placed nest boxes (Kessel 1957) in trees on the University of New Mexico (UNM) campus in Albuquerque (1978–1981; 28 boxes maximum) and near Los Lunas (1979–1980; 12 boxes maximum). The UNM site is in an urban area characterized by lawns, buildings and trees; the Los Lunas site is agricultural and riparian, approximately 40 km south of Albuquerque.

I placed ligatures (pipe cleaners) around the necks of nestling starlings to prevent food from being swallowed (Willson 1966). The nestlings were left in this condition no more than 2 hr. Prey items delivered by parent birds were collected with forceps and preserved in 70% ethanol.

Although the ligature method allows repeated sampling of individual birds and can yield intact prey, it has potential disadvantages. These include possible slippage of prey through the constriction, strangulation, failure of nestlings to gape properly, and loss of disgorged prey (see Johnson et al. 1980). I therefore carefully examined possible sources of bias in data resulting from the ligature method (discussed fully in Moore 1983). The ligature treatment neither impeded vigorous begging by the nestlings, nor affected rates of parental nest box visits. I always searched nest boxes for disgorged prey. I also examined the stomach contents of 105 nestlings after pipe cleaner sessions and found little evidence of slippage. Although young nestlings could have strangled, and thus were sampled sparingly, I found little apparent ligature-induced mortality in nest-

lings over four days old. As chicks older than 17 days may leave the nest if disturbed, I did not ligature nestlings beyond this age.

I collected 876 samples from a total of 195 nestlings in 55 broods. Prey were identified to family whenever possible, and reported and analyzed on a per item basis. As nestlings were rarely fed plant material, I report only animal prey. Depending on the amount of exoskeleton damage and evaporation, wet weight measurements may be misleading. Because I dissected and examined all prey for internal parasites (Moore 1983), I did not directly measure the dry weight or energy content of intact prey. Large prey may be somewhat underrepresented if parents removed conspicuous disgorged items and ate them in the nest box (L. Best, pers. comm.). I never saw parents leaving with prey. I arbitrarily designate Brood I as those hatched before 16 May, intermediate broods hatched 16 to 31 May, and Brood II hatched after 31 May. Thus, there was a maximum of three cohorts per site during a breeding season, with *cohort* defined as all nestlings hatched during one of the three brood periods above. I divided the foraging period into four segments: dawn to 1000, 1000 to 1300, 1300 to 1600, 1600 to dusk.

For each brood, dietary diversity was calculated following Rotenberry (1980), who used the reciprocal transformation of Simpson's (1949) index of diversity, that is,

$$\text{Dietary diversity} = 1/\Sigma \, p_i^2$$

where p_i is the proportion of the ith prey category in the prey collection (= all samples from a brood) under consideration. Peet (1974) and Rotenberry (1980) have discussed this index in detail. In determining diversity, I used ordinal taxonomic categories for arthropods. Other categories included non-arthropods (largely oligochaetes) and larval/adult subdivisions of both Coleoptera and Lepidoptera. Because brood size often changes between hatching and fledging, when exploring the relationship between dietary diversity and brood size, I subdivided the prey collection according to brood size (large, $n > 3$; small, $n < 3$), and calculated this diversity for each of the subdivisions. Similarly, I compared the dietary diversities calculated for older (> 10 days) and younger (≤ 10 days) broods. I used Wilcoxon two-sample test (two-tailed; $\alpha = 0.05$) for two-sample comparisons, and Pearson's correlation to relate dietary diversity and brood size within age classes ($\alpha = 0.05$).

Many field investigations of foraging attempt to assess prey abundances and to compare these abundances with diet choices, but serious problems attend such assessments (see Wiens 1984 for review). In my examination of dietary convergence, I did not measure existing food supply; I compared foraging choices, as reflected by nestling diets, within each of four groups of parent birds under virtually identical conditions of site, time, and weather. Because compared nest boxes were no more than 90 m apart, parent birds had access to approximately the same food supply. Brood sizes and nestling ages did not vary by more than one bird or day within groups. Sampling periods were simultaneous and of approximately equal duration. One group (UNM1) consisted of four broods on the University of New Mexico campus and each brood was sampled for a total of 4 hr, 5 and 7 days posthatching (late April 1979). UNM2 contained two broods and was sampled five times (10 hr total for each brood, ages 6 to 14 days, 9–17 June). Four broods near Los Lunas (LL1) were sampled three times (5 hr total for each brood, ages 6 to 11 days, early May 1980). Three broods (LL2) in the same location were sampled for four days (8 hr total for each brood, ages 6 to 12 days, mid-June 1980).

