

Intersexual variation and factors affecting parental care in Western Bluebirds: a comparison of nestling and fledgling periods

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We compared factors affecting parental feeding rates in Western Bluebirds (*Sialia mexicana*) between the nestling and fledgling periods to evaluate intersexual variation in parental care. Parents did not adjust the frequency of feeding visits between modal (five young) and below-modal (four or less young) broods during the nestling period. The frequency of parental feeding visits also was not significantly affected by offspring age during the nestling period. Males and females exhibited no significant differences in provisioning offspring, although males maintained a constant level of care throughout the nestling period, whereas females increased feeding visits following the brooding period. During the fledgling period, offspring from below-modal broods were fed at higher rates with increasing age than offspring from modal broods. Broods remained together (siblings averaged 8 m apart) within 200 m of the nest box for a week after fledging. As fledglings became more mobile, they would pursue parents while parents were foraging; parental feeding rates thus tended to increase with fledgling age and distance moved from the nest. Offspring sex did not influence parental care during the fledgling period. Both adults fed fledglings, with males taking sole care of fledglings if females initiated a second clutch soon (7-10 days) after fledging of the first brood. Parental feeding rates increased by 60% during the fledgling period compared with the nestling period. No evidence for brood division during the fledgling period was found. Although brood division represents one way of reducing energetic costs attributable to feeding fledglings, Western Bluebirds exhibit an alternate behavior in which the energetics of raising a brood are shared equally between the parents throughout both the nestling and fledgling periods. This is further facilitated by a close association of young during the fledgling period that may reduce energetic costs related to locating and feeding young.

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Nous avons comparé les facteurs qui affectent les taux d'alimentation par les parents chez le Merle-bleu de l'ouest (*Sialia mexicana*) au cours de la période où les oisillons sont au nid et au cours de la période où ils sont prêts à l'envol, afin d'évaluer les variations dans la contribution des deux parents aux soins des oisillons. Les parents n'ont pas modifié la fréquence de leurs visites en fonction du nombre de petits dans la couvée (couvée modale, cinq oisillons ou couvée sous-modale, quatre ou moins oisillons). La fréquence des visites des parents n'était pas significativement affectée par l'âge des oisillons au nid. Mâles et femelles pourvoyaient aux petits avec la même efficacité, mais les mâles ont toujours apporté les mêmes soins aux petits durant toute la période de nidation, alors que les femelles ont augmenté le rythme de leurs visites au nid après la fin de la ponte. Durant la période de l'envol, les petits des couvées sous-modales étaient nourris en fonction de leur âge à des taux plus élevés que les oisillons des couvées modales. Les couvées restaient unies (les petits restaient en moyenne à 8 m de distance les uns des autres) à moins de 200 m du nid au cours de toute la première semaine après l'envol. À mesure qu'ils devenaient plus mobiles, les oisillons suivaient leurs parents à la recherche de nourriture; les taux d'alimentation par les parents avaient donc tendance à augmenter en fonction de l'âge des oisillons et de la distance parcourue depuis le nid. Le sexe des oisillons n'influait pas les soins parentaux durant la période d'envol. Les deux adultes nourrissaient les oisillons, et les mâles devenaient entièrement responsables des soins si les femelles pouvaient une seconde fois tôt après l'envol des petits de la première portée (7-10 jours). La fréquence des soins parentaux a augmenté de 60% entre la période de nidation et la période de l'envol. Il ne semble pas y avoir eu division de la couvée au cours de l'envol. Bien que cette stratégie représente une façon de réduire les coûts énergétiques reliés à l'alimentation des petits prêts à l'envol, les Merles-bleus de l'ouest utilisent plutôt une stratégie de rechange dans laquelle les coûts reliés à l'élevage des petits sont partagés également par les deux parents au cours des périodes de nidation et d'envol. De plus, l'association étroite entre les oisillons au cours de l'envol contribue à réduire davantage les coûts reliés au repérage et à l'alimentation des oisillons.

[Traduit par la revue]

Introduction

Comparative studies of the nestling and fledgling periods in birds are rare (but see Smith 1978), undoubtedly owing to difficulties in obtaining data on fledged young in many species. The importance of such comparative studies, however, has been recognized for more than 2 decades since Royama (1966) first suggested that the fledgling period is a "period of crisis" in terms of energetic demands by young on parents; this hypothesis can be evaluated only by a comparison of parental care during the nestling and fledgling periods. Feeding offspring may provide an important bottleneck that limits reproductive success in nidicolous birds (Murphy and Haukioja 1986; Martin 1987). Factors affecting parental feeding rates during the nestling

period thus have figured prominently in discussions of optimum clutch or brood sizes (Lack 1947; Klomp 1970; Hussenell 1972; Nur 1984b; Murphy and Haukioja 1986; Finke et al. 1987) and the evolutionary implications of parental investment patterns and mating systems (Trivers 1974; Drent and Daan 1980; Power 1980; Gowaty 1983; Leffelaar and Robertson 1986). Ignorance of the postfledgling period, when the young are still dependent upon parents, renders our understanding of the multifaceted factors (both intrinsic and extrinsic) that influence the reproductive characteristics of a species (proximately and ultimately) incomplete at best and erroneous at worst.

Parental care during the postfledgling period usually has been addressed only with regard to the occurrence of brood division (Davies 1976; Smith 1978; Moreno 1984; Edwards 1985; Harper 1985; McLaughlin and Montgomerie 1985). The primary benefit generally attributed to this behavior of each parent preferentially caring for certain offspring and not others is

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increased efficiency in caring for young (e.g., locating, feeding, and protecting fewer offspring). The increased mobility of young following fledging may increase the difficulty of finding young or increase parental foraging distances (McLaughlin and Montgomerie 1985). Brood division thus might be expected to occur if the fledgling period is energetically more stressful for parents relative to the nestling period. Indeed, the only other comparative study of parental care during the nestling and fledgling periods demonstrated a 44% increase in postfledging feeding rates for Song Sparrows (*Melospiza melodia*), which subsequently were found to divide their broods (Smith 1978).

