THE FORAGING BEHAVIOR OF MOUNTAIN BLUEBIRDS

With Emphasis on Sexual Foraging Differences

BY

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Frontispiece: Plate I (upper left). Male Mountain Bluebird on top of his nest box carrying orthopteran prey for his young. Plate II (upper right). Female Mountain Bluebird with orthopteran prey at entrance to nest box. Note dull coloration of folded wings and tail. Plate III (lower left). Female Mountain Bluebird with wings and tail extended. Note the contrasting colors of the flight surfaces and body. Plate IV (lower right). West-facing view of the study area at Calvert, Montana, showing the savanna-like ecotone between Douglas Fir forest and short grass prairie. Note that trees in the savanna are concentrated on northeasterly slopes, i.e., those facing toward the right and bottom.

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To
Nelson G. Hairston
who taught me that
there is no substitute for an experiment

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CHAPTER 1

EVOLUTIONARY BASES OF SEXUAL FORAGING DIFFERENCES

Sexual dimorphism is the set of all differences between males and females in a single species. Sexual foraging differences are an aspect of this dimorphism that can be defined as differences in the ways males and females exploit prey. In the study of sexual foraging differences, evolutionary events should be considered along with ecological ones because evolutionary and ecological events are equally dynamic (Ford 1965; Hutchinson 1965) and feed back into and condition each other continuously. Thus, there can be no profound understanding of present ecological interactions in the absence of an understanding of their historical context and the direction in which selection is currently driving them.

This report is primarily concerned with sexual differences in the behavioral pattern of foraging in Mountain Bluebirds (*Sialia currucoides*). It details observations on foraging behavior from several breeding seasons, and the results of experiments designed to critically evaluate alternative hypotheses of the proximate and ultimate causes of sexual foraging differences. I begin with a review of different possible evolutionary origins of sexual foraging differences: (1) sexual selection, (2) intersexual competition, (3) division of labor, (4) foraging efficiency, and (5) intersexual exploitation. I consider how to separate these origins in practice and discuss factors inhibiting their production of sexual foraging differences.

SEXUAL SELECTION

Darwin's (1871) theory of sexual selection often can account for sexual foraging differences whether other factors are involved or not. Sexual selection can be defined as non-random differential reproduction of individuals in the contexts of (1) within-sexes competition, and (2) between-sexes choice. Within-sexes competition is exemplified by male-male combat over access to fertile females, and between-sexes choice by females mating only with males possessing particular secondary sexual structures, such as bright plumes.

Sexual selection can result in sexual foraging differences by producing morphological, physiological, or behavioral differences preadapting males and females for different types of prey exploitation; e.g., the favoring of large males in male-male combat could secondarily result in males taking larger prey than females because males would be better equipped to capture larger prey. The mating system of a species can influence the expression of sexual foraging differences by affecting the degree to which sexual selection produces sexual dimorphism. Polygynous and polyandrous species will usually be more sexually dimorphic than monogamous ones because of more intense within-sexes competition and between-sexes choice (Verner and Wilson 1969). The greater the dimorphism in structure, function, and behavior, the more divergent will be the foraging tactics that males and females are preadapted to perform.

Sexual selection is always at the root of sexual foraging differences, irrespective of the presence of other factors, because it is the only form of selection acting on the sexes *per se,* and thus the only form of selection producing incipient sexual foraging differences. It may seem that other forms of selection could produce sexual foraging differences by themselves because they favor the sexes being different. However, in the absence of preadaptions tending to make males consistently different in one way and females in another, differences of a particular kind probably would appear in one sex as often as the other and thus result in ecological polymorphisms not following strictly sexual lines. Other forms of selection tending to produce sexual foraging differences are, thus, subordinate to sexual selection, effectively operating only after it has produced at least small differences between the sexes.

For a particular species, one can infer that any factor important in the maintenance of sexual foraging differences has also been important in their evolution. Thus, one can infer that sexual selection is a cause of sexual foraging differences if (1) sexual foraging differences exist, and (2) they derive from sexual dimorphism in structure, and/or function, and/or nonforaging behavior.

INTERSEXUAL FOOD COMPETITION

Rand (1952) and Selander (1966) have hypothesized that intersexual food competition can be an evolutionary cause of sexual foraging differences. In Rand's scheme, intersexual competition is related to structural sexual dimorphism by sexual foraging differences. If sexual foraging differences alleviate intersexual competition, and structural sexual dimorphism enforces and makes sexual foraging differences more efficient, then an environment of intersexual competition will favor males and females that are structurally different from one another.

Selander (1966) reviewed a largely anecdotal literature supporting Rand's idea, correlated morphological and ecological dimorphism in *Centurus* woodpeckers, and postulated that intersexual competition could generate purely behavioral sexual foraging differences in the absence of structural sexual dimorphism. Selander's treatment greatly enhanced the plausibility of intersexual competition as an important factor in sexual foraging differences.

Intersexual competition may be related to the question of altruism. Altruism can be defined as the promotion of another's reproductive success while reducing one's own genetic fitness (Power 1975). Whether altruism is involved depends upon which individual(s) is (are) the primary recipient(s) of the benefit(s) of decreased competition. This benefit can apply either to each competition-reducing individual, or to some other individual(s). Whenever the benefit of an act goes to an individual other than the actor itself, altruism will appear to have occurred. Such appearance may be deceiving because the donation of a benefit can be a way of increasing one's own genetic fitness (Hamilton 1964; Trivers 1971; Alexander 1974).

Individuals that act to escape the effects of intersexual competition benefit themselves by acquiring either more food or the same amount of food at less cost, e.g., by reducing foraging time. The ecological strategy of such individuals can appropriately be called "selfish competition-reduction." An example of a behavior effecting this strategy would be the use of separate wintering grounds by each sex, as occurs in a number of water birds (Selander 1966). This would reduce the density of foraging individuals in a given area.

Individuals that donate the benefits of reduced competition increase the amount of food or decrease the cost of foraging to others. Such a donor can be favored only if the recipient of the benefit consequently promotes the genetic fitness of the donor. The strategy of donating the benefits of reduced competition in order to promote the genetic fitness of the donor can be called "beneficent competition-reduction." An example of a tactic appropriate to this strategy is found in Henslow's Sparrow (*Ammospiza henslowii*) where the male forages near the periphery of the territory leaving food near the nest at the territory center for his incubating mate (Robins 1971). Such a male directs the benefit of the food available near the nest to his mate at the cost of increasing his own caloric expenditure in finding food by foraging over a greater area. He increases his genetic fitness by promoting the nutritional welfare of his mate who thereby is able to be a better parent for their joint offspring. Phenotypic sacrifice in beneficent competition-reduction can be favored (as in this example) provided that it does not prevent a bird from successfully finishing its current breeding effort or breeding in the future.

Because the cost of beneficent competition-reduction can be high (e.g., exhaustion through use of inefficient foraging techniques), directing the benefit to an appropriate individual will be favored strongly. If the benefit is not properly directed, the donor's genetic fitness will decrease because the donor will both lose the benefits and promote the reproductive success of a genetic competitor. Beneficent competition-reduction thus can be expected to be most common between monogamous pair partners and mates in those cases of polygyny and polyandry where the paternity and maternity, respectively, of offspring are most certain. Contrarily, individuals of species in which parenthood is highly uncertain will be at a selective disadvantage if they make phenotypic sacrifices. Thus, in such species, any sexual foraging differences clearly deriving from intersexual competition are probably attributable to selfish competition-reduction rather than beneficent competition-reduction.

One can infer that intersexual competition is a cause of sexual foraging differences if (1) sexual foraging differences exist, (2) intersexual competition occurs, and (3) sexual foraging differences reduce intersexual competition. Competition reduction is beneficent if (4) the donor and recipient are related or jointly involved in reproduction. The fourth requirement is demanded by the difficulty of evolving altruistic behavior because the genes underlying altruistic behavior in the donor are driven to extinction by the genes underlying aid-accepting behavior in the recipient (Williams 1966). If this requirement is not met, then competition-reduction is entirely selfish.

Selander (1972:188) has proposed a different test for identifying the presence of intersexual competition: "Only when the trophic structures alone are modified can we conclude that the dimorphism results primarily or wholly from selection for differential niche utilization." I find this test inferior to the one I propose because sexual differences in trophic structures can result from (1) sexual selection (trophic structures are frequently used in sex combat and display) and/or (2) selection for division of labor. For example, male Strickland's Woodpeckers (*Dendrocopos stricklandi*) excavate nest cavities alone, and, thus, larger, heavier bills are favored in this sex (Ligon 1968).

DIVISION OF LABOR AND FORAGING EFFICIENCY

Selection for division of labor and/or individual foraging efficiency can produce sexual foraging differences if sexual selection has created at least incipient sexual differences. Selection for division of labor can magnify incipient sexual foraging differences by favoring males and females foraging in ways to which they are separately preadapted and that maximize their collective harvest. This selection should always minimize the cost of collective harvest to a group of males and females (e.g., a pair), but not the cost to individuals (e.g., females in monogamous pairs may be more efficient at a task than their mates, and performing it may promote the reproductive success of pairs; however, the task still may be so arduous that females are exhausted and/or endangered by it).

Selection for individual foraging efficiency is a component of selection for division of labor because collective harvest can be maximized by maximizing the efficiency of each individual in a group. But selection for individual foraging efficiency is different from that for division of labor because it (1) promotes the phenotypic welfare of individuals apart from benefits to a pair or other group, and (2) can occur in any context. Division of labor can occur only when there is some common labor to divide among the individuals of a group; thus division of labor is restricted to efforts of common reproduction if altruistic errors are to be avoided.

One can infer that selection for division of labor is a cause of sexual foraging differences if (1) sexual foraging differences exist based on sexual dimorphism in structure, and/or function, and/or nonforaging behavior preadapting the sexes to be more efficient at different tasks, (2) males and females really are more efficient at their respective tasks, and (3) there is a common reproductive effort by those males and females dividing labor. If only the first two requirements are met, sexual foraging differences derive only from selection for individual foraging efficiency.

INTERSEXUAL EXPLOITATION

Trivers (1972) hypothesized that sexual differences in parental care may not indicate division of labor so much as intersexual exploitation in the form of unequal parental investment for equal genetic reward. Trivers followed Bateman's (1948) reasoning that anisogamy favors males that fertilize the eggs of many females while favoring females that provide care for their own eggs and offspring. Bateman's theorem is clearly vindicated in many polygynous bird species. Trivers (1972:156) suggested that anisogamy will produce unequal parental investment even in socially monogamous birds. Because females' investment in eggs is so large relative to males' investment in sperm, "females appear to be caught in a situation in which they are unable to force greater parental investment out of the males and would be strongly selected against if they unilaterally reduced their own parental investment."

The critical assumption in Trivers' argument is that males' total investment is less than females' because males make no individual investment comparable in magnitude to females' investment in eggs. This assumption, in turn, relies heavily on his definition of parental investment, "any investment . . . in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of . . . ability to invest in other offspring" (Trivers 1972:139). Trivers' parental investment is neither synonymous with parental care (anything done for an offspring irrespective of effect on future reproduction), nor easily measured (it is difficult to assess the impact of most present events on future reproduction). Because Trivers' assumption is neither obvious nor easily tested, the reality of intersexual exploitation in socially monogamous birds is questionable.

Ignoring these difficulties (and thereby ignoring whether Trivers' hypothesis is an adequate explanation of intersexual exploitation in monogamous birds, if it exists), it is possible to ask what criteria are sufficient to demonstrate intersexual exploitation. I believe that intersexual exploitation is present if all these criteria are met: (1) the members of one sex coerce the members of the other sex into changing their behavior with the consequence that (2) the members of the coercing sex gain and (3) the members of the coerced sex lose. Gain and loss can be measured in terms of phenotypic detriment (phenotypic exploitation) or in terms of fitness (fitness exploitation). Coercion may be overt or subtle. Kilham (1970) found that male Downy Woodpeckers (*Dendrocopos pubescens*) forced their mates to forage at lower heights in trees by attacking them whenever they foraged in the upper parts of trees. In Chapter 9 I discuss whether male Mountain Bluebirds force their mates to use costly foraging behaviors more often than they otherwise would during the nestling period by simply not using those foraging methods very often themselves; if one sex does not perform an action contributing to reproductive success, then the other may be forced to perform it by that fact of omission alone.

It is possible to infer that intersexual exploitation is a cause of sexual foraging differences if (1) sexual foraging differences exist and (2) the criteria of intersexual exploitation are met when applied to those foraging differences.