Because choice of patch, as well as diet item, is important in foraging behavior (Pyke et al. 1977), the possibility that prey were unevenly distributed might seem to present problems when comparing parent birds' choices. Proximity of the nest boxes used within a group rendered patches, as well as diet items within those patches, accessible to all parents. I saw no interference among adult foragers. Thus, I assume that foraging decisions of these parents were directly comparable and reflect both patch and diet item choice from an unknown array of equally available patches and items. Prey categories for a brood were ranked according to number of items in the categories. I tested the null hypothesis of no difference in ranks among broods for the four independent data sets using Friedmann's Rank Sums, correcting for ties (Hollander and Wolfe 1973), and using the Wilcoxon paired-sample test in the case of UNM2 (Zar 1974). Because the latter test is based on the rank of differences between each prey type, numbers of prey were converted to proportions of the sample before analysis.

RESULTS

GENERAL DIET

Except for one cohort, Lepidoptera and Coleoptera were the most frequent prey categories (79.9% of the diet in Albuquerque (UNM) and 80.5% at Los Lunas; Table 1). Albuquerque nestlings were fed mostly Lepidoptera (47.8%),

TABLE 1. Percent composition of starling nestling diet (animal prey) by item in central New Mexico. Brood I, before May 16; int. brood, May 16–31; Brood II, after May 31. (L = larva, int. = intermediate.)

Columns 1–12: **Albuquerque**; Columns 13–17: **Los Lunas**.

	1978		1979			1980			1981			Group total	1979	1980			Group total
Brood:	Int.	II	I	Int.	II	I	Int.	II	I	Int.	II		II	I	Int.	II	
Orthoptera	1.2L	–	–	–	–	–	1.8	3.9	–	–	–	0.2	18.0	0.6	1.1	4.5	4.5
Hemiptera	8.3	7.1	–	–	1.4	–	–	–	6.2	–	–	1.5	4.0	–	1.5	0.9	1.4
Homoptera	–	–	–	–	–	0.9	–	–	1.5	–	9.1	0.9	–	–	0.5	0.9	0.4
Coleoptera (total)	24.7	28.6	42.9	10.0	13.3	78.0	35.7	57.6	46.2	28.6	36.4	32.1	31.0	40.2	79.9	41.0	51.7
(Larva total)	1.2L	–	34.9L	0.9L	10.4L	40.3L	19.7L	19.2L	26.2L	–	9.1L		6.0L	32.3L	68.8L	22.7L	
(Adult total)	23.5	28.6	8.0	9.1	2.9	37.7	16.0	38.4	20.0	28.6	27.3		25.0	7.9	11.1	18.3	
Larva (type unknown)	1.2L	–	34.1L	–	1.0L	38.6L	17.9L	11.5L	20.0L	–	9.1L		6.0L	2.1L	1.6L	21.8L	
Adult (type unknown)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	
Carabidae	–	–	0.8	0.9	1.7	3.5	5.3	11.5	–	–	9.1		21.0	1.1	0.5	–	
Staphylinidae	1.2	14.3	0.8	–	0.4	–	5.3	–	3.1	–	9.1		2.0	6.2	2.7	6.4	
Scarabaeidae	–	14.3	–	0.9	–	1.7L	–	19.2	–	14.3	9.1		–	–	–	–	
Coccinellidae	4.7	–	4.0	5.5	–	–	1.8	7.7L	6.2L / 16.9	–	–		–	–	11.7L / 6.8	0.9L	0.9L
Chrysomelidae	15.3	–	2.4	–	9.4L	33.3	1.8	7.7	–	–	–		2.0	0.6	–	4.6	
Curculionidae	–	–	–	1.8	0.4	–	–	–	–	14.3	–		–	30.2L	55.5L / 1.1	7.3	
Others*	2.3	–	0.8	0.9	0.4	0.9	3.6	–	–	–	–		–	–	–	–	
Lepidoptera (total)	44.7	50.1	46.8	69.8	61.1	14.1	46.4	38.5	24.6	57.1	27.2	47.8	25.0	45.3	12.2	33.7	28.7
Larva	16.5	50.1	4.8	40.4	37.6	9.7	14.3	26.9	4.6	28.6	27.2		22.0	34.1	10.1	19.2	
Pupa	–	–	–	0.9	1.4	–	–	3.9	–	–	–		3.0	–	2.1	1.8	
Adult	28.2	–	42.0	28.5	22.1	4.4	32.1	7.7	20.0	28.5	–		–	11.2	–	12.7	
Diptera	–	–	0.8	6.5	7.3	0.9	–	–	4.6	–	–	3.8	1.0	1.7	1.1	2.7	1.6
Hymenoptera (total)	4.7	7.1	–	–	0.4	0.9	–	–	3.0	14.3	9.1	1.2	–	–	0.5	1.8	0.5
Formicidae	2.3	7.1	–	–	–	0.9	–	–	1.5	14.3	9.1		–	–	–	1.8	
Isopoda	14.1	7.1	6.3	12.8	12.6	1.7	12.5	–	3.1	–	–	9.2	16.0	2.2	–	11.8	5.7
Araneida	–	–	–	–	–	–	–	–	–	–	–	–	5.0	6.1	–	0.9	2.9
Non-arthropods	2.3	–	3.2	0.9	3.5	3.5	3.6	–	10.8	–	–	3.3	–	3.9	3.2	1.8	2.6
Total animal prey	85	14	126	109	285	114	56	26	65	7	11	898	100	179	189	110	578