We selected Western Bluebirds (*Sialia mexicana*) for a comparative study of parental care during the nestling and fledgling periods because this species readily uses nest boxes, and family groups remain in the vicinity of the nest box following fledging; thus, adults and offspring were accessible for detailed observation during both developmental stages. We examined factors affecting parental feeding rates to provide an understanding of how parental care is allocated to offspring and how this relationship might be affected differentially during the nestling and fledgling periods. Further, we investigated parental roles in provisioning young for intersexual variation during these two developmental stages. Our objectives were to determine behaviorally the following:

- (1) The effects of brood size and offspring age on the frequency of parental feeding visits during the nestling and fledgling periods. Brood size and offspring age are frequently evaluated, as they are readily obtainable data, to assess effects on parental care during the nestling period (e.g., Royama 1966; Hussell 1972; Pinkowski 1978; reviews in Klomp 1970; Drent and Daan 1980). Feeding rates generally increase with increasing brood size and offspring age, but this increase in parental care generally is not proportional to an increase in brood size (i.e., chicks of larger broods receive less food than individuals in smaller broods). The implications of this may be higher mortality in larger broods owing to "malnourished" young (Klomp 1970) or decreased adult survival owing to the increased energetic stress of feeding more young (Nur 1984a). Little information is available regarding the relationship of these factors to parental care and thus offspring survival during the fledgling period, which led Murphy and Haukioja (1986) to remark that "the postfledging period of parental care may be a critical phase in the production of the offspring to breeding age."
- (2) The additional effects of offspring sex, dispersal distance of fledglings from nest, and intersibling distance on parental care during the fledgling period. Parents may preferentially care for offspring of the opposite sex, as has been found for Blackbirds (*Turdus merula*) (Snow 1958) and Robins (*Erithacus rubecula*) (Harper 1985), two species that divide their broods. Investing in young of the opposite sex may influence future mate choice of offspring (offspring imprint on parent of opposite sex; Bateson 1978) or reduce intrasexual competition (in species in which females are the dispersive sex, males may prefer to invest in daughters that are less likely to compete with them; Harper 1985). We were able to study the effect of offspring sex on the allocation of parental care during the fledgling period because bluebird offspring can be sexed as a result of the darker blue coloration of the rectrices and remiges in males (following Pinkowski 1974).
- (3) Whether brood division occurs during the fledgling period.
- (4) Intersexual variation in parental care during the nestling

and fledgling periods. Biparental care is typical of most passerines, but sex differences have been documented as to the extent of male contribution in feeding offspring during the nestling period (e.g., Verner and Willson 1969) and in division of labor between sexes during the nestling (e.g., sexual foraging differences, Power 1980) and fledgling periods (e.g., brood division, sole care of early brood fledglings by males while female initiates second clutch, Edwards 1985).

A nontechnical summary of some of the results of this study was reported elsewhere (With 1988). In this paper, we seek to analyze and interpret our results in an ecological and evolutionary framework and to integrate our findings with previous research on factors affecting parental care.

Methods

We conducted this study during the breeding seasons (March–August) of 1986 and 1987 on an 8.5-ha plot within the United States Department of Agriculture Forest Service Beaver Creek Watershed (WS-17), Coconino National Forest, Coconino County, approximately 43 km south of Flagstaff, Arizona. The study area is at 2100 m elevation and vegetation is primarily ponderosa pine (*Pinus ponderosa*) and Gambel's oak (*Quercus gambelii*). Mature ponderosa pine possess open canopies crowning the upper third of the tree. In 1969, vegetation on this plot was thinned to about 25% of its original foliage volume and all snags were removed (see Szaro and Balda (1979) for vegetation profiles and additional information). These features of the vegetation provided an open habitat that facilitated observation of adult and fledgling bluebirds.

As part of a different study (Brawn 1985; Brawn et al. 1987), 30 nest boxes with an entrance hole diameter of 38 mm were installed at various heights on this plot in 1980. We lowered these boxes to 3 m in March 1986 to facilitate observation of the nests. Breeding densities of Western Bluebirds exhibited a significant fourfold increase on this plot following the introduction of nest boxes in 1980; breeding densities doubled with respect to a control plot (Brawn et al. 1987; Brawn and Balda 1988). Subsequently, breeding densities apparently have stabilized, as the average breeding densities during the 2 years of our study were comparable but less variable than in the years immediately following the introduction of nest boxes (mean breeding density 1986–1987 = 49.5 ± 9.97 pairs/40 ha; mean breeding density 1981–1983 = 43 ± 20.7 pairs/40 ha (Brawn and Balda 1988)).

The contents of boxes were checked weekly beginning in mid-March. Nests with young were checked at least twice a week to determine brood size, and nests with eggs near hatching or young about to fledge were checked daily to establish the date of these events. Young were uniquely color banded between 13 and 16 days ($\bar{x} = 15.0 \pm 1.04$, $n = 57$) after hatching, an average of 5 days before young typically fledged (see Results). Since Hartshorne (1962) warned that nestling Eastern Bluebirds (*Sialia sialis*) would fledge prematurely if handled 2–3 days prior to normal fledging, banding young at 15 days in our study thus should have had little effect on age of fledging. Only two broods fledged prematurely as a consequence of handling; these were deleted from analysis. Adults were not banded, although three banded young from the first year of study returned the 2nd year to breed on the plot. Although Western Bluebirds sometimes have helpers (Skutch 1961; G. C. Bateman and J. D. Brawn, personal communication), no evidence for brood helpers was observed during the 1st year of this study (i.e., only a pair of birds were observed attending each nest). Additional birds would have been detected, given the length of observation at each nest box, and adults generally were visible in the area while foraging owing to the open habitat). During the 2nd year, an additional male occasionally participated in feeding the young at one nest. This nest was deleted from subsequent analyses. Young from first broods were never observed feeding their second-brood siblings. We therefore assume that the role of helpers was minimal in this study.

Nestling period

Study of parental care during the nestling period was restricted to observations of parental feeding visits to broods in nest boxes. We

recognize that frequency of parental visits only approximates the energy requirements of young; parental visits may represent some other aspect of parental care (e.g., nest sanitation), or prey biomass may compensate for food-delivery rate (e.g., small prey delivered at a higher rate than large prey). It was not always possible to ascertain whether parents had prey, since they did not always alight before entering a box, and the distance from which the nests were observed made it difficult to determine size of prey. Royama (1966) found a strong inverse relationship between feeding frequencies and food biomass for Great Tits (*Parus major*), however. Our measure of parental care therefore represents an approximation of energetic demands of young but should provide a relative measure for comparison between brood sizes and offspring ages and between nestling and fledgling periods.

Each nest box was observed for 1 h on 9 days throughout the nestling period. Boxes were systematically observed throughout the day to minimize the effects of temporal variation (e.g., temperature, insect activity, satiation of young) on parental provisioning of young. Observations were made from inconspicuous locations (e.g., observers were shielded by vegetation) at least 50 m from the box. Data were recorded on frequency of feeding visits (number of visits per hour), brood size, offspring age, and sex of visiting parent.

Separate analyses of covariance (Dixon and Brown 1979; pp. 540–580) were run to test for differences in number of feeding visits to the brood for both parents combined (i.e., total number of feeding visits to brood), for males, and for females as a function of brood size and brood age. Since boxes were observed on 9 days, analyses incorporated a repeated-measures sampling design and included both brood size and brood age as covariates that were not constant over trials (trials = days of observation). Brood age obviously changed with each day of observation, but brood size sometimes changed as a result of death of young. The nestling period was divided into four stages: 1–5, 6–10, 11–15, and > 15 days after hatching. Brood sizes were categorized into two groups for analysis, four or less and five nestlings, because of the low frequency of smaller broods. As the modal brood size was five (see Results), analyses represented a comparison between modal and below-modal brood sizes.