INTERACTIONS AMONG FACTORS UNDERLYING SEXUAL FORAGING DIFFERENCES

Sexual foraging differences can evolve in the context of several selective factors operating simultaneously. Sexual selection must always be present, at least to a slight degree, for other forms of selection to operate along strictly sexual lines. Selection for individual foraging efficiency is implicit in selection for division of labor. Selection for reduced intersexual competition can interact with selection for individual foraging efficiency insofar as competition may be best reduced by maximizing individual efficiency. Selection for reduced intersexual competition can similarly interact with selection for division of labor to divide labor in a manner reducing intersexual competition. However, division of labor and/or individual foraging efficiency can be favored for their own benefits even if no intersexual competition exists, as in monogamous pair territories with an abundance of food but a strict feeding schedule for nestlings. Selection for intersexual exploitation can interact with selection for division of labor to produce a division of labor more advantageous to the members of one sex than the other.

FACTORS INHIBITING SEXUAL FORAGING DIFFERENCES

Because not all birds exhibit sexual foraging differences and because in those that do such differences change geographically and seasonally, sexual foraging differences must be the product of inhibiting as well as promoting selection pressures. Factors having the power to inhibit the evolution of sexual foraging differences are (1) selection for common parental care, (2) lack of stable resource units on which the sexes can specialize, and (3) preemption of resources by interspecific competitors.

(1) Selection for parental care by both males and females opposes the development of sexual foraging differences by opposing structural sexual dimorphism, one source of preadaptation for sexual foraging differences. This occurs because similar tasks generally are best performed by similar morphs. One expects that sometimes male and female morphologies converge because morphs intermediate between the initial male and female morphs are favored, but more often one expects males to converge toward females because females are already adapted to care for offspring as eggs, nestlings, and fledglings. Indeed, one expects females to converge toward males only when the morph most adapted to egg laying and incubation is less adapted for providing food for nestlings and fledglings than is the male morph; this must be vanishingly rare. Of the factors inhibiting sexual foraging differences, selection for common parental care is probably the most powerful because it favors sexual monomorphism *per se* while the other two factors only tend to inhibit sexual dimorphism.

(2) A lack of stable resource units can inhibit sexual foraging differences by preventing the sexes from specializing on different prey, or on the same prey in different places. Lack of stability probably also inhibits the evolution of structural sexual dimorphism to the extent that such dimorphism results in fairly great differences in prey optima for males and females and, thus, requires the sexes to partition resources.

Bock's (1970) and Ligon's (1973) studies of woodpeckers in which structural sexual dimorphism did not coincide with sexual foraging differences illustrate the importance of resource stability for resource partitioning. In their study species, the sequential appearance of prey populations resulted in only temporary availability of particular resources and, thus, allowed no long-term specialization on them. Ligon's (1973) study of White-headed Woodpeckers (*Dendrocopos albolarvatus*) also shows how extreme specialization can prevent resource partitioning. The members of this species heavily exploit Ponderosa Pine (*Pinus ponderosa*) seeds, a resource not readily divisible. No stable resource partitioning can occur where the basic resource cannot be divided. Of course, the seeds of a single species are not necessarily an indivisible resource; conceivably, they could have a very broad or bimodal size distribution allowing stable sexual differences in size preference.

Despite the difficulty, sexual foraging differences can also occur in the absence of stable resource units if they can be facultatively expressed for short periods. Morse (1968), Robins (1971), Williamson (1971), and I (see below) have shown short-term microgeographic sexual allopatry made possible by high prey abundances throughout territories during the nestling stage.

(3) Interspecific competition can inhibit sexual foraging differences by limiting the range of available resources (Van Valen 1965; Selander 1966; Wallace 1974) and, thus, preventing them from being partitioned into long-term stable sets. However, interspecific competition does not always inhibit sexual foraging differences because sometimes even a narrow range of resources can be partitioned. Raptors may be examples of narrow-niched species facing intense interspecific competition (e.g., *Accipiter* hawks, Storer 1966) yet having long-term sexual partitioning of prey by size-class.

CHAPTER 2

STUDY SPECIES, STUDY AREA, AND GENERAL METHODS

CHOICE OF THE MOUNTAIN BLUEBIRD

Desiring to explore the several alternative hypotheses for the evolution of sexual foraging differences, I sought a species in which there were *a priori* grounds for considering more than one hypothesis. I chose the Mountain Bluebird primarily because I already knew its general biology (Power 1966), but also because bluebirds are (1) nearly monomorphic structurally (males are slightly larger than females but trophic structures do not differ significantly, Table 1); (2) dichromatic with brightly colored males and duller colored females (Plates I–III); (3) limited by availability of nest sites; (4) monogamous; and (5) easily identified as individuals and experimentally manipulated.

(1) Choosing a structurally monomorphic species, I avoided the chicken-and-egg question plaguing previous studies of whether the size or ecological dimorphism came first. In a structurally monomorphic species sexual foraging differences cannot be simple reflections of structural sexual dimorphism.

(2) The importance of sexing birds in a study of sexual dimorphism is patent. Dichromatism reliably correlates with gender and allows ready sex identification (Power, unpubl. data).

(3) Miller (1970) and his group corroborated my hypothesis (Power 1966) that Mountain Bluebirds are nest-site limited; they generated a striking increase in the bluebird breeding population in Manitoba in only a few years by erecting hundreds of nest boxes. It is reasonable to expect that in a nest-site limited species, selection will favor individuals that use nest sites nearly anywhere they can be found. Thus, such a species can be expected to have a wide habitat tolerance. Some habitats are, inevitably, less productive than others, and the least productive acceptable ones may be so food impoverished that males and females are in food competition. Thus, there are *a priori* grounds for considering intersexual competition in Mountain Bluebirds.

(4) The importance of monogamy is simply that the potential difficulty of altruism is avoided in cases of intersexual competition (see above); beneficent competition-reduction is, thus, a possible outcome of intersexual competition if that competition occurs.

(5) Identification and manipulation of every individual in the breeding population was facilitated by birds breeding in nest boxes where they could be located, captured, marked, or collected. Individual identification and manipulation made possible the rigorous testing of alternative hypotheses.

STUDY AREA

Bluebirds were studied in the Calvert rural school district of southern Cascade County, Montana. The study area (hereafter Calvert) covered about 16,000 ha; a core area of 1200 ha was covered frequently by car, foot, and horseback. Calvert is a prairie-forest ecotone (Plate IV) where scrub Douglas Fir (*Pseudotsuga menziesii*) forest breaks up into savanna or parkland of clumped trees and short-grass foothills prairie (see Küchler 1964). Elevations at Calvert range from 1524–1740 m above sea level. Mountain Bluebirds occur naturally at Calvert having been

TABLE 1
BLUEBIRD MENSURAL DATA

Character[1]	N	Mean[2]	S.D.	Range
Birds in the University of Michigan Museum of Zoology Collection				
Males				
Bill length	45	10.01	0.62	9.0–11.5
Bill width	46	6.13	0.62	5.0–8.0
Bill depth	46	4.83	0.40	4.0–5.5
Tarsus	45	22.01	0.91	19.0–24.0
Wing length P9	41	113.20***	2.76	108.0–118.0
Wing length P5	41	88.85***	2.54	83.0–94.0
Wing shape, P5/P9	41	0.78	0.01	0.76–0.81
Females				
Bill length	38	10.04	0.55	9.0–11.5
Bill width	38	6.13	0.62	5.0–8.0
Bill depth	38	4.75	0.38	4.0–5.0
Tarsus	38	22.06	1.01	20.0–25.0
Wing length P9	32	109.40***	3.50	100.0–117.0
Wing length P5	32	86.00***	1.87	82.0–91.0
Wing shape, P5/P9	32	0.79	0.02	0.71–0.85
Birds at Calvert in 1972				
Males				
Bill length	10	10.15	0.28	9.5–10.5
Bill width	10	8.85	1.00	7.0–10.0
Bill depth	9	5.22	0.26	5.0–5.5
Tarsus	8	23.19	0.75	22.0–24.5
Wing length P9	8	114.63***	3.29	111.0–120.0
Wing length P5	8	90.88*	4.85	87.0–102.0
Wing shape, P5/P9	8	0.79	0.03	0.76–0.85
Females				
Bill length	13	9.92	0.40	9.0–10.5
Bill width	14	8.71	0.75	7.0–10.0
Bill depth	14	5.18	0.25	5.0–5.5
Tarsus	13	23.27	1.01	21.0–25.0
Wing length P9	14	108.79***	3.42	104.0–115.0
Wing length P5	13	85.39*	4.66	75.0–92.0
Wing shape, P5/P9	13	0.78	0.03	0.71–0.81

[1] All measurements in mm. P9 = primary 9, P5 = primary 5.

[2] Each character compared between males and females with significant differences noted as: * = $p < 0.05$; *** = $p < 0.001$; other differences non-significant.

seen annually during 80 years of ranching settlement (J. G. Gasvoda, pers. comm.).

A few nest boxes (inside measurements 12.70 × 12.70 × 20.32 cm) were erected at Calvert in the early 1960's (Power 1966). Twenty-two were available at the beginning of 1970, and more were added for a total of 59 boxes during 1972. These boxes were erected along a zig-zagging trail nearly 32 km long.

GENERAL METHODS

I concentrated on foraging behavior but also noted other activities in order to provide a context for foraging behavior. Data were recorded orally on a casette tape in the field and later transcribed onto paper and analyzed.

(A) *The foraging event.* I used a set of six parameters to describe and measure the foraging behavior of individual birds. The six parameters comprising what I call the "foraging event" are:

- (1) Proximity to large perches
  - (a) near-large-perches: the bird was within 6 m of a large perch [see (2) below] at the point of capture or capture attempt;
  - (b) away-from-large-perches: the bird was more than 6 m from a large perch.
- (2) Staging points: places from which foraging patterns were initiated
  - (a) large perches: trees, fences (especially posts), utility lines, cliffs, buildings or other objects more than 0.5 m tall;
  - (b) small perches: low bushes and other objects less than 0.5 m tall, the soil surface, and rock outcroppings;
  - (c) aerial positions: hovering positions or points of flight deviation for hawking [see (3) below].
- (3) Foraging patterns
  - (a) perch-foraging: the bird searched for prey from an elevated perch; when it observed a prey item, it flew down to the ground or vegetation and attempted to capture the item; whether it was successful or not, it usually returned to the perch from which it initiated the pattern, or a similar one; I previously reported (Power 1966) that birds generally ate prey at the capture site, but, in fact, prey often was eaten on a perch;
  - (b) ground-foraging: similar to perch-foraging except that the pattern was initiated from the ground;
  - (c) flycatching: similar to perch-foraging except that the bird attempted to take prey from the air;
  - (d) hover-foraging: the bird searched for prey from a hovering position; when it spotted a prey item, it flew down to the earth or vegetation and attempted to capture it; this pattern was often repeated in rapid sequence when initial tries were unsuccessful;
  - (e) perch-foraging/hover-foraging: elements of perch-foraging and hover-foraging were used sequentially; the pattern was usually initiated from a high perch (more than 4 m tall); the bird dropped from its perch to a point usually about 1 m above ground, then hovered before attempting to take prey from the ground or vegetation; this pattern was used when the bird appeared to want to look more closely at an item it had spotted from a height;
  - (f) hawking: the bird deviated strongly from a flight course in pursuit of a large flying insect; similar to the foraging behavior typical of swallows except more clumsily performed.
- (4) Vegetation types
  - (a) normal prairie: short-grass prairie with plants of varying heights and some shrubs [see Küchler (1964) for description of central Montana foothills prairie];
  - (b) uniform prairie: prairie with plants of uniform, short height, often kept short by heavy grazing pressure from cattle and grasshoppers;

- (c) simple hayfield: a cultivated field with one crop species, spring wheat or, especially, oats;
- (d) mixed hayfield: a cultivated field and grass mixed with alfalfa;
- (e) cut hayfield: a mown hayfield;
- (f) bare area: a fallow field, road surface, or other area of denuded earth;
- (g) rock outcropping: a cliff, boulder field, or slab of exposed rock surface.

(5) Vegetation height: four heights measured against the body of a foraging bluebird

- (a) vegetation less than or equal to tarsal height;
- (b) vegetation between tarsal and shoulder height;
- (c) vegetation between shoulder and head height;
- (d) vegetation more than head high.

Because the two extreme categories were represented by vegetation on all territories while the intermediate ones were represented on only some territories, or on only small or remote parts of territories, I reduced the four height categories to two in the data tables. Birds foraging on bare substrate, vegetation less than tarsal length in height, or the surface of mats of vegetation (e.g., swaths of mown hay, and grass growing horizontal because of heavy grazing) were all scored as foraging in "short" vegetation because these places all had the same effect on bird visibility, freedom of movement, and ability to detect predators and prey. Birds hunting in vegetation more than tarsal length in height were scored as foraging in "tall" vegetation. Actually, birds scored in the "tall" category usually foraged in vegetation more than head high because cattle grazing tended to leave grass either shorter than tarsal length or greater than bluebird height.