* Dermestidae, Cleridae, Tenebrionidae, Bruchidae.

TABLE 2. Percent composition of starling nestling diet (animal prey) in central New Mexico by nestling age and diet item. Brood I, before May 16; intermediate (int.) brood, May 16–31; Brood II, after May 31.

	Albuquerque													
	1978				1979						1980			
	Int.		II		I		Int.		II		I		Int.	
Brood age (days):	≤10	>10	≤10	>10	≤10	>10	≤10	>10	≤10	>10	≤10	>10	≤10	>10
Orthoptera	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—
Hemiptera	8.5	—	—	—	—	—	—	—	0.8	—	—	—	2.7	—
Homoptera	—	—	—	16.7	—	—	—	—	3.0	—	—	1.8	—	—
Coleoptera														
Larvae	1.2	—	—	—	35.5	20.0	1.2	—	6.1	14.4	35.1	45.6	24.3	10.5
Adults and pupae	24.4	—	12.5	49.9	8.3	—	10.3	4.5	1.5	3.9	47.3	28.0	13.5	21.1
Lepidoptera														
Larvae	15.9	33.3	75.0	16.7	4.1	20.0	35.6	59.1	31.8	42.5	14.0	5.2	18.9	5.3
Adults	29.3	—	—	—	42.2	40.0	29.9	27.3	22.0	24.8	1.8	7.0	35.2	26.3
Diptera	—	—	—	—	0.8	—	8.0	—	15.9	—	—	1.8	—	—
Hymenoptera	4.9	—	—	16.7	—	—	—	—	0.8	—	—	1.8	—	—
Isopoda	12.2	66.7	12.5	—	5.8	20.0	13.8	9.1	14.4	11.1	1.8	1.8	5.4	26.3
Non-arthropods	2.4	—	—	—	3.3	—	1.2	—	3.8	3.3	—	7.0	—	10.5
Total animal prey	82	3	8	6	121	5	87	22	132	153	57	57	37	19

and those in Los Lunas were fed primarily coleopteran larvae. In 12 of 15 cohorts, combined Lepidoptera and Coleoptera accounted for at least 70% of diet items, and in no group did they comprise less than 50%.

The sites differed in that Lepidoptera predominated in seven of eleven Albuquerque cohorts, but in only one of the four Los Lunas groups. Larvae dominated this category in Los Lunas, but not in Albuquerque. In general, curculionids, carabids and coccinellids were among the major coleopteran taxa fed to Los Lunas nestlings. In addition, staphylinids, scarabaeids, and chrysomelids were well-represented at Albuquerque. Moreover, some prey exhibit a diel pattern of abundance (Moore 1981; see also Tinbergen 1981).