Residuals generated by analyses were examined for homogeneity of variance, fit to normality, and detection of outliers (Draper and Smith 1981, pp. 141–182) using time-sequence plots of residuals against order of data collection or against predicted values. None of the assumptions was violated for any analysis; data transformation or nonparametric procedures were not required.

Fledgling period

Owing to difficulties in locating fledged young, the following sampling scheme was adopted. An observation period was concluded after 1 h or when fledglings were lost from sight ($\bar{x} = 49.0 \pm 11.5$ min; $n = 110$ observation periods). Fledglings generally remained together (see Results), but rarely could all fledglings from a brood be observed simultaneously. Individual offspring thus served as the focal point of observation, rather than the entire brood as during the nestling period. Only one fledgling was fed per parental visit, so data on food delivery rates were unbiased when only a subset of offspring could be watched. Data were recorded on food-delivery rate (number of visits per minute), sex of visiting parent, actual distance to siblings (nearest 0.1 m), and distance of fledgling from nest box (m); all distances were visually estimated (K.A.W. conducted all of the field observations and had trained to make visual estimates as part of another study; Block et al. 1987). Observations of less than 20 min duration were discarded.

Linear regression was used to evaluate the relationships between parental feeding rates and fledgling attributes that might affect parental care (e.g., age, dispersal distance from nest box, mean distance between fledglings in brood) with respect to brood size. Data were analyzed separately for below-modal and modal brood sizes, using *F*-tests. Differences between modal and below-modal broods were analyzed by comparing the slopes of the regression lines with *F*-tests (Dixon and Brown 1979, p. 392).

The effect of offspring sex on parental care during the fledgling period was also evaluated with linear regression using sex as a grouping factor. The relationship between parental feeding rates and various

attributes of the fledgling period (same factors as above; e.g., fledgling age) were examined separately for each sex and for differences between sexes, using the tests discussed above.

To evaluate which variables were the best descriptors of variation in parental feeding rates of fledglings, all possible subsets regression (Dixon and Brown 1979, pp. 418–436) was conducted to provide a regression equation giving the smallest value for Mallows's C_p (Dixon and Brown 1979, p. 424).

We also determined if brood division occurred during the fledgling period; that is, whether one parent primarily or solely fed particular offspring and not others. Demonstrating that one parent relative to the other significantly devoted more care to particular offspring is not in itself evidence for brood division unless it can be shown that this care was disproportionate to the care that this same parent provided to the brood as a whole (Harper 1985). We tested two hypotheses: (i) equality of visits by both parents to a particular fledgling (Harper's hypothesis A), and (ii) proportionate visits from a parent to a particular fledgling relative to those received by the entire brood by this same parent (Harper's hypothesis B). The proportions of male feeding visits were considered in these analyses. Normal approximations for two-tailed binomial tests, corrected for continuity, were used to test these two hypotheses (Zar 1984, p. 386). Rejection of both hypotheses is evidence for brood division. Only offspring observed for at least 10 feeding visits were included in these analyses.

Intersexual differences

Sexual differences in feeding nestlings were evaluated using a simple contrast between the two parents in feeding frequencies (e.g., male visits minus female visits). This contrast was then subjected to an analysis of covariance to test for intersexual differences in feeding frequencies over brood sizes and offspring ages during the nestling period.

Intersexual variation in providing for nestlings and for fledglings was evaluated further by assessing the proportion of male parental care during each developmental period. During the fledgling period, we additionally examined the effect of second broods on male parental care of first-brood fledglings.

Comparison of nestling and fledgling periods

To facilitate comparisons of parental care during the nestling period with that of the postfledgling period (where focal offspring were observed rather than entire broods in nest boxes during the nestling period), data for feeding visits during the nestling period were expressed as feeding rate per individual (number of visits/min per individual). Average feeding rates were obtained for each brood during both the nestling and fledgling periods. A paired-sample *t*-test (Zar 1984, pp. 150–152) was used to evaluate the mean differences in parental feeding rates between the nestling and fledgling periods.

Parental care during the nestling and fledgling stages were compared by testing the proportionality of male feeding visits during the nestling period with respect to the fledgling period by using a two-tailed binomial test corrected for continuity. The overall contribution of the male to feeding the offspring (summed over both nestling and fledgling periods) was then evaluated with a binomial two-tailed test to examine equality of parental care for each brood. This then provided a test of intersexual differences in parental care summed over both developmental stages.

Results

Clutch size in Western Bluebirds ranged from four to six with a mode of five; 89% of all nests contained four or five eggs (total $n = 27$; With 1988). All but 10% of eggs hatched, and broods during the nestling period averaged about four young, although the modal size was five (88% of broods contained four or five nestlings; With 1988). Seventy-five percent of nestlings fledged so that broods during the fledgling period averaged three young, but the mode remained five young (90% of broods contained four or five fledglings; With 1988). Overall breeding success was 66% of eggs resulting in fledged young.

Nestling period

The nestling period lasted 17–23 days ($\bar{x} = 20.0 \pm 1.48$; $n = 21$ nests) and followed an incubation period averaging 14 days ($\bar{x} = 13.9 \pm 1.12$, range = 13–17 days, $n = 23$ nests). Nestling sex ratios were skewed in favor of females (1.44 : 1, $n = 78$ chicks from 18 nests).

Although parents visited modal broods more frequently than below-modal broods (modal broods: $\bar{x} = 12$ visits/(brood · h), $n = 11$; below-modal broods: $\bar{x} = 9$ visits/(brood · h), $n = 8$), the difference was not significant (analysis of covariance; Fig. 1A). Parental care was not significantly affected by nestling age in either below-modal or modal broods (Fig. 1A). Frequency of male feeding visits was consistent throughout the nestling period and was unaffected by brood size; below-modal broods were visited five times per hour, and modal broods were visited six times per hour (Fig. 1B). Females similarly did not adjust feeding visits to brood size (below-modal broods = 4 visits/h, modal broods = 6 visits/h); female visits were, however, affected slightly by nestling age (although $P = 0.07$, $n = 19$, analysis of covariance; Fig. 1C).

Fledgling period

Fifty-three offspring from 16 broods were observed during the fledgling period. Fledged Western Bluebirds were almost entirely dependent upon their parents for food for the first 3–5 days after fledging but rapidly developed foraging skills and after 2 weeks were essentially independent. They continued to solicit food from their parents for a month or more if the adults did not initiate a second clutch. No significant difference was found in age of fledging between young from below-modal and modal broods (≤ 4 : $\bar{x} = 20.2 \pm 1.64$ days, $n = 9$ broods; 5: $\bar{x} = 19.83 \pm 1.40$, $n = 12$; Mann-Whitney U -test = 105.0, $P > 0.05$).