(6) Distance to nest box: estimated in meters by sight; thus, distances were accurate only on an ordinal scale; the greater the distance, the less accurate the measurement.

While I always attempted to do so, I was not always able to obtain information on all six parameters of a foraging event. Consequently sample sizes for the different parameters vary. Moreover, I only took data on proximity to large perches, foraging patterns, and staging points prior to 1972.

(B) *Foraging rate.* In 1971–72 I measured the foraging rate by counting the number of foraging patterns executed per minute of foraging. A minute of foraging was arbitrarily defined as a 1-min interval beginning with an observed foraging pattern. This rate indicated the rapidity with which a bird foraged once it had begun foraging although it also included loafing if the bird stopped foraging before 60 secs were up.

(C) *Parental care.* Activities directed toward young were quantified to obtain a measure of parental care. Included were the number of box visits per hour (a measure of feeding as food appeared to be brought on every trip), and the number of fecal sac removals per hour (a measure of nest sanitation).

(D) *Statistical analysis.* Computer analysis was performed primarily using the MI-DAS console statistics program of The University of Michigan Statistical Research Laboratory. Choice of test was determined by consulting Siegel (1956) and the personnel of the Statistical Research Laboratory. Chi-square analysis and Fisher's Exact Probability Test were used on nominal level data. The Wilcoxon Matched-Pairs Test was used on before-after data. The Spearman Rank Correlation coefficient was used to detect correlation between ordinal and interval level parameters. The Mann-Whitney U Test was used on ordinal level parameters. Both the Mann-Whitney U Test and Student's T-test were used on mensural data because the U Test makes no assumptions about normality or homoscedasticity while the T-test has greater power-efficiency (Siegel 1956; Sokal and Rohlf 1969).

Chi-square testing was based on complete tables unless there were zero entries or more than 20% of the cells had expected values of less than 5. When this occurred, chi-squares were based on reduced tables made by joining columns and/or rows until there were no zero entries, and all cells had expected values of at least 5.

I treated results having less than a 5% probability of random error as significant, results having more than a 10% probability of random error as not significant, and results having a probability of random error between 5 and 10% as significant or not significant on the basis of relevant factors not considered in the statistical analysis itself. Probabilities of random error for all cases are provided in the data tables.

CHAPTER 3

NON-EXPERIMENTAL OBSERVATIONS

All stages of nesting were observed at Calvert during June–August, 1970 and May–September, 1971 and 1972. In particular, sexual foraging differences in relation to different nesting stages and seasonal changes in foraging behavior were noted. The breeding season is conveniently divisible into seven stages: preincubation, first brood incubation, first brood nestling, first brood fledgling, second brood incubation, second brood nestling, and postbreeding flock stages. The preincubation stage includes all those activities from spring arrival through egg laying. It is the least realistic division because it includes events as disparate as territory acquisition and nest building. However, it was convenient to combine periods of preincubation activities because the length of any one of them for any pair was so short that it was exceedingly difficult to gather sufficient data to analyze foraging behavior in each. There was no distinct second brood fledgling stage because postbreeding flocks were attracted to fledglings and often formed around them.

SEXUAL FORAGING DIFFERENCES OUTSIDE THE NESTLING STAGES

Most sexual foraging differences were restricted to the first and second brood nestling stages, but differences in foraging rates and use of staging points occurred in other stages. In this and the following section I argue that only differences in resource use during the nestling stages are significant because the differences during other stages represent biological events other than differential resource partitioning.

Table 2 shows number of foraging patterns per foraging minute by nesting stage and sex. Significant intersexual differences occurred only during the first brood incubation period when females perch-foraged more frequently than males. More rapid foraging by females probably occurred because they had little time to spend off their nests; tarrying would allow eggs to chill and/or increase vulnerability to nest predators. More rapid foraging by females did not necessarily cause the sexes to exploit different resources. Merely reducing the interval between foraging patterns would not necessarily cause females to encounter different prey populations from males, or the same prey populations with different frequencies.

The recorded foraging rate for females is much lower for the second brood incubation stage than the first (Table 2). A lower rate and absence of sexual differences may have been produced by warmer ambient temperatures (July vs. May–June) causing a slower chilling rate for untended eggs, or it may have been an artifact of smaller sample size.

Outside the nestling stages, intersexual differences in the foraging event were restricted to the use of foraging patterns during the first brood incubation stage (Table 4), and the use of staging points during the preincubation and first brood incubation stages (Table 5). Females flycaught significantly more often than males during the first brood incubation stage (Table 4), but this difference is only apparent because it is based on observations of females during short periods of high fly density that were not balanced by similar observations on males. Fly densities were highly variable on a day-to-day basis because of frequent high winds and cold snaps.

TABLE 2

NUMBER OF FORAGING PATTERNS PER MINUTE OF FORAGING

Nesting Stage	No. timed sequences	Mean	Range
		Males	
Preincubation	14	1.78	1.0–5.0
Incubation I[1]	47	2.01	1.0–10.0
Nestling I	44	2.61	1.0–9.0
Fledgling	17	2.51	1.0–6.0
Incubation II	12	1.79	1.0–4.0
Nestling II	18	2.74	1.0–4.0
Postbreeding flocks	21	5.61	1.0–16.0
		Females	
Preincubation	8	1.35	1.0–3.0
Incubation I[1]	44	3.02	1.0–7.5
Nestling I	38	2.87	1.0–12.0
Fledgling	8	2.67	1.0–6.0
Incubation II	8	1.63	1.0–3.0
Nestling II	21	3.01	1.0–14.0
Postbreeding flocks	5	3.67	1.0–6.0

[1] Significant difference between sexes by Mann-Whitney U test, $p < 0.001$; all other intersexual comparisons non-significant.

Males made greater use of trees than females did during the preincubation and first brood incubation stages (Table 5). This difference represents a division of labor in which males guard territories more than females do, but it does not represent a difference in actual foraging. Examination of data on staging points

TABLE 3

PROXIMITY OF FORAGING BIRDS TO LARGE PERCHES DURING NON-EXPERIMENTAL OBSERVATIONS OF VARIOUS STAGES OF THE NESTING CYCLE[1]

	NLP[2]	AFLP		NLP	AFLP
		1970–1972			
	Preincubation			First brood incubation	
♂♂	40 (95)[3]	2 (5)	♂♂	98 (94)	6 (6)
♀♀	32 (100)	0 (0)	♀♀	81 (98)	2 (2)
	First brood nestling***			First brood fledgling	
♂♂	422 (87)	62 (13)	♂♂	50 (89)	6 (11)
♀♀	338 (61)	219 (39)	♀♀	28 (87.5)	4 (12.5)
	Second brood incubation			Second brood nestling*	
♂♂	43 (83)	9 (17)	♂♂	41 (77)	12 (23)
♀♀	17 (100)	0 (0)	♀♀	46 (61)	29 (39)
	Postbreeding flock				
♂♂	31 (97)	1 (3)			
♀♀	9 (100)	0 (0)			
		1974–1975[4]			
	Fledgling			Postbreeding Flock	
♂♂	85 (84)	16 (16)	♂♂	41 (85)	7 (15)
♀♀	104 (81)	24 (19)	♀♀	72 (86)	12 (14)

[1] Male vs female differences in each stage non-significant unless noted; * = $p < 0.05$; *** = $p < 0.001$.

[2] NLP = Near-large-perches; AFLP = away-from-large-perches.

[3] Number (%).

[4] No second broods in 1974–75.

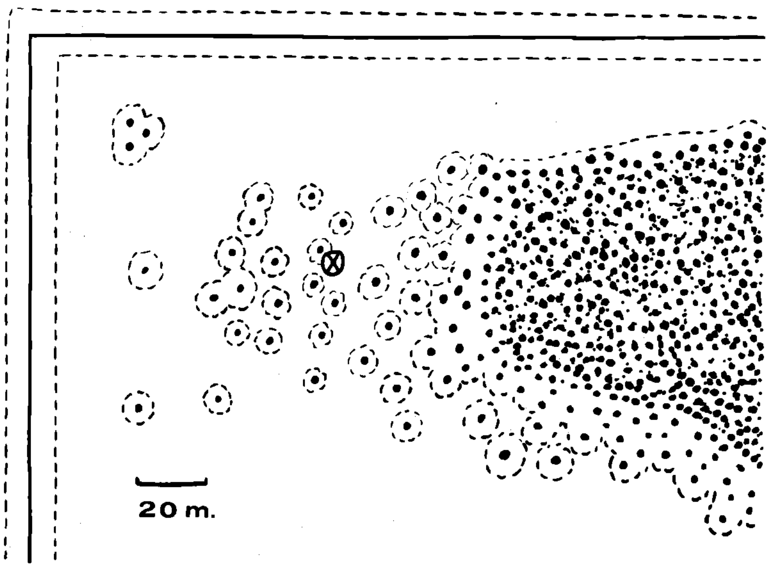

Fig. 1. Areas near- and away-from-large-perches in a corner of territory 28 in 1970. Circled X is the nest box; dots are trees; solid line is a barbed-wire fence; dashed lines indicate the boundaries between the areas near- and away-from-large-perches. Bluebirds foraged everywhere except within the dense grove of trees at the right.

actually used in perch-foraging (as opposed to the total use of staging points shown in Table 5) showed no significant intersexual differences in tree use. Males probably used trees as perches near territorial boundaries because trees are high. The absence of an equivalent male-female dichotomy in the use of trees in the nesting stages following first brood incubation (Table 5) is coincident with greatly reduced territorial advertising behavior by males. During the nestling stage, males mainly advertise by dawn song flights that precede the day's foraging and by crepuscular singing. Reduced advertising activity presumably reflects the prior learning of territorial boundaries by adjacent males and the feeding demands of nestlings.

SEXUAL FORAGING DIFFERENCES DURING THE NESTLING STAGES

During both nestling stages, females were away-from-large-perches significantly more often than males (Table 3). This was accompanied by more frequent hover-foraging and hawking (Table 4), and greater use of aerial staging points (Table 5). Females used aerial staging points more frequently because hover-foraging and hawking were initiated from them, and they hover-foraged and hawked more frequently because these are the principal patterns by which the area away-from-large-perches is exploited. (But I have observed all foraging patterns except perch-foraging/hover-foraging away-from-large-perches.) Males, contrarily, perch-foraged and used trees and fences more frequently than females; this enabled them to exploit the area near-large-perches more intensively. The crux of these intersexual differences was relative use of the area away-from-large-perches. (The areas near- and away-from-large-perches are illustrated in Figure 1).

By foraging in the area away-from-large-perches more frequently, females in-

TABLE 4
USE OF FORAGING PATTERNS DURING NON-EXPERIMENTAL OBSERVATIONS OF VARIOUS STAGES OF THE NESTING CYCLE

Nesting stage[1]	PF[2]	PF/HF	GF	HF	Fly	Ha
			1970–1972			
Preincubation						
♂♂	26 (70)[3]	0 (0)	1 (3)	2 (5)	8 (22)	0 (0)
♀♀	26 (70)	0 (0)	6 (16)	0 (0)	5 (14)	0 (0)
First brood incubation**						
♂♂	125 (81)	2 (1)	14 (9)	4 (3)	6 (4)	3 (2)
♀♀	125 (73)	1 (1)	26 (15)	1 (1)	18 (10)	1 (1)
First brood nestling***						
♂♂	369 (75)	10 (2)	9 (2)	58 (12)	40 (8)	4 (1)
♀♀	307 (51)	20 (3)	7 (1)	214 (35)	29 (6)	20 (3)
First brood fledgling						
♂♂	20 (24)	1 (1)	49 (60)	7 (9)	4 (5)	1 (1)
♀♀	13 (32)	1 (2)	21 (51)	6 (15)	0 (0)	0 (0)
Second brood incubation						
♂♂	30 (57)	1 (2)	4 (8)	11 (21)	4 (7)	3 (6)
♀♀	10 (50)	0 (0)	1 (5)	0 (0)	8 (40)	1 (5)
Second brood nestling						
♂♂	31 (51)	0 (0)	0 (0)	11 (18)	13 (21)	6 (10)
♀♀	30 (41)	0 (0)	0 (0)	19 (26)	15 (21)	9 (12)
Postbreeding flock						
♂♂	24 (20)	0 (0)	89 (75)	0 (0)	5 (4)	0 (0)
♀♀	8 (32)	0 (0)	16 (64)	0 (0)	1 (4)	0 (0)
			1974–1975			
Fledgling						
♂♂	84 (71)	4 (3)	10 (8)	3 (3)	14 (12)	4 (3)
♀♀	125 (78)	2 (1)	10 (6)	6 (4)	12 (8)	5 (3)
Postbreeding flock						
♂♂	28 (46)	2 (3)	13 (21)	0 (0)	16 (26)	2 (3)
♀♀	56 (54)	0 (0)	15 (15)	7 (7)	22 (21)	3 (3)

[1] Male vs female differences in each stage non-significant unless noted; ** = $p < 0.01$; *** = $p < 0.001$.
[2] PF = perch-foraging; HF = hover-foraging; GF = ground-foraging; Fly = flycatching; Ha = hawking.
[3] Number (%).

vested a greater part of their time and energy and took a greater part of their total harvest there than did males. This resulted in horizontal spatial separation of the sexes. Vertical spatial separation also was statistically significant. Females hawked significantly more often than males during the first brood nestling stage (Table 4) and thus took a greater proportion of prey from the volume of air above the grassland. But, as hawking amounted to only 3% of the foraging effort of females and 1% of that of males, vertical spatial separation was probably only of marginal significance in resource use compared to horizontal spatial separation.