TEMPORAL VARIABILITY

In Albuquerque (all years), the proportion of Coleoptera decreased over the course of the breeding season, paralleling a decrease in the ratio of Coleoptera larvae to adults (Table 1). Coleoptera families showed no identifiable trends, and no single family exhibited consistent relative abundance rank on a year-to-year scale. The proportion of Lepidoptera, especially larvae, in samples, increased during the breeding season, as did dipteran larvae and Isopoda when they were relatively common diet items (1979). Other prey occurred too infrequently to identify seasonal trends. The dietary diversity of early broods ($\bar{x}$ = 2.5 ± 0.78, n = 27) and late broods ($\bar{x}$ = 3.0 ± 1.30, n = 29) did not differ significantly, however, for the entire data set.

NESTLING AGE, BROOD SIZE, AND DIET COMPOSITION

In Albuquerque nestling diets, the hemipteran, coleopteran larvae, hymenopteran and non-arthropod portions decreased steadily with nestling age. In Los Lunas, the percentage of Lepidoptera in the diet increased with nestling age, while dipteran and isopod fractions decreased (Table 2). The dietary diversity of younger birds at Los Lunas ($\bar{x}$ = 3.3 ± 1.14 SD, n = 17) was significantly larger (P < 0.02) than that of older animals ($\bar{x}$ = 2.3 ± 1.08, n = 15). A similar tendency (P = 0.09) can be observed using the data from Albuquerque for younger ($\bar{x}$ = 2.6 ± 0.99, n = 38) and older nestlings ($\bar{x}$ = 2.1 ± 0.94, n = 27). Holding brood size constant for all sites, in my combined data set, the partial correlation between dietary diversity and age was negative (r = −0.280) and highly significant (P < 0.005).

Brood size seemed especially influential in the diets of early broods (Table 3). In this group, a larger brood size was associated with larger proportions of adult Coleoptera, Diptera, Hymenoptera and Isopoda, and fewer coleopteran larvae. Intermediate clutches showed few consistent trends, although the proportion of coleopteran adults was larger in large broods, and smaller broods were more likely to be fed non-arthropod prey. In Albuquerque, larger late broods were generally fed a greater percentage of lepidopteran larvae and a smaller proportion of adult beetles than were small brood counterparts.

I found a significant and positive partial correlation (r = 0.203, P < 0.05) between brood

TABLE 2. Extended.

Albuquerque								Los Lunas							
1980		1981						1979		1980					
II		I		Int.		II		II		I		Int.		II	
≤10	>10	≤10	>10	≤10	>10	≤10	>10	≤10	>10	≤10	>10	≤10	>10	≤10	>10
6.3	—	—	—	—	—	—	—	18.9	17.0	—	1.3	1.3	—	7.5	—
—	—	8.9	—	—	—	—	—	7.6	—	—	—	1.3	—	—	2.3
—	—	2.2	—	—	—	—	100.0	—	—	—	—	0.6	—	1.5	—
31.2	—	28.9	20.0	—	—	10.0	—	9.4	2.1	31.4	33.7	69.0	70.0	28.4	14.0
12.5	80.0	26.7	5.0	—	40.0	30.0	—	7.6	44.7	6.9	9.1	12.0	6.7	14.9	23.3
31.2	20.0	—	15.0	50.0	20.0	30.0	—	24.5	19.2	40.2	26.0	9.5	13.3	13.4	27.9
18.8	—	8.9	45.0	—	40.0	—	—	—	6.4	1.0	24.7	1.3	6.7	14.9	14.0
—	—	2.2	10.0	—	—	10.0	—	1.9	—	2.9	—	1.3	—	3.0	2.3
—	—	4.4	—	50.0	—	10.0	—	—	—	—	—	0.6	—	1.5	2.3
—	—	2.2	5.0	—	—	10.0	—	20.8	10.6	2.9	1.3	—	—	13.4	9.3
—	—	15.6	—	—	—	—	—	9.4	—	9.8	1.3	—	—	—	2.3
								—	—	4.9	2.6	3.1	3.3	1.5	2.3
16	10	45	20	2	5	10	1	53	47	102	77	159	30	67	43

size and dietary diversity when age was held constant. This was most apparent in younger chicks, where large broods had significantly more diverse diets ($\bar{x}$ = 3.2 ± 1.22, n = 28; P < 0.05) than small broods ($\bar{x}$ = 2.6 ± 1.11, n = 30).

DIETARY CONVERGENCE

In two of the four comparisons (LL2 and UNM2), ranks of prey were significantly different (P < 0.05, and in another (UNM1), they tended to differ (P < 0.10; Table 4). Combining probabilities from all four tests revealed a highly significant (P < 0.005) likelihood that ranks were different.