Parental feeding rates increased significantly ($P < 0.01$, Table 1) with age for fledglings from below-modal broods but not for fledglings from modal broods (Table 2). Fledglings from below-modal broods were fed at significantly ($P = 0.001$, Table 1) higher rates than fledglings from modal broods (Table 2).

Broods remained together for at least a week following fledging. Fledglings from modal broods were generally within 5 m of each other ($\bar{x} = 5.5 \pm 1.31$, $n = 60$ observation periods), and siblings from below-modal broods were 13 m apart ($\bar{x} = 12.6 \pm 5.31$, $n = 49$ observation periods) (Table 2); this difference between brood sizes was significant ($P = 0.05$, Table 1). Parental feeding rates were unaffected by intersibling distance (Table 1).

There was a general trend for fledglings to disperse farther from their nests with age (3 m/day, $P = 0.05$, Table 3), but broods usually remained within 200 m of the nest. Fledglings from modal broods were generally 125 m from the nest ($\bar{x} = 125.3 \pm 18.88$, $n = 60$ observation periods) and young from below-modal broods were 113 m from the nest ($\bar{x} = 113.3 \pm 29.78$, $n = 49$ observation periods) (Table 2), but this difference between broods was not significant (Table 1). Parental feeding rate was found to increase with dispersal distance from nest, especially for fledglings in below-modal broods (Table 1).

Parents did not alter feeding rates according to offspring sex during the fledgling period. Fledglings behaved similarly, irrespective of sex, with regards to dispersal distance from nest box and intersibling distance (Table 3).

Parental feeding rates significantly increased with distance from nest box, decreased with fledgling age, and decreased with brood size during the fledgling period ($P < 0.01$, all possible

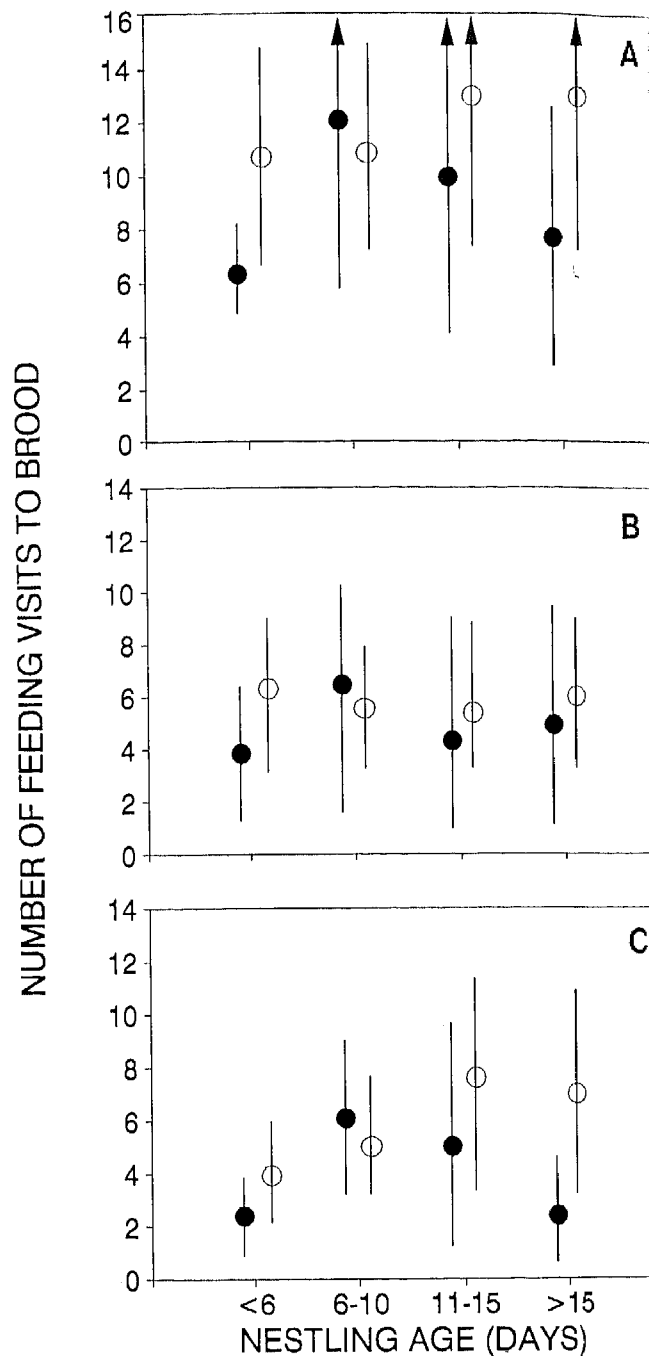


FIG. 1. Western Bluebird parental-feeding visits to broods as a function of nestling age for both parents combined (A), for males (B), and for females (C) during 1986 and 1987 in northern Arizona. ●, below-modal (≤ 4 young) broods; ○, modal (5 young) broods. Vertical lines indicate ± 1 SD; arrowheads indicate that SD extends beyond graph.

subsets regression: $Y = 0.070 + 1.41 \times 10^{-4} (\text{distance}) - 1.77 \times 10^{-3} (\text{age}) - 1.38 \times 10^{-2} (\text{size})$). The model substantiated the weak relationships between these variables and parental feeding rates indicated by the univariate tests. Brood size explained only 7.9% of the variation in parental feeding rates, followed by dispersal distance from nest box (3.2%), and finally fledgling age (2.0%).

Brood division during the fledgling period was virtually nonexistent in Western Bluebirds; of the seven fledglings that

TABLE 1. Linear regression analysis of the effects of offspring age (AGE), dispersal distance from nest box (DIST), and intersibling distance (SIB) on parental feeding rates as a function of brood size in Western Bluebirds during the fledgling period in northern Arizona during 1986 and 1987

Relationship	Group ^a	n ^b	Model	R ²	P ^c	P ^d
Feeding rate vs. age	≤4	48	-0.06+0.01 (AGE)	0.191	0.002	0.001
	5	61	0.07-0.40×10 ⁻³ (AGE)	0.001	0.791	
	B	109	0.04+0.13×10 ⁻² (AGE)	0.012	0.254	
Dispersal distance vs. age	≤4	49	4.69+4.74 (AGE)	0.078	0.052	0.427
	5	61	95.41+1.09 (AGE)	0.004	0.635	
	B	110	44.11+3.09 (AGE)	0.036	0.046	
Feeding rate vs. dispersal distance	≤4	48	0.04+0.35×10 ⁻³ (DIST)	0.140	0.009	0.018
	5	61	0.05+0.67×10 ⁻⁴ (DIST)	0.011	0.432	
	B	109	0.05+0.15×10 ⁻³ (DIST)	0.036	0.048	
Intersibling distance vs. age	≤4	41	2.28+0.41 (AGE)	0.011	0.513	0.050
	5	59	10.17-0.16 (AGE)	0.004	0.616	
	B	100	12.63-0.19 (AGE)	0.004	0.535	
Feeding rate vs. intersibling distance	≤4	42	0.07-0.17×10 ⁻³ (SIB)	0.002	0.780	0.393
	5	60	0.06-0.40×10 ⁻⁴ (SIB)	0.000	0.950	
	B	102	0.07+0.92×10 ⁻⁵ (SIB)	0.000	0.983	

^a≤4, below-modal broods; 5, modal broods; B, both groups combined.