PRELIMINARY CONSIDERATIONS OF SEXUAL FORAGING DIFFERENCES

Before considering alternative hypotheses to account for sexual foraging differences during the nestling stages, it is appropriate to comment on the possibil-

TABLE 5
USE OF STAGING POINTS DURING NON-EXPERIMENTAL OBSERVATIONS OF VARIOUS STAGES OF THE NESTING CYCLE

Nesting stage[1]	Tree	UL[2]	Fence	SP[2]	Rock	Ground	Aerial	Bale
				1970–1972				
Preincubation*								
♂♂	42 (48)[3]	1 (1)	36 (41)	1 (1)	0 (0)	3 (3)	4 (5)	
♀♀	17 (26)	0 (0)	40 (62)	0 (0)	1 (1)	7 (11)	0 (0)	
First brood incubation***								
♂♂	64 (23)	37 (14)	118 (43)	17 (6)	14 (5)	13 (5)	11 (4)	
♀♀	21 (9)	44 (19)	111 (47)	5 (2)	20 (9)	29 (12)	4 (2)	
First brood nestling***								
♂♂	361 (32)	78 (7)	443 (39)	39 (3)	40 (4)	40 (4)	123 (11)	
♀♀	254 (20)	76 (6)	387 (30)	55 (4)	33 (3)	34 (3)	439 (34)	
First brood fledgling								
♂♂	25 (18)	1 (1)	19 (14)	12 (9)	15 (11)	55 (40)	11 (8)	
♀♀	22 (26)	4 (5)	8 (9)	5 (6)	14 (16)	25 (29)	7 (8)	
Second brood incubation								
♂♂	16 (22)	9 (12)	28 (38)	6 (8)	2 (3)	4 (5)	8 (11)	
♀♀	9 (24)	4 (11)	22 (58)	0 (0)	0 (0)	1 (3)	2 (5)	
Second brood nestling*								
♂♂	15 (14)	6 (6)	65 (60)	0 (0)	1 (1)	5 (5)	16 (15)	
♀♀	7 (5)	7 (5)	64 (50)	3 (2)	1 (1)	9 (7)	38 (29)	
Postbreeding flock								
♂♂	0 (0)	5 (4)	31 (24)	0 (0)	5 (4)	88 (68)	1 (1)	
♀♀	0 (0)	4 (14)	9 (31)	0 (0)	0 (0)	16 (55)	0 (0)	
				1974–1975				
Fledgling**								
♂♂	44 (18)	54 (23)	65 (27)	12 (5)	8 (3)	7 (3)	13 (5)	35 (15)
♀♀	58 (20)	33 (12)	91 (32)	24 (8)	17 (6)	7 (2)	28 (10)	25 (9)
Postbreeding flock								
♂♂	3 (3)	2 (2)	58 (66)	1 (1)	11 (13)	10 (11)	3 (3)	0 (0)
♀♀	1 (1)	16 (11)	87 (61)	0 (0)	1 (1)	21 (15)	16 (11)	1 (1)

[1] Male vs female differences in each stage non-significant unless noted; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.
[2] UL = utility line; SP = small plant.
[3] Number (%).

ities (1) that excessive observations of females away-from-large-perches falsely generated the appearance of sexual foraging differences, and (2) that prey away-from-large-perches were superior in quality or quantity to those near-large-perches.

I countered possible sex bias in observing foraging behavior by stationing myself in a place where I could see all or nearly all of a territory, focusing my binoculars on the nest box, and visually following the first bird leaving the box vicinity until it completed its foraging expedition and returned to its nest. I then visually followed its mate in the same way and, thus, alternated observations between pair partners. Some of my observations were made on birds initially encountered away from their nests, but those birds probably did not bias my results because I watched them only briefly before turning my attention to their mates or nest boxes. Sometimes, I was able to watch pair partners simultaneously. Whenever I was able to watch entire foraging expeditions, no observational bias toward any type of behavior by any bird was possible. I did sometimes lose sight of foraging birds, and this happened more frequently with females because of the flash pattern they manifested when alighting (see below). But, I do not believe my sample is biased toward females foraging away-from-large-perches because females were more frequently lost to view when foraging there. This occurred because the area away-from-large-perches is much larger than the area near-large-perches. Moreover, it is more difficult to predict where a bird will reappear after a temporary disappearance away-from-large-perches because it does not focus its activity on large, easy-to-see staging points as it does when near-large-perches. Insofar as visual losses of birds biased my total sample, they biased it against observation of birds foraging away-from-large-perches, especially females, and thus against observation of sexual foraging differences. My estimate of sexual foraging differences is, therefore, conservative.

Evidence suggests that prey away-from-large-perches was not superior in quality or quantity to prey near-large-perches. Prey near and away from fences and utility lines probably was not different in quality or quantity because fences and lines were built without reference to soil type, moisture, and vegetation, the determinants of arthropod species number and abundance. Moreover, prey may have been more accessible near fences than away from them because cattle wore trails along some fences forming bare places where bluebirds could more easily find and capture arthropods. Prey near and away from trees may have been different because most trees were on moist, northeasterly slopes (Plate IV). However, moister conditions near trees may have resulted in more abundant prey just as it resulted in lusher grass and forbs.

In 1976 I searched for differences in prey quality and quantity between the areas near- and away-from-large-perches by sweep netting and pit trapping at places of equivalent vegetation height. On one territory, I sampled for 10 consecutive days from a pair of 100 m courses running parallel to a fence where birds frequently foraged; one course was 1 m from the fence, the other 10 m. On five other territories, I collected on 1–4 consecutive mornings from two strips running 10 m out from nest boxes; one strip bordered a fence while the other ran at right angles to it. Species composition, size, and abundance of prey did not differ between areas near- and away-from-large-perches according to analysis by the Mann-Whitney U Test and Wilcoxon Matched Pairs Test ($p \gg 0.05$ in all comparisons).

Despite my conclusion that the body of prey occurring away-from-large-perches is not superior to that near-large-perches and therefore could not reward birds sufficiently to compensate for their far greater caloric expenditure in hover-foraging,[1] I am not dismissing the possibility that the *average* item taken by hover-foraging is larger or otherwise superior to the average item taken by perch-foraging. To the contrary, I think that bluebirds do take larger and, perhaps, otherwise better prey when hover-foraging; they search for such a short time

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[1] Insofar as bluebirds are like hummingbirds (Trochilidae), hovering costs 4–8 times the calories perching does (see Lasiewski 1963; Wolf and Hainsworth 1971). If bluebirds are less adapted for hovering (and that is probable), then it may be even more costly than in hummingbirds. The relative costs of hovering and perching are difficult to estimate under field conditions because hovering is most frequent on gusty days when the wind provides part of the required lift, but hovering also commonly occurs on still days. Females could take advantage of wind more than males only if they were shaped differently, which they are not (see below).

when hover-foraging (a few seconds) compared to perch-foraging (up to many minutes) that they probably have time only to discover larger or otherwise more noticeable individuals. But, whatever differences may exist between prey taken near- and away-from-large-perches, I suspect that prey taken away-from-large perches seldom will be *sufficiently* superior to repay the greater cost of hover-foraging. Comparisons between prey in the diet and the environment (e.g., Royama 1966, 1970) show that birds generally capture the largest prey they can find and subdue. Thus, prey taken by either foraging mode probably has the same upper size limit even if prey taken by perch-foraging averages somewhat smaller than prey taken by hover-foraging.

POSSIBLE CAUSES OF SEXUAL FORAGING DIFFERENCES

The pattern of sexual foraging differences observed during the nestling stages initially seemed consistent with several alternative explanations of origin and maintenance. These were (1) intersexual food competition, (2) female superiority at hover-foraging, (3) division of labor in which females contribute more food to young and males search more often for intruding conspecifics, (4) male coercion of females into foraging away-from-large-perches, and (5) sexual dichromatism resulting in greater predation upon males than females while foraging away-from-large-perches. All but the first of these possibilities are indirect reflections of sexual selection producing morphological and/or behavioral differences.

(1) The partial spatial separation of the sexes during the nestling periods could have reduced intersexual food competition if there were any. Intersexual food competition could have existed if there were an incipient competition between pair partners prior to the hatching of their young, and if the arrival of those young made that competition actual. Spatial separation could have reduced intersexual food competition by spatially partitioning the resource base of each pair and thereby lowering the probability that males and females simultaneously foraged for the same item.

(2) If females were better hover-foragers, then they would be better able to exploit the area away-from-large-perches, and their superiority in hover-foraging would generate sexual foraging differences. However, there was no evidence for this as males and females had the same aerodynamic properties and apparently were equally successful at hover-foraging.

Were females aerodynamically better hoverers than males, then their wings should be shaped differently [as Vaughan (1959) found in bats] or have lighter loading in proportion to females' greater frequency of hover-foraging. I estimated wing shape by comparing the lengths of the fifth and ninth primaries. As number 5 approaches number 9 in length, the wing becomes round, whereas it is elongated when number 5 is much shorter than number 9 (Fig. 2). The ratio of primaries 5 to 9 was not significantly different between males and females (Table 1). Thus, I concluded that the wings of males and females are the same shape.

The greater wing length of males (Table 1) suggests that they are heavier than females according to Hamilton's (1961) hypothesis, and this, coupled with equivalent wing shape for the sexes, means that females may have lighter wing loading. To determine relative wing loading, I weighed pair partners at 7 nests during the first brood nestling stage of 1977. Males averaged 32.4 g (range 29–38), and females averaged 32.7 g (range 27–36). These differences are insignificant by both

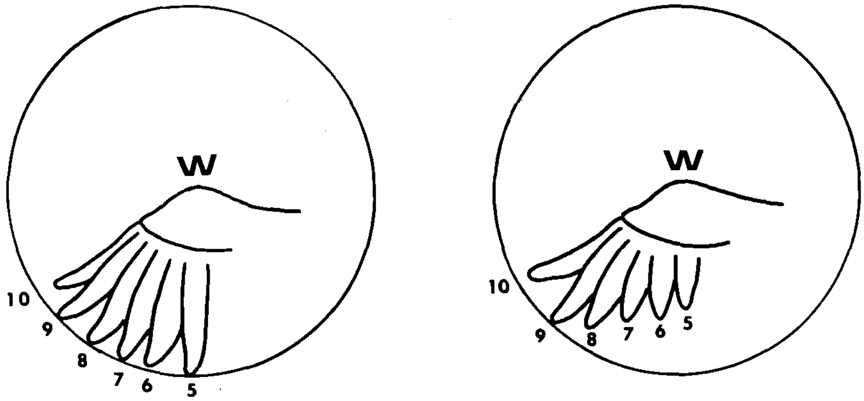


Fig. 2. Diagrammatic representation of passerine wing shapes. Numbers refer to primaries; W = wrist. In a rounded wing (left), the length of primary 5 is similar to that of primary 9. In an elongated wing (right), primary 5 is substantially shorter than primary 9. Thus, the ratio of the length of primary 5 to the length of primary 9 is an index of wing shape. When the ratio is low, the wing is elongated; when the ratio is high, the wing is rounded.

the Mann-Whitney U Test (U = 26) and the Wilcoxon Matched Pairs Test (T = 12). Even if a larger sample were to show that females are significantly lighter than males (and thus have lower wing loading), I predict that the difference in loading would be insufficient to account for the difference in frequency of hover-foraging because females hover-foraged 338% more often than males during the two nestling stages (Table 4).

Males and females appeared to be equally successful hover-foragers. Males made capture attempts (dropped to the ground or vegetation while hover-foraging) 49% of the times when they stopped to hover (n = 119), while females attempted captures during 51% of their hover stops (n = 419) during the first brood nestling period (compares Tables 4 and 5). This difference is not statistically significant.

The actual number of captures was not used as an index of success because birds were usually too far away to determine whether attempts were successful. The number of capture attempts is itself an upper limit of success as some attempts must not have been successful. Apparent equal success at hover-foraging by males and females suggests that males did not hover-forage and go away-from-large-perches less than females because they were less able to do so.