DISCUSSION

GENERAL DIET

My results are generally consistent with those reported by others in the United States and abroad (Kalmbach and Gabrielson 1921; Lindsey 1939; Dunnet 1955; Gromadzki 1969; Westerterp 1973; Smith 1975; Moeed 1975, 1980; Coleman 1977; Tinbergen 1981). Feare (1984) noted that, despite geographic differences in the species, most studies show that the most frequent diet items are coleopteran and lepidopteran larvae, especially those that live close to the soil surface. Additionally, Diptera have been found to be important in Holland (Gromadzki 1969, citing Kluijver 1933; Westerterp 1973; Tinbergen and Drent 1980; Tinbergen 1981) and Scotland (Dunnet 1955). Of course, comparisons must be made circumspectly, because methods of collecting and reporting data vary among workers and even within studies, ranging from stomach content studies to photographic studies and based on prey weight or item frequency.

Isopods were unusually abundant in my samples (Table 1), although they have been reported in few other studies (Moeed 1975, Coleman 1977), where they did not exceed 2.1% of the diet. It has been argued that isopods are infrequent items because of distastefulness or unavailability (Gorvett 1956). A subset of the isopods in my study areas, however, were intermediate hosts for the acanthocephalan *Plagiorhynchus cylindraceus,* which alters the behavior of infected isopods. Parasite prevalence has not been reported heretofore in other starling diet studies, but it may play a role in diet composition of this and other predators (Moore 1984a, b).

The New Mexico birds are also unusual in their coleopteran prey. Scarabaeids, an apparent staple in most areas, were absent from the Los Lunas samples, although present in the Albuquerque collections. Moreover, coccinellids were more plentiful in the New Mexico diets than reported elsewhere (Kalmbach and Gabrielson 1921; Lindsey 1939; Gromadzki 1969; Smith 1975; Moeed 1975, 1980; Coleman 1977). Starlings are thought to avoid coccinellids because they are distasteful (Coleman 1977, but see Brooks 1952) and rarely encountered (Moeed 1980).

TEMPORAL VARIABILITY

While Tinbergen and Drent (1980) found considerable annual variation in the food given to chicks, Coleman (1977) found annual similar-

TABLE 3.   Percent composition of starling nestling diet (animal prey) by item and brood size in central New Mexico.

A. Brood 1: Hatched Before May 16.
(Orthoptera, Homoptera, and Hymenoptera did not exceed 4% of any group's diet.)

	Albuquerque							Los Lunas			
	1979			1980		1981		1980			
Brood size:	2	3	4	3	4	1	2	3	4	5	6
Hemiptera	—	—	—	—	—	—	—	7.4	—	—	—
Coleoptera											
Larvae	76.7	15.0	23.7	26.0	51.5	66.7	40.0	20.4	34.8	5.3	50.0
Adults	—	5.0	11.8	42.0	34.4	—	—	24.1	8.7	12.5	3.8
Lepidoptera											
Larvae	3.3	10.0	3.9	8.0	10.9	33.3	—	1.8	28.2	46.4	29.5
Adults	16.7	60.0	47.4	10.0	—	—	40.0	20.4	19.6	17.9	1.3
Diptera	—	—	1.3	2.0	—	—	—	5.6	2.2	—	2.6
Araneida	—	—	—	—	—	—	—	—	4.3	7.1	6.4
Isopoda	3.3	—	9.2	2.0	1.6	—	—	3.7	—	3.6	2.6
Non-arthropods	—	10.0	2.6	8.0	—	—	20.0	11.1	2.2	5.4	3.8
Total items	30	20	76	50	64	6	5	54	46	56	78

B. Intermediate Brood: Hatched May 16–31.
(Orthoptera and Homoptera did not exceed 4% of any group's diet. Araneida were not observed.)