^bNumber of observations.

^cProbability value for test of regression line in each group.

^dProbability value for test of regression lines between modal and below-modal groups.

TABLE 2. Parental feeding rates (visits/(min·individual)) and average distance (m) between siblings and from nest box as a function of age (days since hatching) for fledgling Western Bluebirds from modal (five young) and below-modal (four or fewer young) broods during 1986 and 1987 in northern Arizona

Brood size	Age	n ^a	Feeding rate		Intersibling distance		Distance from nest	
			\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Modal	20-22	21	0.01	0.030	5.6	6.19	121	43.0
	23-25	25	0.01	0.033	6.7	8.24	109	58.8
	≥25	14	0.04	0.063	4.1	4.34	146	71.1
Below-modal	≤19	14	0.03	0.047	14.9	13.77	96	40.4
	20-22	16	0.01	0.034	4.9	5.64	107	45.0
	23-25	13	0.07	0.095	13.4	17.54	93	71.1
	≥25	6	0.07	0.052	17.0	7.82	157	35.4

^aNumber of observation periods.

received disproportionate parental care (i.e., rejection of hypothesis A), only one (offspring 1 from brood A) received disproportionate care relative to that received by the entire brood (rejection of hypothesis B) (Table 4). This bird fledged 3 days earlier than its siblings and was cared for solely by the female during this time. Following fledging of the rest of the brood, the female continued to provide almost all of the care to this offspring relative to the male, even when all young flocked together.

Intersexual differences

Western Bluebirds exhibited no significant intersexual differences in number of feeding visits to nestlings either as a function of brood size or nestling age (Fig. 1).

Both parents contributed equally to feeding offspring in 71%

of the broods during the nestling period but in only 57% during the fledgling period (Table 5). Males assumed sole care of first-brood fledglings if females initiated a second clutch soon (7-10 days) after fledging of first brood but provided about half of all feeding visits if second broods were delayed (2-3 weeks) or never attempted (Fig. 2).

Comparison of nestling and fledgling periods

Parental feeding rates increased by 60% during the fledgling period, with 4.8 ± 2.05 visits/(h·bird) relative to 2.9 ± 1.00 visits/(h·bird) during the nestling period $P < 0.01$, paired *t*-test; Table 6). Removal of brood D from the analysis resulted in an increase in parental feeding rate of 65% between the two periods ($P < 0.001$). Both parents cared for offspring during both the nestling and fledgling periods; significant differences in paren-

TABLE 3. Linear regression analysis of the effects of offspring age (AGE), dispersal distance (DIST), and intersibling distance (SIB) on parental feeding rates as a function of offspring sex in Western Bluebirds during the fledgling period in northern Arizona during 1986 and 1987

Relationship	Group ^a	n ^b	Model	R ²	P ^c	P ^d
Feeding rate vs. age	M	45	-0.03+0.41×10 ⁻² (AGE)	0.086	0.051	0.190
	F	58	0.08-0.31×10 ⁻³ (AGE)	0.001	0.824	
	B	103	0.04+0.13×10 ⁻² (AGE)	0.012	0.273	
Dispersal distance vs. age	M	45	53.73+3.24 (AGE)	0.034	0.225	0.213
	F	59	19.85+3.88 (AGE)	0.069	0.045	
	B	104	42.21+3.27 (AGE)	0.043	0.035	
Feeding rate vs. dispersal distance	M	45	0.04+0.17×10 ⁻³ (DIST)	0.045	0.164	0.709
	F	58	0.05+0.16×10 ⁻³ (DIST)	0.047	0.102	
	B	103	0.05+0.16×10 ⁻³ (DIST)	0.041	0.039	
Intersibling distance vs. age	M	39	11.94-0.14 (AGE)	0.002	0.790	0.728
	F	57	10.98-0.17 (AGE)	0.005	0.620	
	B	96	11.86-0.18 (AGE)	0.004	0.531	
Feeding rate vs. age	M	39	0.06+0.49×10 ⁻³ (SIB)	0.011	0.523	0.642
	F	56	0.07+0.53×10 ⁻⁴ (SIB)	0.000	0.928	
	B	95	0.06+0.22×10 ⁻³ (SIB)	0.002	0.636	

^aM, male; F, female; B, both sexes combined.

^bNumber of observations.

^cProbability value for test of regression line in each group.

^dProbability value for test of similarity of regression lines between males and females.

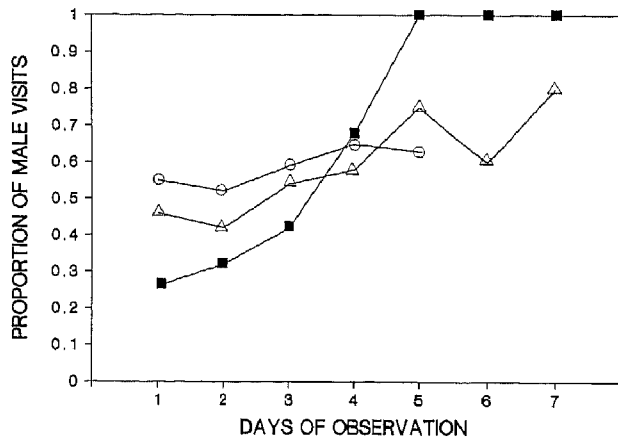


FIG. 2. Average daily proportion of male parental care during the fledgling period in Western Bluebirds during 1986 and 1987 in northern Arizona. Broods ($n = 3$) in which second clutches were initiated soon (7–10 days) after young from first brood fledged are indicated by squares. Broods ($n = 2$) with a longer interbrood interval (2–3 weeks) are indicated by circles. Broods ($n = 7$) in which second clutches were never attempted are indicated by triangles.

tal care between these two periods were found for only 4 of 14 broods (Table 5). Overall, both parents contributed equally to the feeding of offspring in all but two broods (Table 5).