(3) Sexual foraging differences could be explained by division of labor if females were away-from-large-perches more often than males because they contributed more food to young and both sexes had the same thresholds for initiation of the same foraging behaviors, and/or because males searched more often for intruding conspecifics. However, observation showed this could not have been an important cause of sexual foraging differences.

During the field seasons of 1970–72, I recorded frequency of nest visits while observing foraging behavior and found that males and females visited their nests equally often (Tables 6, 7, 13). However, frequency of nest visits is only an indirect and sometimes incorrect measure of actual food delivery to nestlings (Royama 1966). Therefore, in 1977 I simultaneously watched the interior and exterior of four nests during the nestling stage via closed circuit television and with binoc-

TABLE 6

VISITS TO THE NEST BOX DURING NON-EXPERIMENTAL OBSERVATIONS[1]

Group	No. observ.	Visits/hour	
		Mean	Range
♂♂	107	6.1	0–19.1
♀♀	133	7.1	0–29.5

[1] Male vs female difference non-significant.

ulars, and saw 491 food deliveries. Males provided nearly all of the food to young and much of the food to females for the first few days after hatching, while females brooded. Thereafter, females provided about 60% of the items delivered to young. Large (>15 mm long) caterpillars (Lepidoptera) and grasshoppers (Orthoptera) were the most important prey given nestlings, comprising 27% and 33%, respectively, of the 491 feedings. They probably comprised more than 90% of the biomass given young because other prey items tended to be much smaller. Most of the other food items were unidentified, but spiders (Araneae) were sometimes seen. No sexual differences were found in the kinds of prey or relative abundances of different prey types delivered to nestlings when data were analyzed across the entire nestling stage, but temporary differences occurred at individual nests. For example, male 72 brought mostly grasshoppers to his 11 day old nestlings while female 72 brought a variety of very small, unidentified insects more frequently than grasshoppers. These results are similar to those of Royama (1966) on Great Tits (*Parus major*), and Hartshorne (1962) on Eastern Bluebirds (*S. sialis*).

Results from all years suggest that males and females feed young equally when the nestling stage is considered as a whole but that there is a division of labor in relative amounts of feeding during the brooding and post-brooding segments of that stage. This division of labor does not explain the origin(s) of sexual foraging differences in bluebirds because those 1977 males providing most of the food during the brooding period were not observed hover-foraging; thus, males do not automatically forage like females when they provide more food than females.

It is possible that part of the sexual foraging differences were ascribable to territorial males watching for intruding conspecifics. However, this probably accounted for only a small part of the sexual differences because the frequency of conspecific intrusion declined as the season progressed and never exceeded a few times per day. Intruding males almost always headed directly for nest sites where they attempted to investigate nest cavities and to display and where they were discovered irrespective of the mode of foraging or proximity to large perches of the residents. Unmated females were never observed intruding upon territories during the nestling periods except when males had lost their mates; thus, females probably did not intrude frequently enough to favor males that stayed on large perches and, thus, were better able to spot and copulate with them. Moreover, a female probably would not copulate unless she had a nest site of her own (Power and Doner 1980).

(4) The apparently equal hover-foraging ability of the sexes suggests that males' disproportionately high use of the area near-large-perches effectively forced females to use the area away-from-large-perches disproportionately often

and, thus, also to hover-forage disproportionately often in order to adequately feed offspring. Because hovering may require 4–8 times the energy perching does, any increase in the share of hover-foraging may cause at least short-term harm to females. The coupled possibilities of male coercion and female harm are consistent with the hypothesis that male exploitation causes sexual foraging differences (see below).

(5) The most obvious physical difference between the sexes is sexual dichromatism with brightly colored males and relatively dull colored females (Plates I–III). Sexual dichromatism is presumably the product of sexual selection (Darwin 1871). In the case of Mountain Bluebirds, I believe sexual dichromatism developed in the context of male-male competition for nest sites.

Sexual dichromatism is potentially important in bluebird foraging behavior. Although hovering females are conspicuous, they blend into the background when they alight during capture attempts. Females have bright blue wings and tails but mousey brown bodies (Plates II, III). When they fold their wings, their entire visual stimulus pattern changes abruptly and, to an untrained observer, confusingly; it is, then, very easy to lose track of them. Robinson (1969) described such sudden changes in visual stimuli as "flash patterns," stating that they are very common in insects heavily preyed upon by visually-oriented predators, particularly birds, and are effective in confusing these predators.

By contrast, males do not blend into the background when they alight while hover-foraging because their entire bodies are bright blue. Thus, males should be more vulnerable than females to visually-oriented predators, particularly hawks.

Because Mountain Bluebirds nest and forage in very open prairie-forest ecotone terrain (Plate IV), they are visible most of the time. This might make one think that plumage brightness is unrelated to predation, but the presence of bright plumage is not evidence against the importance of predation because defense against visually-oriented predators in open terrain does not entail hiding so much as maintaining a flight distance from predators.

Mountain Bluebirds spend most of their time on large perches whether foraging or not; this obviously protects them from ground predators and probably also provides some protection against approaching aerial predators. Perched bluebirds appear to spend a large amount of time observing the area outside the immediate vicinity where they make capture attempts, which suggests that they are alert for predators. Although conspicuous on perches, they are less conspicuous than when hovering or hawking simply because they are not in motion. Moreover, hovering birds direct their attention to what is immediately below them, having little time for searching a larger area. Also, hovering produces a turbulent air flow over birds' wings, probably reducing hearing ability temporarily (Griffin and Hopkins 1974). Birds on perches, because they are elevated, see farther than birds on the ground.

The pattern of sexual foraging differences, sexual dichromatism itself, and the inherently different risks in perch-foraging and hover-foraging all are consistent with the hypothesis that sexual selection has indirectly produced sexual foraging differences via differential predation on the sexes. The critical evidence required to support this hypothesis, predation on birds away-from-large-perches, especially males, was not obtained, but interactions between raptors and bluebirds suggested predation may be important even if somewhat irregular in occurrence.

Several species of raptor were observed at Calvert, and bluebirds showed different responses to them. Bluebirds always hid from Merlins (*Falco columbarius*) and Cooper's Hawks (*Accipiter cooperii*) but showed a more variable response to American Kestrels (*Falco sparverius*) and Marsh Hawks (*Circus cyaneus*). Kestrels and Marsh Hawks were common on the study tract but usually were ignored. On two occasions single kestrels chased adult bluebirds, but the bluebirds escaped by outmaneuvering their pursuers. Bluebirds in postbreeding flocks frequently hid when groups of ca. four kestrels flew over. I once saw a male bluebird intercept a male kestrel flying toward a fledgling bluebird and chase that kestrel about a km and out of sight. Several adult bluebirds were probably taken by kestrels as they emerged from their nest boxes in 1975–77 (Power 1980). Marsh Hawks were common in late summer following their dispersal from lower elevation nesting grounds. They usually were ignored by adult bluebirds although they once were implicated in the deaths of a group of fledglings (Power 1966) and probably can take juveniles and nonalert adult bluebirds by surprise (Helmut Mueller, pers. comm.).

Douglass Morse (pers. comm.) suggested that sexual dichromatism may have been important in bluebird foraging success, i.e., males may have perch-foraged more frequently than females when feeding nestlings because their brighter color makes them more conspicuous to prey, and hover-foraging would increase their conspicuousness. However, I doubt that differential visibility to prey was an important cause of sexual foraging differences because hovering females are about as conspicuous as hovering males; females are truly less conspicuous only when perched.

YEARLY CHANGES IN FORAGING BEHAVIOR

Few snowstorms occurred during the breeding seasons of 1970–72, years of high reproductive success at Calvert (Power 1974). During the years 1974–75, the weather was persistently cold and wet with frequent snowstorms; there was mass reproductive failure. These differences in climate and reproductive success coincided with differences in foraging behavior. Because the early and late years of the study were so different, they will be considered separately.

1970–1972

Frequency of perch-foraging, the most important foraging pattern during the first two stages of nesting, declined during the first brood nestling stage and remained low for the remainder of the season (Table 4). This seasonal decline was probably a function of the replacement of perch-foraging by hover-foraging during the two nestling stages, and the increased importance of ground-foraging during some of the later stages. Perch-foraging was the most important pattern for males during the early stages of nesting partly because it was staged from trees, fences, etc., all of which were used as song perches in territorial displays. One reason perch-foraging was important for both males and females early in the breeding season was that large perches provide good positions from which to scan the ground for prey; this was especially important when days were generally cool and overnight frosts common, making insects both less abundant and less active than later in the year. A second reason was that grass was longer during the first brood incubation and nestling stages than later in the year. This strongly interfered with good horizontal visibility from ground staging points but affected visibility from perches to a lesser degree.

As the season progressed, perch-foraging generally was replaced by ground-foraging except when birds had second broods. This accompanied a reduction of grass height from trampling and grazing, and the formation of family groups and postbreeding flocks. Flocks probably reduced the need for individual birds to constantly watch for predators, so the role of large perches as lookout posts declined. The importance of ground-foraging during the fledgling stage and its replacement by perch-foraging during the second brood incubation stage may have been related to the training of young birds. Fledglings depended entirely on their parents for food for the first few days out of the nest. As soon as they could, they followed their parents about, begging frequently and imitating the actions of their parents, quickly learning to ground-forage. Parents fed near-large-perches during most of this time (Table 3) whether ground-foraging or perch-foraging, possibly to reduce predation risk for their following fledglings as well as for themselves.

During the second brood incubation period, females tended their eggs, leaving the care of first brood fledglings entirely to males. Males acted as much like shepherds as like food-providers during that stage. They were frequently harassed by begging fledglings that seemed fully capable of feeding themselves. Males fed themselves mostly by perch-foraging (Table 4), but fledglings continued to ground-forage. Females also fed themselves by perch-foraging, possibly to provide themselves some protection against predation; they foraged singly, so there were no accompanying birds to act as lookouts. Contrarily, males probably perch-foraged frequently during this time because they acted as lookouts for fledglings, they escaped some harassment from fledglings by removing themselves to perches, and their increased use of perch-foraging appeared to stimulate fledglings to begin perch-foraging.

During the second brood nestling stage, first brood fledglings were driven away by their parents. Adults foraged similarly during both first and second brood nestling stages except for the increased frequency of flycatching and hawking during the second (Table 4) that paralleled the relative abundance of flying insects during the warm days of late June and July.

Perch-foraging/hover-foraging was always rare, its use bearing no obvious relationship to changes of environment or food demand (Table 4). Many changes in frequency of use of staging points throughout the breeding season (Table 5) followed changes in use of particular foraging patterns and the areas near- and away-from-large-perches. To some extent trees and fence lines, but especially trees and fence posts, were mutually exchangeable as staging points in foraging behavior. The combined fluctuations in the use of trees and fences tended to follow fluctuations in the frequency of perch-foraging, the pattern most often staged from them. Why use of utility lines fluctuated was not apparent from non-experimental observations, but the 1972 experiment provided some insight into this (see below).

1974–1975

The area away-from-large-perches was used more commonly during the fledgling and postbreeding flock stages in 1974–75 than it was in 1970–72 (Table 3). This was probably due to colder, wetter weather in 1974–75, and more observation may have more accurately depicted use of that area.

Birds mostly perch-foraged, especially during the fledgling stage (Table 4). Perch-foraging was more common in 1974–75 than 1970–72 (Table 4) because all pairs with fledglings in 1974–75 had territories with high numbers of perches, and postbreeding flocks roamed among places with many perches. Perch-foraging declined during the postbreeding flock stage because birds frequently ground-foraged in groups on the county road. Prey from adjacent grassland was blown in by almost constant wind, and exposed on the road surface. Birds probably were relatively safe on roads during this stage because flock members could warn one another of approaching danger.

The use of different staging points, of course, coincided with the use of different foraging patterns (Table 5). Trees were used more frequently during the fledgling stage than during the postbreeding flock stage while fences were used more frequently during the latter because families used trees on or near their territories whereas postbreeding flocks centered their activities on roadways and their bordering fences. Hay bales were ephemeral but important large perches on some territories during the fledgling stage. Bales were unavailable to postbreeding flocks because they had been picked up and stacked. Utility lines were of variable use as staging points depending on their availability. For example, they were less available to postbreeding flocks than to birds with fledglings because the stretch of road most frequented by flocks did not have an adjacent utility line.

Males and females did not differ in their foraging behavior during the fledgling and postbreeding flock stages of 1974–75 except in the use of staging points during the fledgling stage (Table 4), and that may not have been biologically significant. Males used bales and utility lines more often than females, but I believe these differences represent individual idiosyncrasies rather than sexual characteristics. Female 41 foraged less frequently than her mate and fledglings who frequently staged foraging patterns from bales; this resulted in underrepresentation of female use of bales. Similarly, male 64a in 1975 frequently foraged from a utility line above his well-hidden fledglings while his mate was hardly seen for the first week after fledging.