	Albuquerque											Los Lunas	
	1978			1979			1980			1981		1980	
Brood size:	2	3	4	2	3	4	2	3	4	1	3	3	4
Hemiptera	—	29.4	4.6	—	—	—	—	—	—	8.3	—	1.5	—
Coleoptera													
Larvae	—	—	—	—	—	—	—	21.2	9.1	25.0	—	61.8	86.0
Adults	20.0	5.9	2.3	3.6	3.2	11.9	37.5	9.1	27.3	25.0	28.6	14.5	3.5
Lepidoptera													
Larvae	16.0	17.6	16.3	60.7	22.6	38.1	50.0	18.2	—	16.7	28.6	10.7	8.8
Adults	8.0	47.1	32.6	25.0	48.4	21.4	12.5	33.3	36.3	25.0	28.6	3.0	—
Diptera	—	—	—	—	3.2	14.3	—	—	—	—	—	0.8	—
Hymenoptera	12.0	—	2.3	—	—	14.3	—	—	—	—	14.2	0.8	1.7
Isopoda	32.0	—	9.3	7.1	19.4	—	—	15.2	18.2	—	—	—	—
Non-arthropods	8.0	—	—	3.6	—	—	—	3.0	9.1	—	—	4.6	—
Total items	25	17	43	28	31	42	8	33	11	12	7	131	57

TABLE 3. Continued.

C. Brood II: Hatched After May 31.
(Non-arthropods did not exceed 5% of any group's diet.)

	Albuquerque										Los Lunas					
	1978		1979			1980			1981		1979			1980		
Brood size:	2	3	2	3	4	1	2	3	2	3	3	4	5	3	4	5
Orthoptera	—	—	—	—	—	—	6.7	—	—	—	11.1	7.4	23.4	3.3	7.3	2.6
Hemiptera	—	—	—	—	0.5	—	—	—	—	—	—	3.7	4.7	3.3	—	—
Homoptera	16.7	—	—	—	1.8	—	—	—	11.1	—	—	—	—	—	2.4	—
Coleoptera																
Larvae	—	—	—	34.5	4.4	12.5	13.3	66.7	11.1	—	11.1	14.8	1.6	16.7	17.1	33.3
Adults	49.9	12.5	—	1.7	3.1	87.5	20.0	—	33.4	—	22.2	3.7	34.4	30.0	22.0	5.1
Lepidoptera																
Larvae	16.7	75.0	100.0	24.1	41.3	—	46.7	—	11.1	100.0	22.2	37.1	15.6	26.7	19.5	12.7
Adults	—	—	—	24.1	22.7	—	13.3	33.3	—	—	—	7.4	1.6	6.7	17.1	18.0
Diptera	—	—	—	—	9.3	—	—	—	11.1	—	—	—	1.6	3.3	2.4	2.6
Hymenoptera	16.7	—	—	—	0.5	—	—	—	11.1	—	—	—	—	—	2.4	2.6
Araneida	—	—	—	—	—	—	—	—	—	—	—	11.1	3.1	3.3	—	—
Isopoda	—	12.5	—	13.9	12.4	—	—	—	11.1	—	33.4	14.8	14.0	6.7	9.8	18.0
Total items	6	8	2	58	225	8	15	3	9	2	9	27	64	30	41	39

ity in diet. Seasonal dietary variation has also been noticed, and Gromadzki (1969) speculated that this resulted from increased difficulty in meeting nestling energy requirements, noting higher second-brood mortality. I also observed progressive seasonal decrease in survivorship (Moore 1984c). This may be a function of nutrition or other variables, but apparently this is not related to within-brood dietary diversity.

NESTLING AGE, BROOD SIZE, AND DIET COMPOSITION

Tinbergen and Drent (1980) suggested that supranormal broods might approximate "hungry" nestlings. Tinbergen (1981) found that the same parents fed small and normal-sized broods different prey species with different consequences for the nestlings. My data support the notion of a relationship between brood size and diet; diversity increased with brood size, independently of age.

Nestling diets also vary with nestling age, probably because of changes in both prey availability and developmental requirements of nestlings (Feare 1984). This variation includes prey size (Kessel 1957, and citing Kluijver 1933) and texture (Coleman 1977) and proportion of prey species (Kalmbach and Gabrielson 1921, Tinbergen 1981), and may increase with age (Kessel 1957, Coleman 1977, Tinbergen 1981, but see Gromadzki 1979).

Demands on parents increase with nestling age (Westerterp 1973). If changing demands on parents affect prey choice across the categories I used, one might expect parallel trends for diversity with increasing brood size and with age. My analysis shows the opposite result and may indicate that age-related differences in nutritional requirements can overshadow the simple increase in demand placed on parents of larger, older nestlings. When feeding older nestlings or large clutches, parents must support increased offspring biomass. The ways in which they do so, as indicated by dietary diversity indices, are not the same for both cases.