Discussion

Factors affecting parental care

Western Bluebirds did not significantly adjust the frequency of feeding visits between modal (five young) and below-modal (four or less young) broods during the nestling period. Unlike its two congeners, little information has been published on the reproductive behavior of Western Bluebirds to provide a basis for comparison. Eastern Bluebirds (Pinkowski 1978) and other

cavity nesters such as Great Tits (Royama 1966) also did not adjust feeding rates to brood size during the nestling period. Mountain Bluebirds (*Sialia currucoides*) apparently increased feeding rate with increasing brood size but at the cost of incorporating energetically demanding foraging behaviors (Power 1980). Feeding rates generally increase with brood size in most open-nesting passerines (e.g., Hussell 1972). Nestlings in cavities may suffer smaller thermal losses and thus have reduced energy needs relative to nestlings in open nests (O'Connor 1975).

Feeding frequency also was not significantly a function of offspring age, although female Western Bluebirds fed nestlings slightly more than males after day 5 and decreased feeding visits to below-modal broods with respect to males after day 15. Nestling age influences feeding rate differently between the sexes in many species (Royama 1966; Wittenberger 1982). This has generally been attributed to a greater feeding contribution by males during the early days of the nestling period while the female was brooding. Male Mountain Bluebirds likewise provided most of the food during the brooding period, after which time females contributed about 60% of feeding visits (Power 1980). In Eastern Bluebirds, however, males and females contributed equally during the brooding period (Pinkowski 1978). After the brooding period, females alone increased feeding rates to offspring, whereas males remained constant. Western Bluebirds are a composite of these two patterns, with males resembling male Eastern Bluebirds in maintaining a constant level of feeding visits throughout the nestling period regardless of brood size and females initially providing less care during the brooding period, as in Mountain Bluebirds.

Fledglings remained together in the vicinity of the nest box for a week after fledging. Young from below-modal broods were fed at higher rates than modal broods, as perhaps fewer young could be located and fed more quickly. Feeding rates of

TABLE 4. Postfledging parental care in Western Bluebirds during 1986 and 1987 in northern Arizona

Brood ^a	Brood size	Young	Sex	Days of observation	Male visits ^b	Total male visits ^c
A	4	1	F?	7	1/27***†	11/51
A'	4	1	M	4	7/15	14/32
		2	F?	3	3/10	
B	3	1	?	2	4/10	11/23
		2	?	2	6/12	
C	4	1	M	4	9/13	40/66
		2	M	5	8/12	
		3	F	6	7/14	
		4	M	6	16/27	
D	2	1	M	3	3/17**	5/28
		2	F	1	2/11*	
E	1	1	?	2	5/14	5/14
F'	2	1	F	3	0/20***	1/34
		2	F?	3	1/14***	
H	4	1	M	5	4/13	20/50
		2	F	4	5/12	
		3	F?	3	5/12	
		4	F	4	4/13	
I	5	1	F	8	10/23	36/78
		2	F	7	7/11	
		3	F	5	3/10	
J	5	1	F	4	8/10*	31/47
		2	F?	3	7/10	
		3	F	3	9/10***	
K	5	1	M	7	9/12	33/58
		2	F	6	6/11	
		3	F	5	6/11	

^aPrime denotes second brood.
^bProportion of male feeding visits to focal offspring. *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$; hypothesis A, see text for description. †, $P \leq 0.05$; hypothesis B, see text for description.
^cProportion of male feeding visits to entire brood.

TABLE 5. Comparison of nestling and fledgling parental care in Western Bluebirds during 1986 and 1987 in northern Arizona

Brood ^a	Brood size		Male visits ^b			Parental care ^c		
	NP	FP	NP	FP	Total	NP	FP	Total
A	4	4	60/93	11/51***	71/144	M	F	B
A'	5	4	81/138	14/32	95/170	B	B	B
B	4	3	36/88	11/23	47/111	B	B	B
C	5	4	57/114	40/66*	97/180	B	M	B
D	4	2	71/92	5/28***	76/120**	M	F	M
E	1	1	23/45	5/14	28/59	B	F	B
F	5	5	67/153	11/23	78/176	B	B	B
F'	2	2	14/76	1/34	15/110***	F	F	F
G	5	5	62/118	10/19	72/137	B	B	B
H	5	4	63/109	20/50	83/159	B	B	B
I	5	5	39/86	36/78	75/164	B	B	B
J	5	5	50/93	31/47	81/140	B	M	B
K	5	5	38/105	33/58**	71/163	F	B	B
L	5	5	51/95	18/30	69/125	B	B	B

^aPrime denotes second brood.
^bProportion of male visits to entire brood during the nestling period (NP), the fledgling period (FP), and both periods combined (Total). *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.
^cFeeding visits primarily (>60%) by male (M), female (F), or by both parents (40-60%; B).

TABLE 6. Comparison of average parental feeding rates (visits/(h · young)) to Western Bluebird broods between the nestling and fledgling periods during 1986 and 1987 in northern Arizona

Brood ^a	Nestling		Fledgling	
	\bar{x}	SD	\bar{x}	SD
A	2.9	1.85	3.8	2.28
A'	3.6	1.97	4.1	1.71
B	2.4	1.14	4.0	2.60
C	2.6	0.71	5.0	3.23
D	3.3	1.46	11.1	8.69
E	5.0	3.20	6.6	2.54
F	3.4	0.84	4.8	3.58
F'	4.2	1.68	5.4	2.24
G	2.6	1.09	4.5	3.14
H	2.7	0.65	3.9	2.50
I	1.9	0.79	3.2	2.35
J	2.1	0.83	3.2	2.10
K	2.3	0.82	3.1	1.81
L	1.0	0.37	4.4	1.03
Average	2.9	1.00	4.8	2.05

^aPrime denotes second brood.

fledglings also increased with age and distance moved from nest box. Since fledglings dispersed farther from nest with age, this represents the increasing mobility of young and perhaps their corresponding "aggressiveness" in obtaining food. Parents foraged away from nests, and as young became more skillful in flight they were able to pursue their foraging parents and perhaps obtain food more readily (i.e., faster). Fledgling Wheatears (*Oenanthe oenanthe*) also began to chase their parents about a week after fledging, and parents tended to feed only young that were actively following them (Moreno 1984). This "aggressiveness" in obtaining food was correlated with an initial decrease in parental feeding rates (i.e., "parental meanness," forcing offspring to become independent by decreasing feeding rates; Davies 1978).