CHAPTER 4

DESIGN OF THE WORK LOAD EXPERIMENTS

Three experiments were run in 1972 to test hypotheses deriving from observations in 1970–71 and proposed to explain the evolution of bluebird sexual foraging differences. Because changes in foraging and sexual foraging differences coincided with the nestling stages, it was reasonable to suppose that some proximate factor of the increased work load associated with those stages, especially feeding nestlings, was responsible for both. Alternatively, it was possible that some factor(s) other than increased work load, but associated with the presence of nestlings, was responsible.

EXPERIMENT I

The first experiment was designed to test the importance of work load by comparing the behavior of birds with high and low work loads. Seventy-six birds were divided into two groups of 19 pairs each. Pairs in the first group had broods of five (1 pair) and six (18 pairs) young, in the second group, broods of three. Brood size was established within the first week of each nestling period, usually within the first three days. Broods designated for the first group were examined but left intact, while broods designated for the second group were reduced to three young. Nests were assigned alternately to each group on the basis of hatching date to eliminate temporal differences between groups. Brood sizes of six and three were chosen because they were the normal upper limit to brood size and half that limit, respectively (Power 1974). Eggs or young could have been added to establish broods of more than six young, but that would have required trading eggs or young between nests in which incubation had begun on the same day to prevent mixing of different aged young. This was not practical, for nesting synchrony was not exact.

The choice of broods for the two groups imparted a bias into the experiments, i.e., broods of six young were unmolested, but the almost equally common broods of five were in all but one case reduced to three. This had the advantage of maximizing difference in brood size (six vs three rather than five vs three), but the disadvantage of preselecting birds to have large and small broods. This preselection was justifiable in terms of the aims of the experiments because it had the effect of making *a priori* judgments of foraging behavior more difficult to realize, as shown by the following argument.

It is reasonable to suppose that birds try to match their brood size to the number of young a territory can support if Lack (1968) is right in concluding that food ultimately controls clutch size. Thus, birds with five young can be expected, on average, to inhabit poorer territories than birds with six, other things equal. (Even if birds with smaller clutches are younger, they are still likely to inhabit poorer quality territories because their inexperience should make them inferior competitors for territories.) Comparing birds with presumably high quality territories (those with six young) to those with low quality territories (those with three young) made it more difficult for predictions of differences between groups to be demonstrated because the comparison tended to minimize differences in effective work load. Effective work load can be thought of as proportional to the ratio of food need to food availability. Large broods have higher work loads because the food need, expressed in number of young, is higher even if food availability is equal between groups. By the same reasoning, birds with small broods can have higher effective work loads than would be predicted solely on the basis of number of young if the food availability per nestling is lower than with large broods. Because the operating hypothesis of the first experiment was that the behavioral changes characteristic of the nestling stage and the degree of sexual dimorphism in those changes increases with greater work load, then tending to equalize work load by including mostly birds with territories of lower food availability in the group of birds with smaller broods would tend to counter realization of the predictions. Thus, if the predictions were still met despite this bias, then the hypothesis from which they derived would be strongly supported.

The behavior of adults at all nests was observed on both the 10th and 11th days of nestling life for periods of 30–60 min per nest per day. Length of observation time was determined by the number of pairs observed per day. Results were compared between groups for each sex and between sexes for each group.

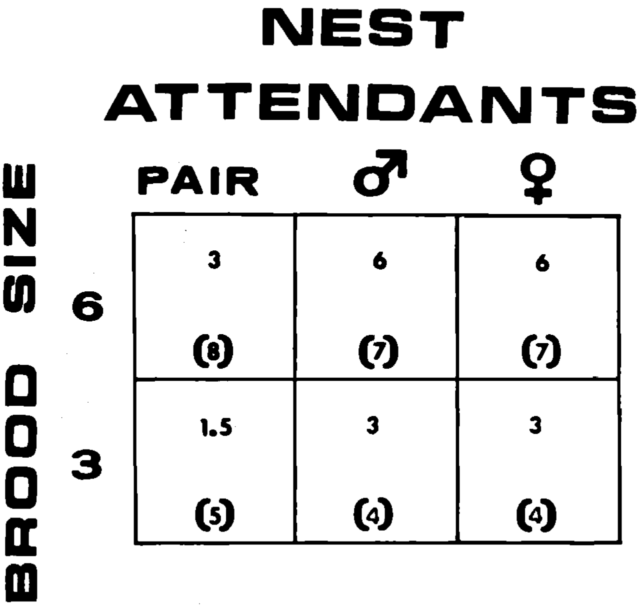
EXPERIMENT II

The second experiment was designed to sort out four possible factors of work load (given that the first experiment showed that work load was involved) and three possible explanations of sexual foraging differences during the nestling periods. The work load factors were the following: (1) Total number of nestlings, i.e., brood size; this is a measure of the work load per pair. (2) Number of nestlings per attendant adult, i.e., the brood size divided by the number of adults present; this is a measure of the work load per parent, given that each parent works equally hard. (3) Number of adults per territory, i.e., the number of adults attending young, one bird or two. (4) Total number of birds per territory, including young and adults.

The second experiment was built upon the first by collection of certain adults and banding of young on the 12th day of nestling life (see Fig. 3) or as quickly thereafter as possible (never later than Day 14). At 13 nests, young were banded, but no adults were collected. Seven of these nests had six young, and six nests had three young. At another 13 nests, females were collected and young banded leaving only males to care for young. Six of these nests had six young, and seven nests had three. At the remaining 12 nests, males were collected and young banded leaving only females to care for young. Six of these nests had six young, and six had three young.

Day 12 of nestling life was chosen for manipulations because flight feathers were unsheathed by then in most nestlings, an event probably signaling achievement of thermoregulation (Dawson and Evans 1960). It was important that nestlings be able to thermoregulate following loss of their mothers because males do not brood (Power 1966, unpubl. data). If females brooded following day 12 but males did not, and females succeeded in rearing their young but males did not, then differences in success might be solely attributable to sexual differences in brooding regimes. Nest failure by males following day 12 also would have detracted from the sample of male behavior. Thus, manipulations were performed on day 12 in order to maximize the chances of success by unpaired males, thereby allowing a strong basis for intergroup and intersexual comparison.

Day 12 manipulations produced four different series of work load, one for each



NEST ATTENDANTS

BROOD SIZE	PAIR	♂	♀
6	3 (8)	6 (7)	6 (7)
3	1.5 (5)	3 (4)	3 (4)

Fig. 3. Complete block design of work load Experiment II. Number and sex of nest attendants are indicated across the top of the block, brood size along the side. The upper number in each square indicates the number of young per attendant adult. The lower number (in parentheses) indicates the total number of birds per territory.

possible factor. The first series, total number of nestlings (3 or 6), collapsed the six groups of the second experiment to the two of the first experiment. The second series, number of nestlings per attendant adult, followed levels from 1.5 to 3 to 6 young per attendant adult. The third series, number of adults per territory, proceeded from 1 to 2 adults per territory. The last series, total number of birds per territory, ranged from 4 to 5 to 7 to 8 birds per territory. None of these series overlapped (see Fig. 3), making it possible to separate the factors by noting which series birds actually followed in their foraging behavior.

The second experiment was also designed to test the (1) intersexual food competition, (2) sexual dichromatism-differential predation, and (3) male exploitation hypotheses of sexual foraging differences. The logic of these tests is better explained during consideration of the experimental results.

Adult behavior at each nest was observed on the first two days following collecting (if any) and banding for 30–60 min per nest per day. Results were compared between sexes within groups and between groups for each sex.

EXPERIMENT III

The third experiment was designed to test the effects of mate loss on foraging behavior. Testing was done by comparing the behavior of birds before and after the day 12 manipulations. The first experiment provided the "before" data, the second provided the "after" data.

Although comparison of paired and unpaired adults in the second experiment measured the importance of having or not having a mate, the results were influenced by the small number of adults in each group and the fact that each bird resided on a different territory. By comparing the behavior of individual birds before and after mate loss, differences in territory between birds were controlled.

LIMITED SAMPLE SIZE

The sample size of only 38 pairs in the experiments of 1972 may seem small. Sample size was limited by the number of pairs that could be visited on any day. I found that I could visit no more than 11 pairs per day because of the wide geographic distribution of nests. This, the relative synchrony of nesting in 1972, and the progression of the breeding season prevented inclusion of more than 38 first brood nests. Birds at second brood nests were omitted to avoid seasonally produced habitat and prey differences.

METHOD OF PRESENTATION OF EXPERIMENTAL RESULTS

Foraging behavior was complex and, therefore, divided into the many categories of the foraging event for analysis (see Chapter 2). Because an account of all results of the work load experiments presented as components of the foraging event would almost certainly exhaust the reader (see Power 1974), I have grouped the results most important for understanding the outcome of the experiments into a single parameter, "high cost score." This parameter has an ordinal level value indicating relative work output by showing the relative energy expenditure of birds in different experimental groups during foraging; it also may reflect relative predation risk.

High cost score incorporates birds' use of aerial staging points and tall vegetation in a manner similar to the way grade point average (G.P.A.) incorporates results of student performance in different academic subjects. High cost score is easily understood by a brief consideration of the familiar G.P.A. Because G.P.A. lumps qualitatively different categories, it is intrinsically limited to an ordinal level of measurement. A student with a G.P.A. of 3.8 cannot be said to have performed better than a student with a G.P.A. of 3.7 because of the inherent inaccuracy of combining grades from subjects as different as political science and mathematics. Nor can a student with a G.P.A. of 3.7 be said to have performed better than a student with a G.P.A. of 3.0 by exactly the same amount that a student with a G.P.A. of 3.0 could be said to have performed better than a student with a G.P.A. of 2.3 despite the fact that the difference is 0.7 in each case. And G.P.A. becomes a very poor performance indicator when compared between students sharing no courses in common or attending different schools. Nevertheless, educators find that students with similar educational experiences widely separated in G.P.A. are usually truly different in academic performance and, therefore, that G.P.A. can be a useful partial measure of student performance when used carefully.

I chose use of aerial staging points as an indicator of energy expenditure because it includes all of the most energy-costly behaviors: hover-foraging, hawking, and attempts at those behaviors (Tables 17, 18). Use of aerial staging points also may indicate increased predation risk because birds hover-forage from those points and, thus, reduce their ability to detect approaching aerial predators; they also increase their vulnerability while capturing prey on the vegetation or ground.

I chose use of tall vegetation as a cost indicator because birds almost always avoided it even when it was abundant very close to the nest and contained more prey than short vegetation. Costs of using tall vegetation seemed to include reduced ability to see predators and prey, easier ability of prey to escape, and impeded movement. All but the first of these costs should have increased rate of energy expenditure, and the first should have increased predation risk. Bluebirds may be subject to effective ambushers when foraging in tall vegetation. For example, I occasionally have flushed Long-tailed Weasels (*Mustela frenata*) from tall grass where they were nearly invisible.

High cost scores for each experimental group were calculated by (1) ranking each group separately for use of aerial staging points and tall vegetation according to each group's percentage use of each type, (2) clustering groups when statistically they were not significantly different in use of each type, thereby reducing the number of ranks below the number of groups, (3) assigning values to each group according to its rank so that the groups using each type most frequently received the highest value for that parameter, and (4) adding values between groups to generate scores. High cost scores were then plotted against some factor of work load to visually relate behavior to work load.

An artificial example illustrates the scoring procedure. Imagine 2 categories of behavior, A and B, and 3 groups of birds, 1, 2 and 3. Suppose that the groups could be ranked (Raw Group Rank) 2, 1, 3 in use of A, and 1, 3, 2 in use of B. Further suppose that groups 1 and 2 did not differ significantly in use of A, and groups 2 and 3 did not differ significantly in use of B. Groups would then be reclustered (Significant Group Rank):

Behavior	Raw Group Rank	Significant Group Rank
A	2 > 1 > 3	(2,1) > 3
B	1 > 3 > 2	1 > (3,2)

Values reflecting significant ranks would then be assigned:

Behavior	Group	Value
A	1	2
	2	
	3	1
B	1	2
	2	1
	3	

Addition of values between behaviors would generate the scores:

Group	Group Values (A + B)	Score
1	2 + 2	4
2	2 + 1	3
3	1 + 1	2

The scores, representing behavioral output from greatest (4) to least (2), would then be plotted against some appropriate parameter.