DIETARY CONVERGENCE

I did not attempt to assess prey availability in this study, and it might be argued that fluctuations in prey populations were largely responsible for my observations. My comparisons within four sets of parent birds foraging under similar conditions reveal significant differences in foraging choices that may not be solely attributable to differences in prey abundance (Table 4). These results indicate that parent starlings did not select the same kinds

TABLE 4.   Numbers of prey delivered to four groups of nestling starlings.

	Orthoptera	Hemiptera	Homoptera	Hymenoptera	Coleoptera		Lepidoptera		Diptera	Isopoda	Araneida	Non-arthropods
					Larvae	Adults	Larvae	Adults				
UNM1	—	—	—	—	13	4	4	18	1	7	—	—
UNM2	—	—	1	—	2	3	37	15	—	7	—	3
LL1	—	—	—	—	20	11	38	19	1	2	4	4
LL2	4	1	1	1	18	12	13	8	2	9	—	2

of food, even when prey were grouped at rather inclusive taxonomic levels.

In part, this may reflect a response to food shortage. The nestlings in this study exemplified the tendency for weight and survival of starling hatchlings to decrease as the breeding season progresses (Moore 1984c). The LL2 and UNM2 broods hatched approximately one month later than the other two groups, and given their relatively low weights, it is possible that food shortage prompted the within-group foraging divergence exhibited by parents.

In contrast, the significant positive partial correlation between brood size and dietary diversity indicates that individual parents are likely to diversify prey delivered to large broods, a condition not strictly analogous to food shortage. This will not necessarily yield differences between prey ranks such as those observed in LL2 and UNM2 unless parents diversify in different ways. As shown above, dietary diversity did not differ for early and late broods. Demands of large broods may thus prompt parents to diversify prey and may result in greater dietary diversity within broods. On the other hand, food scarcity (as inferred from late season, lighter-weight nestlings) may result in divergence of foraging tactics among parents and inter-brood differences in diet composition.

Despite the extent of this study, my sample size is regrettably small if limited to samples that are strictly comparable (i.e., the diet convergence study). It does, however, yield nonrandom differences. Can we be confident that these differences reflect true discrepancies in foraging decisions?

My assumption that patch and diet item availability were similar for the parent birds in this comparison may be faulty. Prey may be patchily distributed within superficially homogeneous study sites. Such qualifications have bedeviled attempts to address prey abundance in many studies. I tried to minimize patch effects by comparing data only from similar broods in close proximity, and I assumed that parent birds had access to the same patches. Nonetheless, one alternate interpretation of my diet convergence study is that it reflects unknown differences in availability or response to patchy prey. Rigorous evaluation of these interpretations is very difficult under general field conditions and awaits experimentation. When my results are combined with the remainder of the data, however, they strongly support the notion of a broad range of starling foraging tactics (Feare 1984).

Of course, one may question whether taxonomic groups are good criteria for evaluating choices. What about size criteria, energy content, or unknown limiting nutrients, to name a few? Perhaps the parents themselves differed in quality, and their choices reflect this? These and similar criticisms can be directed at many foraging studies, and imperfect knowledge of these topics is certainly a constraint on data interpretation.

Beyond such qualifying remarks, however, the general success of the starling as a colonizing species argues in favor of behavioral plasticity in many aspects of its biology. Foraging studies and foraging theories often do not clearly discriminate between animals with narrow ranges of prey and broadly foraging colonizers such as the starling. Faced with the prey diversity of the latter, a knowledge of the functional significance of prey types (e.g., Tinbergen 1981, Westerterp et al. 1982) is necessary before we can begin to formulate algorithms that might relate the behavior of a few thoroughly studied individuals to events at the population level.

ACKNOWLEDGMENTS

Department of Colorado State University provided clerical assistance.

LITERATURE CITED

BROOKS, M. 1952. Starlings, *Sturnus vulgaris*, eating monarch butterflies. Auk 69:89.

COLEMAN, J. D. 1977. The foods and feeding of starlings in Canterbury. Proc. N. Z. Ecol. Soc. 24:94–109.

DUNNET, G. M. 1955. The breeding of the starling *Sturnus vulgaris* in relation to its food supply. Ibis 97: 619–662.

FEARE, C. 1984. The starling. Oxford Univ. Press, New York.

GORVETT, H. 1956. Tegumental glands and terrestrial life in woodlice. Proc. Zool. Soc. Lond. 126:291–314.