Biparental care

Western Bluebirds generally provided equal parental care when feeding visits were totaled over both nestling and fledgling periods, although care was not always equivalent during each of these developmental stages. The importance of male parental care is generally assessed in examining the relative reproductive costs and benefits of uniparental- versus biparental-care systems. It is often implied that biparental care increases reproductive fitness when more offspring can be raised relative to a system of uniparental care (e.g., where the polygyny threshold is not crossed; Orians 1969), but this hypothesis has received varying support, as frequently it is demonstrated that one parent (generally the female) can successfully fledge young. For example, female Eastern Bluebirds were capable of fledging as many young following removal of males as pairs (Gowaty 1983). Single parents may incorporate high costs involving decreased reproductive success or increased mortality, however. Tree Swallows (*Tachycineta bicolor*) were able to increase feeding efforts to offspring following mate removal but could only do so on a short-term basis, which ultimately resulted in reduced reproductive success (Leffelaar and Robertson 1986). Mountain Bluebirds apparently

did not suffer decreases in reproductive success when mates were removed, as single birds were able to increase visits to young (Power 1980). Single birds also increased costly foraging behaviors, however. Furthermore, since feeding offspring can lower adult body weight, which may lead to decreased survival (Nur 1984a), biparental care may represent "cooperation" between parents to minimize risk of mortality or decreased reproductive success incurred by the high costs of single parenthood (Alatalo et al. 1988).

Biparental care may also increase reproductive success relative to a uniparental-care system by facilitating the production of multiple broods. Females may be unable to replenish fat reserves for the ensuing brood if they are concurrently providing care for fledglings. For example, female Song Sparrows did not begin another clutch while caring for more than one fledged young (Smith and Roff 1980). In Blackbirds, females feeding fledglings began second nests about a week later than if males provided sole care to first-brood fledglings (Edwards 1985). In Western Bluebirds, males assumed sole care of fledglings from first broods if females initiated a second clutch within 7–10 days. Males provided equal care, however, if second broods were initiated later (2–3 weeks) or never attempted (Fig. 2). Some factor other than male contribution may determine timing of second clutches (e.g., food abundance), and thus amount of male parental care may not affect when females initiate second clutches but may merely be a consequence of when they are able to do so (e.g., immediate initiation of second clutches would "force" males to care solely for young). Nevertheless, male parental care would seem to be important during the fledgling period, which usually is not addressed when considering the reproductive costs and success of single parenthood relative to biparental care, as males generally provided equal parental care regardless of whether second broods were attempted. Single parenthood apparently was feasible only for very small broods (e.g., one or two young; Table 5) where care by both parents perhaps was not required to meet the energetic demands of the young.

Comparison of nestling and fledgling periods

Western Bluebirds increased feeding rates by 60% between the nestling and fledgling periods. They did not, however, divide their broods. Smith (1978) found a 44% increase in feeding rate during the fledgling period for Song Sparrows, and this species exhibited a division of labor in feeding young. Evidence of brood division has been used to suggest that the fledgling period is an energetically stressful time for the parents that may serve to limit brood size. For breeding Great Tits, Yom-Tov and Hilborn (1981) developed a model of energy budgets that identified two periods of energetic stress: one at the end of the incubation period that was independent of clutch size, and one at the end of the fledgling period that was dependent upon clutch size. Although Western Bluebirds did not divide their broods, we cannot conclude that parents are not stressed without accompanying physiological data (e.g., corticosterone levels).

Just as a lack of brood division does not indicate the absence of stress, neither does an increase in feeding rate during the fledgling period demonstrate stress. Elevated feeding rates may reflect a close association between parents and offspring (Hegner and Wingfield 1987) (e.g., young follow parents, thereby reducing commuting costs of adults; Moreno 1984). If commuting distances are shorter, it may be energetically more feasible to bring smaller food loads at a more rapid rate than a

larger load less frequently (Orians and Pearson 1979). This is a salient point, especially since Pinkowski (1978) observed that adult Eastern Bluebirds fed smaller items to fledglings than nestlings. Further, elevated feeding rates during the fledgling period may indicate abundant food that is easy to procure (Lack 1947; Perrins 1970). Without data on energy budgets and hormonal or other physiological correlates of stress, it is difficult to assess the stress factor of parents during the fledgling period, let alone to compare the two periods with only behavioral data on feeding rates.

Parental care in Western Bluebirds

Despite the advantages, brood division may not be a common pattern in birds that has merely been overlooked (e.g., Smith 1978; McLaughlin and Montgomerie 1985) for it entails costs as well as benefits (see Harper 1985). Further, the existence of brood division had not been satisfactorily documented in most studies because of the failure of rigorously testing whether parents disproportionately fed certain offspring more than others (and not just that offspring were fed mostly by one parent) and because of the short time period during which fledglings were studied. We searched for this behavior in Western Bluebirds in many broods, which were studied over a 4-day period on average ($\bar{x} = 4.3 \pm 1.81$, $n = 27$ fledglings from 11 broods, Table 4), and found no evidence for brood division. Robins only occasionally divided their broods and even then did not practice "perfect" brood division in which young were fed entirely by one parent (Harper 1985). Unlike Western Bluebirds, fledgling Robins did not pursue their parents to obtain food, and in fact brood division became more marked as fledglings became older and more mobile. This led Harper (1985) to hypothesize that brood division may enable parents to monitor food intake of fledglings, as brood division was more pronounced in times of low prey abundance. This same hypothesis regarding the function of brood division was also broached by Edwards (1985). Brood division occurred primarily in second ("late") broods where young tended to fledge at lower weights than first-brood offspring. Feeding could be regulated more efficiently in divided broods, thus enabling parents to delay independence of young to minimize discrepancies in offspring weight that might affect survival.

Western Bluebirds exhibit shared parental care into the fledgling period and an association of young following fledging that may reduce energetic costs of parents related to locating, feeding, and protecting young. Fledglings were within 8 m of each other on average (8.2 ± 10.15 m; $n = 102$ observation periods) and dispersed an average of 115 m from the nest (114.8 ± 56.16 m; $n = 109$ observation periods). In Lapland Longspurs (*Calcarius lapponicus*), a species that divides its brood, male-tended offspring dispersed 171 m from the nest, whereas female-tended offspring dispersed almost four times as far (McLaughlin and Montgomerie 1985). Weak evidence for brood division was found, however, in American Redstarts (*Setophaga ruticilla*) in which broods apparently remained together. Young were within 8 m of each other, and adults only fed particular young despite begging by "wrong" offspring. The evidence is not very convincing, however, as these observations were based on a single brood in which two offspring were fed by the male and one by the female over a period of 2 days (offspring were not banded) (Boxall 1983). Nevertheless, we cannot assert whether the "geometry" of fledglings observed in Western Bluebirds is an alternate behavior to brood division or whether it is a consequence of a lack of brood division without

assessing the effect of offspring distance on the energetics of parental care.