As with G.P.A., these scores are purely ordinal. Although 4 > 3 > 2, one cannot say that 4 > 3 by exactly the amount 3 > 2 despite the fact that the difference in each case is 1. Moreover, the scores themselves reflect both the number of significant ranks in each behavior and the number of behaviors considered. Scoring according to 3 behaviors rather than 2, or according to 5 groups rather than 3, would automatically increase the numerical value of each score. Thus, scores cannot be compared according to their numerical value between experiments having different numbers of behaviors or groups, e.g., between experiments 1 and 2 having 4 and 8 groups, respectively.

It is important for the reader to note that high cost scores are plotted to visually summarize the outcome of experiments but that the outcomes themselves were determined by minute examination of each data table. Therefore, close scrutiny of the data will generate the same conclusions as perusal of the figures.

CHAPTER 5

EXPERIMENT I: BROOD SIZE AND WORK LOAD

The purpose of the first experiment was to determine whether the behavioral changes characterizing both males and females during the nestling periods were functions of work load. Two levels of work load were established by manipulating brood size. Nineteen nests had broods of five or six young, and 19 nests had three young. Adults at each nest were observed on the 10th and 11th day of nestling life.

PARENTAL CARE

As in 1970, males and females visited their nests equally often regardless of brood size, but birds with small broods visited less often than birds with large broods (Table 7). The lower number of visits per hour with reduced brood size was statistically significant for females ($p < 0.001$) and almost significant for males ($p = 0.057$). That males with small broods really did make fewer visits than males with large broods was indicated by the absence of significant intersexual differences at each brood size.

Although fecal sac removals per hour declined with reduced brood size, this decline was not statistically significant (Table 8). Nor were any intersexual differences significant at either brood size. The effect of similar amounts of nest sanitation at both brood sizes was evident, i.e., birds with large broods tended to leave filthy, dung encrusted nests after fledging whereas birds with small broods tended to leave fairly clean nests.

PROBLEM BIRDS

Analysis of foraging behavior results was difficult because of the peculiar nature of the territories of pairs 42 and 43, birds with small broods. Their territories consisted exclusively of strips of growing hay alternating with fallow field. Except for a utility line, upon poles of which boxes 42 and 43 were placed, no large perches existed in these territories. Consequently, nearly all foraging was done away-from-large-perches, most of it in fallow field. This caused an overestimation of use of the area away-from-large-perches by males with small broods. It also produced a bias in the opposite direction for females with small broods because I more frequently lost view of them against the brown background of fallow earth.

Had I omitted pairs 42 and 43 from analysis, I still would have had 17 of 19 pairs in the group of birds with small broods. However, the foraging behavior of these birds was otherwise similar to that of other birds with small broods, and, as both pairs chose their territories, the information cannot be discarded. I therefore have compromised by including observations on these pairs in all data tables, but pointing out in the text changes in the outcome of analysis contingent upon omitting these pairs from analysis.

FORAGING BEHAVIOR

Females with large broods were away-from-large-perches more often than males with large broods or females with small broods (Table 9). When pairs 42 and 43 were left in the analysis, males with small broods were away-from-large-perches as often as males with large broods, and males with small broods were

TABLE 7

VISITS TO THE NEST BOX IN EXPERIMENT I

Group[1]	No. observ.	Visits/hour		Intergroup comparisons[2]
		Mean	Range	
♂♂LB	117	5.9	0–30.0	♂♂LB vs ♀♀LB
♀♀LB	139	5.8	0–14.5	♂♂LB vs ♂♂SB†
♂♂SB	61	3.4	0–9.5	♂♂SB vs ♀♀SB
♀♀SB	56	3.4	0–15.0	♀♀LB vs ♀♀SB**

[1] LB = birds with large broods; SB = birds with small broods.

[2] Differences between groups non-significant unless noted; ** = $p < 0.01$; † = $p = 0.057$.

TABLE 8

FECAL SAC REMOVALS IN EXPERIMENT I[1]

Group[2]	No. observ.	Removals/hour	
		Mean	Range
♂♂LB	18	0.7	0–3.6
♀♀LB	30	1.3	0–8.0
♂♂SB	8	0.5	0–3.0
♀♀SB	12	0.7	0–2.6

[1] All intergroup differences non-significant.

[2] LB = birds with large broods; SB = birds with small broods.

TABLE 9

PROXIMITY OF FORAGING BIRDS TO LARGE PERCHES IN EXPERIMENT I

Group[1]	NLP[2]	AFLP	Intergroup comparisons[3]
♂♂LB	187 (68)[4]	87 (32)	♂♂LB vs ♀♀LB***
♀♀LB	176 (53)	158 (47)	♂♂LB vs ♂♂SB
♂♂SB	148 (67)	74 (33)	♂♂SB vs ♀♀SB*
♀♀SB	145 (78)	42 (22)	♀♀LB vs ♀♀SB***

[1] LB = birds with large broods; SB = birds with small broods.

[2] NLP = near-large-perches; AFLP = away-from-large-perches.

[3] Differences between groups non-significant unless noted; * = $p < 0.05$; *** = $p < 0.001$.

[4] Number (%).

TABLE 10

USE OF FORAGING PATTERNS IN EXPERIMENT I

Group[1]	PF[2]	PF/HF	GF	HF	Fly	Ha
♂♂LB	137 (48)[3]	3 (1)	51 (18)	58 (20)	34 (12)	3 (1)
♀♀LB	130 (38)	3 (1)	77 (22)	115 (33)	18 (5)	1 (1)
♂♂SB	116 (50)	1 (1)	44 (19)	27 (12)	39 (17)	6 (2)
♀♀SB	103 (55)	0 (0)	30 (16)	23 (12)	31 (16)	2 (1)

Intergroup Comparisons[4]

♂♂LB vs ♀♀LB***	♂♂SB vs ♀♀SB
♂♂LB vs ♂♂SB*	♀♀LB vs ♀♀SB***

[1] LB = birds with large broods; SB = birds with small broods.

[2] PF = perch-foraging; HF = hover-foraging; GF = ground-foraging; Fly = flycatching; Ha = hawking.

[3] Number (%).

[4] Difference between groups non-significant unless noted; * = $p < 0.05$; *** = $p < 0.001$.

TABLE 11

USE OF STAGING POINTS IN EXPERIMENT I

Group[1]	Tree	UL[2]	Fence	SP[2]	Rock	Ground	Aerial
♂♂LB	59 (11)[3]	31 (6)	195 (38)	26 (5)	17 (3)	69 (13)	116 (23)
♀♀LB	66 (11)	41 (7)	165 (27)	39 (6)	8 (1)	91 (15)	199 (33)
♂♂SB	59 (15)	48 (12)	124 (32)	14 (4)	19 (5)	63 (16)	59 (15)
♀♀SB	62 (19)	85 (27)	68 (21)	14 (4)	13 (4)	33 (10)	45 (14)

Intergroup Comparisons[4]

♂♂LB vs ♀♀LB*** ♂♂SB vs ♀♀SB***

♂♂LB vs ♂♂SB*** ♀♀LB vs ♀♀SB***

[1] LB = birds with large broods; SB = birds with small broods.

[2] UL = utility line; SP = small plant.

[3] Number (%).

[4] Differences between groups significant; *** = $p < 0.001$.

away-from-large-perches significantly more often than their mates. Omission of these pairs resulted in males with large broods being away-from-large-perches significantly more often than males with small broods ($p < 0.05$) and eliminated the intersexual difference at small broods.

Females with large broods hover-foraged more often and flycaught and perch-foraged less often than their mates (Table 10). Males and females with small broods used foraging patterns equivalently. Birds with large broods used all foraging patterns more frequently than birds with small broods. They also hover-foraged in greater proportion but flycaught in lesser proportion than birds with small broods. Additionally, females with large broods ground-foraged in greater proportion but flycaught less frequently than females with small broods; these differences, like those in hover-foraging between brood sizes, reflected greater use of the area away-from-large-perches by females with large broods.

Females with large broods used aerial staging points more often but fences less often than their mates (Table 11). This correlated with their respective reliances on hover-foraging and perch-foraging. Females with small broods used trees and utility lines more often but fences and ground positions less often than their mates. This was associated with more frequent ground-foraging by males than females with small broods, itself a reflection of observations on pairs 42 and 43. Birds with large broods used fences and aerial positions significantly more often

TABLE 12

USE OF VEGETATION OF DIFFERENT HEIGHTS IN EXPERIMENT I[1]

Group[2]	Short[3]	Tall[4]
♂♂LB	163 (81)[5]	37 (19)
♀♀LB	225 (78)	64 (22)
♂♂SB	110 (79)	29 (21)
♀♀SB	78 (74)	27 (26)

[1] All intergroup differences non-significant.

[2] LB = birds with large broods; SB = birds with small broods.

[3] Column "Short" combines data from columns "Bare" and "Rock" in Table 21, and column $G \leq T$ in Table 22 of Power (1974).

[4] Column "Tall" combines data from columns $T < G \leq S$, $S < G \leq H$, and $H < G$ in Table 22 of Power (1974).

[5] Number (%).

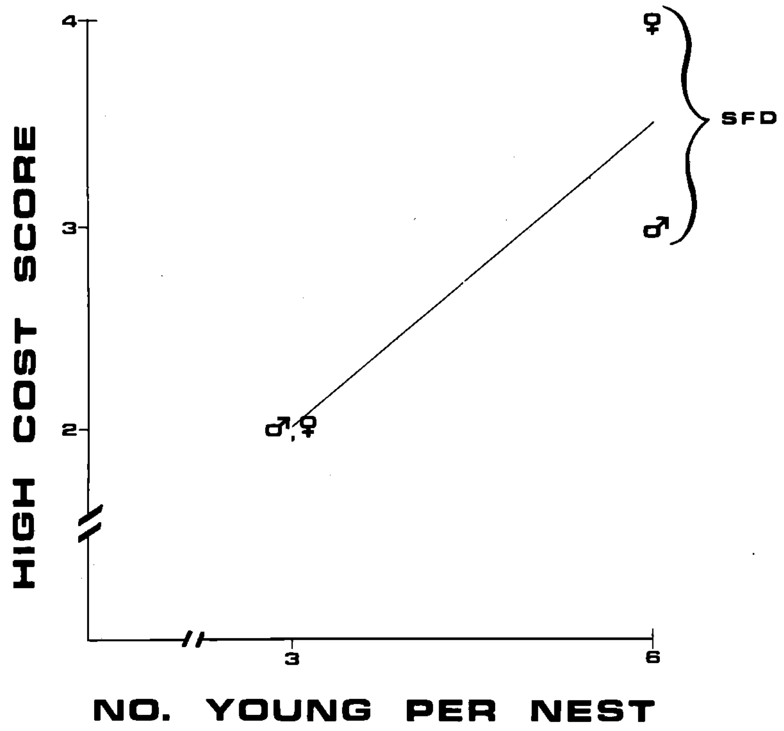


Fig. 4. High cost scores in work load Experiment I. Pairs with small broods (lower left) had lower scores than pairs with large broods (upper right) and showed no sexual dimorphism in use of costly behaviors. Females with large broods used aerial staging points significantly more often than their mates, creating a sexual difference in use of costly behaviors indicated as SFD (for sexual foraging difference) on the figure.

than birds with small broods but utility lines and trees less often. Differences in use of fences and aerial positions reflected the greater foraging effort of birds with large broods. Differences in use of utility lines and trees reflected the more frequent occurrence of lines on territories of birds with small broods and the smaller food need of their young.

Birds most often foraged in short vegetation or barren places irrespective of sex or brood size (Table 12). That birds chose to forage in those places was shown by the fact that they frequently foraged in small spots of short vegetation or barren ground in the midst of the more widely distributed tall vegetation.

High Cost Scores

A comparison of the use of aerial staging points (Table 11) by the 4 groups of birds in the first experiment shows that males and females with small broods (SB) did not differ statistically but that males and females with large broods (LB) did. Thus, the 4 groups collapse to 3 and have this descending order of use of aerial staging points: ♀♀ LB > ♂♂ LB > (♂♂ SB = ♀♀ SB). The groups are assigned values of 3, 2 and 1, respectively, for their use of aerial staging points.

Table 12 shows that no group was significantly different statistically from any other in use of tall vegetation; thus, each is assigned a value of 1. High cost scores were obtained by adding values for each group across both parameters, giving results of 4 for ♀♀ LB, 3 for ♂♂ LB, and 2 for both ♀♀ SB and ♂♂ SB. These scores are plotted in Figure 4, showing (1) equivalence of costly behavior for birds with small broods, (2) greater costs for birds with large broods, and (3) greater costs for females with large broods than their mates.

CONCLUSION

These results support the hypothesis that increased work output by both males and females was produced by increased work load. The results do not suggest which of several possible factors of work load were important or why sexual dimorphism in work output occurred.