GROMADZKI, M. 1969. Composition of food of the starling, *Sturnus vulgaris* L., in agrocenoses. Ekol. Pol. Ser. A. 17:287–311.

GROMADZKI, M. 1979. Food requirement and effect of starling, *Sturnus vulgaris* L., on agriculture in Zulawy Wislane. Acta Ornithol. 16:467–492.

HOLLANDER, M., AND D. A. WOLFE. 1973. Nonparametric statistical methods. Wiley and Sons, New York.

HUBBARD, J. P. 1970. Check-list of the birds of New Mexico. New Mexico Ornithol. Soc. Publ. No. 3.

JOHNSON, E. J., L. B. BEST, AND P. A. HEAGY. 1980. Food sampling biases associated with the "ligature method." Condor 82:186–192.

KALMBACH, E. R., AND I. N. GABRIELSON. 1921. Economic value of the starling in the United States. U.S. Dep. Agric. Bull. #868.

KESSEL, B. 1957. A study of the breeding biology of the European starling (*Sturnus vulgaris* L.) in North America. Am. Midl. Nat. 58:257–331.

LIGON, J. S. 1961. New Mexico birds and where to find them. Univ. of New Mexico Press, Albuquerque.

LINDSEY, A. A. 1939. Food of the starling in central New York State. Wilson Bull. 51:176–182.

MOEED, A. 1975. Diets of nestling starlings and mynas at Havelock North, Hawke's Bay. Notornis 22:291–294.

MOEED, A. 1980. Diets of adult and nestling starlings (*Sturnus vulgaris*) at Hawke's Bay, New Zealand. N. Z. J. Zool. 7:247–256.

MOORE, J. 1981. The ecology of the acanthocephalan (*Plagiorhynchus cylindraceus*) in the isopod (*Armadillidium vulgare*) and the starling (*Sturnus vulgaris*). Ph.D.diss., Univ. of New Mexico, Albuquerque.

MOORE, J. 1983. Responses of an avian predator and its isopod prey to an acanthocephalan parasite. Ecology 64:1000–1015.

MOORE, J. 1984a. Altered behavioral responses in intermediate hosts—an acanthocephalan strategy. Am. Nat. 123:572–577.

MOORE, J. 1984b. Parasites and altered host behavior. Sci. Am. 250:108–115.

MOORE, J. 1984c. Starling reproduction in central New Mexico. J. Field Ornithol. 55:254–257.

PEET, R. K. 1974. The measurement of species diversity. Annu. Rev. Ecol. Syst. 5:285–307.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52:137–154.

ROTENBERRY, J. T. 1980. Dietary relationships among shrubsteppe passerine birds: competition or opportunism in a variable environment? Ecol. Monogr. 50: 93–110.

SIMPSON, E. H. 1949. Measurement of diversity. Nature 163:688.

SMITH, D. G. 1975. Breeding range expansion of the starling in Utah. Great Basin Nat. 35:419–424.

TINBERGEN, J. M. 1981. Foraging decisions in starlings (*Sturnus vulgaris* L.). Ardea 69:1–67.

TINBERGEN, J. M., AND R. H. DRENT. 1980. The starling as a successful forager, p. 83–101. *In* E. N. Wright, I. R. Inglis, and C. J. Feare [eds.], Bird problems in agriculture. Lamport Gilbert Printers Ltd., Reading, Great Britain.

WESTERTERP, K. 1973. The energy budget of the nestling starling *Sturnus vulgaris*, a field study. Ardea 61:137–158.

WESTERTERP, K., W. GORTMAKER, AND H. WIJNGAARDERN. 1982. An energetic optimum in brood-raising in the starling *Sturnus vulgaris*: an experimental study. Ardea 70:153–162.

WIENS, J. A. 1984. Resource systems, populations, and communities, p. 397–436. *In* P. W. Price, C. N. Slobodchikoff and W. S. Gaud [eds.], A new ecology: novel approaches to interactive systems. J. W. Wiley and Sons, Inc., New York.

WILLSON, M. F. 1966. Breeding ecology of the Yellow-headed Blackbird. Ecol. Monogr. 36:51–77.

WRIGHT, E. N., I. R. INGLIS, AND C. J. FEARE [EDS.]. 1980. Bird problems in agriculture. Lamport Printers Ltd., Reading, Great Britain.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J.