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- ALATALO, R. V., GOTTLANDER, K., and LUNDBERG, A. 1988. Conflict or cooperation between parents in feeding nestlings in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scand.* **19**: 31–34.
- BATESON, P. 1978. Sexual imprinting and optimal outbreeding. *Nature (London)*, **273**: 659–660.
- BLOCK, W. M., WITH, K. A., and MORRISON, M. L. 1987. On measuring bird habitat: influence of observer variability and sample size. *Condor*, **89**: 241–251.
- BOXALL, P. C. 1983. Observations suggesting parental division of labor by American Redstarts. *Wilson Bull.* **95**: 673–674.
- BRAWN, J. D. 1985. Population biology, community structure, and habitat selection of birds in ponderosa pine forest habitat. Ph.D. dissertation, Northern Arizona University, Flagstaff.
- BRAWN, J. D., and BALDA, R. P. 1988. Population biology of cavity nesters in northern Arizona: do nest sites limit breeding densities? *Condor*, **90**: 61–71.
- BRAWN, J. D., BOECKLEN, W. J., and BALDA, R. P. 1987. Investigations of density interactions among breeding birds in ponderosa pine forests: correlative and experimental evidence. *Oecologia*, **72**: 348–357.
- DAVIES, N. B. 1976. Parental care and the transition to independent feeding in the young Spotted Flycatcher (*Muscicapa striata*). *Behaviour*, **59**: 280–295.
- . 1978. Parental meanness and offspring independence: an experiment with hand-reared Great Tits *Parus major*. *Ibis*, **120**: 509–514.
- DIXON, W. J., and BROWN, M. B., *Editors*. 1979. BMDP biomedical computer programs P-series. University of California Press, Berkeley.
- DRAPER, N. R., and SMITH, H. 1981. Applied regression analysis. 2nd ed. John Wiley & Sons, New York.
- DRENT, R. H., and DAAN, S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea*, **68**: 225–252.
- EDWARDS, P. J. 1985. Brood division and transition to independence in Blackbirds *Turdus merula*. *Ibis*, **127**: 42–59.
- FINKE, M. A., MILINKOVICH, D. J., and THOMPSON, C. F. 1987. Evolution of clutch size: an experimental test in the House Wren (*Troglodytes aedon*). *J. Anim. Ecol.* **56**: 99–114.
- GOWATY, P. A. 1983. Male parental care and apparent monogamy among Eastern Bluebirds (*Sialia sialis*). *Am. Nat.* **121**: 149–157.
- HARPER, D. G. C. 1985. Brood division in robins. *Anim. Behav.* **33**: 466–480.
- HARTSHORNE, J. M. 1962. Behavior of the Eastern Bluebird at the nest. *Living Bird* **1**: 131–149.
- HEGNER, R. E., and WINGFIELD, J. C. 1987. Effects of brood-size manipulations on parental investment, breeding success, and reproductive endocrinology of House Sparrows. *Auk*, **104**: 470–480.
- HUSSELL, D. J. T. 1972. Factors affecting clutch size in arctic passerines. *Ecol. Monogr.* **42**: 317–364.

- KLOMP, H. 1970. The determination of clutch-size in birds: a review. *Ardea*, **58**: 1-124.
- LACK, D. 1947. The significance of clutch-size. *Ibis*, **89**: 302-352.
- LEFFELAAR, D., and ROBERTSON, R. J. 1986. Equality of feeding roles and the maintenance of monogamy in tree swallows. *Behav. Ecol. Sociobiol.* **18**: 199-206.
- MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annu. Rev. Ecol. Syst.* **18**: 453-487.
- MCLAUGHLIN, R. L., and MONTGOMERIE, R. D. 1985. Brood division by Lapland Longspurs. *Auk*, **102**: 687-695.
- MORENO, J. 1984. Parental care of fledged young, division of labor, and the development of foraging techniques in the Northern Wheatear (*Oenanthe oenanthe* L.). *Auk*, **101**: 741-752.
- MURPHY, E. C., and HAUKIOJA, E. 1986. Clutch size in nidicolous birds. In *Current ornithology*. Vol. 4. Edited by R. F. Johnston. Plenum Press, New York. pp. 141-180.
- NUR, N. 1984a. The consequences of brood size for breeding Blue Tits. I. Adult survival, weight change and the cost of reproduction. *J. Anim. Ecol.* **53**: 479-496.
- 1984b. The consequences of brood size for breeding Blue Tits. II. Nestling weight, offspring survival, and optimal brood size. *J. Anim. Ecol.* **53**: 497-517.
- O'CONNOR, R. J. 1975. The influence of brood size upon metabolic rate and body temperature in nestling blue tits, *Parus caeruleus*, and House Sparrows, *Passer domesticus*. *J. Zool.* **175**: 391-404.
- ORIAN, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.* **103**: 589-603.
- ORIAN, G. H., and PEARSON, N. E. 1979. On the theory of central place foraging. In *Analysis of ecological systems*. Edited by D. J. Horn, B. R. Stairs, and R. D. Mitchell. Ohio State University Press, Columbus. pp. 157-177.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. *Ibis*, **112**: 242-255.
- PINKOWSKI, B. C. 1974. Criteria for sexing Eastern Bluebirds in juvenile plumage. *Inland Bird-Banding News*, **46**: 88-91.
- 1978. Feeding of nestling and fledgling Eastern Bluebirds. *Wilson Bull.* **90**: 84-98.
- POWER, H. W. 1980. The foraging behavior of Mountain Bluebirds with emphasis on sexual foraging differences. *Ornithol. Monogr.* No. 28.
- ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits *Parus major*. *Ibis*, **198**: 313-347.
- SKUTCH, A. F. 1961. Helpers among birds. *Condor*, **63**: 198-226.
- SMITH, J. N. M. 1978. Division of labour by Song Sparrows feeding fledged young. *Can. J. Zool.* **56**: 187-191.
- SMITH, J. N. M., and ROFF, D. A. 1980. Temporal spacing of broods, brood size, and parental care in Song Sparrows (*Melospiza melodia*). *Can. J. Zool.* **58**: 1007-1015.
- SNOW, D. W. 1958. A study of Blackbirds. George Allen and Unwin, London.
- SZARO, R. C., and BALDA, R. P. 1979. Bird community dynamics in a ponderosa pine forest. *Stud. Avian Biol.* No. 3.
- TRIVERS, R. L. 1974. Parent-offspring conflicts. *Am. Zool.* **14**: 249-264.
- VERNER, J., and WILLSON, M. F. 1969. Mating systems, sexual dimorphism, and the role of male North American passerine birds in the nesting cycle. *Ornithol. Monogr.* No. 9.
- WITH, K. A. 1988. Parental care in Western Bluebirds during the nestling and fledgling periods. *Sialia*, **10**: 123-129.
- WITTENBERGER, J. F. 1982. Factors affecting how male and female Bobolinks apportion parental investments. *Condor*, **84**: 22-39.
- YOM-TOV, Y., and HILBORN, R. 1981. Energetic constraints in clutch size and time of breeding in temperate zone birds. *Oecologia*, **48**: 234-243.
- ZAR, J. H. 1984. *Biostatistical analysis*. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.