CHAPTER 6

EXPERIMENT II: WORK LOAD FACTORS AND CAUSES OF SEXUAL FORAGING DIFFERENCES

The purpose of the second experiment was to separate four factors of work load potentially accounting for changes in foraging behavior, and three possible causes of sexual foraging differences during the nestling stages. The four work load factors were separated by making a series of predictions regarding response to work load:

(1) If number of adults per territory is crucial, then response to increasing work load (as measured by high cost scores) should increase from unpaired to paired adults (Fig. 7A).

(2) If total number of birds per territory is crucial, then response to increasing work load should follow the gradient from 4 to 5 to 7 to 8 birds per territory (Fig. 7B).

(3) If total number of nestlings is crucial, then response to increasing work load should increase from 3 to 6 nestlings per nest (Fig. 7C).

(4) If number of nestlings per attendant adult is crucial, then response to increasing work load should follow the gradient from 1.5 to 3 to 6 young per attendant adult (Fig. 7D).

The design of the second experiment mixed these factors in such a way that no two series of expected results would overlap, making it possible to separate the factors. Of course, if more than one factor is important, response to increasing work load may follow more than one gradient.

The three possible causes of sexual foraging differences also were separated by making a series of predictions regarding response to work load:

(1) The importance of intersexual competition is shown if number of adults per territory is an important factor of work load because such competition is possible with paired birds occupying the same territory but not with single birds.

(2) The importance of sexual dichromatism is shown if males that forage like females suffer a higher rate of predation than males that forage in a typical manner *provided* that appropriate predators can be made to respond to the manipulations of the work load experiments. Because I had no means of directly manipulating predator behavior, only a positive outcome (predation) would be interpretable in terms of the hypothesis. A negative outcome (absence of predation) could mean either that sexual dichromatism is irrelevant to predation risk (rejection of the hypothesis), or that predators simply failed to respond to manipulations only indirectly affecting them. For example, alternative prey may have been abundant at the time of the experiments, eliminating any incentive for predators to prey upon bluebirds irrespective of bluebird foraging behavior.

(3) The importance of male exploitation is shown if evidence is obtained of male coercion, consequent damage to females, and consequent male gain. Male coercion is shown if paired females work harder than unpaired females with the same work load, if paired females work harder than paired males with the same work load, if unpaired males work harder than paired males with the same work load, and if unpaired males and females with the same work load work equally hard. All four criteria must be met in order to avoid the possibility that unequal

TABLE 13
VISITS TO THE NEST BOX IN EXPERIMENT II

Group[1]	No. observ.	Visits/hour	
		Mean	Range
P♂♂LB	51	5.8	0–12.4
P♀♀LB	60	6.6	0–22.0
P♂♂SB	25	4.5	0–18.6
P♀♀SB	24	4.3	0–8.6
U♂♂LB	94	14.1	6–26.9
U♀♀LB	76	11.1	0–20.6
U♂♂SB	71	13.3	4–36.0
U♀♀SB	34	5.8	1.9–14.7

Intergroup Comparisons[2]

Paired vs Paired	P♂♂LB vs P♀♀LB	Paired ♂♂ vs Unpaired ♂♂	P♂♂LB vs U♂♂LB***
	P♂♂LB vs P♂♂SB		P♂♂LB vs U♂♂SB*
	P♂♂SB vs P♀♀SB		P♂♂SB vs U♂♂LB***
	P♀♀LB vs P♀♀SB		P♂♂SB vs U♂♂SB**
Unpaired vs Unpaired	U♂♂LB vs U♀♀LB	Paired ♀♀ vs Unpaired ♀♀	P♀♀LB vs U♀♀LB
	U♂♂LB vs U♂♂SB		P♀♀LB vs U♀♀SB
	U♂♂SB vs U♀♀SB		P♀♀SB vs U♀♀LB*
	U♀♀LB vs U♀♀SB		P♀♀SB vs U♀♀SB

[1] P = paired (i.e., mated) birds; U = unpaired (i.e., mate-less) birds; LB = birds with large broods; SB = birds with small broods.

[2] Differences between groups non-significant unless noted; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

work by males and females derives wholly from causes other than male coercion. Damage of females might be inferred from the demonstration of their working harder consequent to coercion, but it is more rigorous to require an independent criterion of damage, e.g., weight loss.

High cost score is an appropriate index of how hard birds work because it measures cost, including relative energy expenditure. I used it to test for male coercion. Subsequent to the work load experiments, I measured male and female weights successively through the nestling stage to try to obtain evidence of damage to females (see Chapter 9).

The 76 birds at the 38 nests of the first experiment were divided into 6 groups for the second experiment by collection of 1 adult at each of 25 nests on day 12 of the first brood nestling period. This left 51 birds or 13 pairs and 25 unpaired birds. Of the unpaired birds, 13 were males and 12 were females. Half of the paired and unpaired birds had large broods while the other half had small broods.

PARENTAL CARE

There were no statistically significant differences within groups of paired or unpaired birds in the frequency of box visits (Table 13) although birds with large broods visited their nests more often. When the frequencies of box visits were compared between groups of unpaired and paired birds, unpaired birds visited their nests significantly more often in most cases. In only one case (unpaired females with small broods) did a group of unpaired birds show a lower number of box visits per hour than any of the groups of paired birds.

In frequency of fecal sac removal, the different groups were statistically indistinguishable with one exception. Paired males with small broods were never ob-

TABLE 14
FECAL SAC REMOVALS IN EXPERIMENT II

Group[1]	No. observ.	Removals/hour	
		Mean	Range
P♂♂LB	7	0.8	0–3.9
P♀♀LB	8	0.8	0–3.9
P♂♂SB	0	—	—
P♀♀SB	4	0.7	0–4.3
U♂♂LB	12	1.5	0–5.0
U♀♀LB	11	1.1	0–4.2
U♂♂SB	6	1.4	0–6.0
U♀♀SB	7	1.0	0–2.7

Intergroup Comparisons[2]

Paired vs Paired	P♂♂LB vs P♀♀LB	Paired ♂♂ vs Unpaired ♂♂	P♂♂LB vs U♂♂LB
	P♂♂LB vs P♂♂SB*		P♂♂LB vs U♂♂SB
	P♂♂SB vs P♀♀SB		P♂♂SB vs U♂♂LB**
	P♀♀LB vs P♀♀SB		P♂♂SB vs U♂♂SB**
Unpaired vs Unpaired	U♂♂LB vs U♀♀LB	Paired ♀♀ vs Unpaired ♀♀	P♀♀LB vs U♀♀LB
	U♂♂LB vs U♂♂SB		P♀♀LB vs U♀♀SB
	U♂♂SB vs U♀♀SB		P♀♀SB vs U♀♀LB
	U♀♀LB vs U♀♀SB		P♀♀SB vs U♀♀SB

[1] P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.
[2] Differences between groups non-significant unless noted; * = $p < 0.05$; ** = $p < 0.01$.

served removing fecal sacs and, thus, had a significantly lower rate of removal than other groups except for their mates (Table 14). However, the frequencies of fecal sac removal were very low for all groups, suggesting that group differences may not be very meaningful.

FORAGING BEHAVIOR

There were no statistically significant intersexual differences among paired birds at either brood size in proximity-to-large-perches (Table 15). Paired birds with large broods were away-from-large-perches significantly more often than paired birds with small broods. Unpaired males with large broods and unpaired females with small broods were both away-from-large-perches significantly more often than unpaired females with large broods. Other comparisons between groups of unpaired birds revealed no statistically significant differences in frequency of foraging away-from-large-perches. All groups of unpaired males were away-from-large-perches significantly more often than all groups of paired males. The only significant difference between paired and unpaired females was that unpaired females with small broods were away-from-large-perches more often than paired females with small broods.

Paired females with large broods hover-foraged and flycaught more frequently than their mates but perch-foraged less often (Table 16). There were no significant intersexual differences for paired birds with small broods. Paired males with large broods flycaught less often than paired males with small broods. Paired females with large broods hover-foraged more often than paired females with small broods. Unpaired females with large broods flycaught more frequently than unpaired males with large broods but perch-foraged less often. Unpaired males and

TABLE 15

PROXIMITY OF FORAGING BIRDS TO LARGE PERCHES IN EXPERIMENT II

Group[1]	NLP[2]	AFLP[2]	Group	NLP	AFLP
P♂♂LB	84 (84)[3]	17 (16)	U♂♂LB	171 (74)	60 (26)
P♀♀LB	50 (79)	13 (21)	U♀♀LB	137 (86)	23 (14)
P♂♂SB	105 (91)	10 (9)	U♂♂SB	116 (73)	42 (27)
P♀♀SB	92 (91)	9 (9)	U♀♀SB	61 (70)	26 (30)

Intergroup Comparisons[4]

Paired vs Paired	P♂♂LB vs P♀♀LB	Paired ♂♂ vs Unpaired ♂♂	P♂♂LB vs U♂♂LB*
	P♂♂LB vs P♂♂SB*		P♂♂LB vs U♂♂SB**
	P♂♂SB vs P♀♀SB		P♂♂SB vs U♂♂LB***
	P♀♀LB vs P♀♀SB***		P♂♂SB vs U♂♂SB***
Unpaired vs Unpaired	U♂♂LB vs U♀♀LB**	Paired ♀♀ vs Unpaired ♀♀	P♀♀LB vs U♀♀LB
	U♂♂LB vs U♂♂SB		P♀♀LB vs U♀♀SB
	U♂♂SB vs U♀♀SB		P♀♀SB vs U♀♀LB
	U♀♀LB vs U♀♀SB***		P♀♀SB vs U♀♀SB***

[1] P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.
[2] NLP = near-large-perches; AFLP = away-from-large-perches.
[3] Number (%).
[4] Differences between groups non-significant unless noted; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

females with small broods showed no significant differences in foraging behavior. Both unpaired males and unpaired females with small broods hover-foraged more often than their unpaired counterparts with large broods. Paired and unpaired males with large broods did not differ significantly, but unpaired males with small broods hover-foraged more frequently than both paired males with large broods

TABLE 16

USE OF FORAGING PATTERNS IN EXPERIMENT II

Group[1]	PF[2]	PF/HF	GF	HF	Fly	Ha
P♂♂LB	85 (77)[3]	1 (1)	3 (3)	7 (6)	13 (11)	2 (2)
P♀♀LB	36 (46)	0 (0)	2 (3)	17 (21)	21 (27)	2 (3)
P♂♂SB	68 (55)	2 (2)	1 (1)	9 (7)	39 (32)	4 (3)
P♀♀SB	73 (62)	1 (1)	0 (0)	8 (7)	35 (30)	0 (0)
U♂♂LB	175 (66)	1 (1)	10 (4)	29 (10)	31 (12)	18 (7)
U♀♀LB	109 (52)	5 (3)	3 (1)	26 (12)	50 (24)	16 (8)
U♂♂SB	91 (54)	1 (1)	5 (2)	47 (28)	24 (14)	1 (1)
U♀♀SB	81 (63)	0 (0)	1 (1)	34 (27)	12 (9)	0 (0)

Intergroup Comparisons[4]

Paired vs Paired	P♂♂LB vs P♀♀LB***	Paired ♂♂ vs Unpaired ♂♂	P♂♂LB vs U♂♂LB
	P♂♂LB vs P♂♂SB***		P♂♂LB vs U♂♂SB***
	P♂♂SB vs P♀♀SB		P♂♂SB vs U♂♂LB***
	P♀♀LB vs P♀♀SB**		P♂♂SB vs U♂♂SB***
Unpaired vs Unpaired	U♂♂LB vs U♀♀LB**	Paired ♀♀ vs Unpaired ♀♀	P♀♀LB vs U♀♀LB*
	U♂♂LB vs U♂♂SB***		P♀♀LB vs U♀♀SB***
	U♂♂SB vs U♀♀SB		P♀♀SB vs U♀♀LB*
	U♀♀LB vs U♀♀SB***		P♀♀SB vs U♀♀SB**

[1] P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.
[2] PF = perch-foraging; HF = hover-foraging; GF = ground foraging; Fly = flycatching; Ha = hawking.
[3] Number (%).
[4] Differences between groups non-significant unless noted; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

TABLE 17
USE OF STAGING POINTS IN EXPERIMENT II

Group[1]	Tree	UL[2]	Fence	SP[2]	Rock	Ground	Aerial
P♂♂LB	31 (16)[3]	4 (2)	121 (62)	10 (5)	5 (3)	5 (3)	18 (9)
P♀♀LB	25 (19)	6 (4)	61 (45)	4 (3)	7 (5)	1 (1)	31 (23)
P♂♂SB	19 (11)	64 (37)	65 (37)	4 (2)	3 (2)	3 (2)	16 (9)
P♀♀SB	14 (9)	90 (58)	37 (24)	2 (1)	2 (1)	1 (1)	9 (6)
U♂♂LB	52 (12)	35 (8)	196 (46)	4 (1)	33 (8)	25 (6)	80 (19)
U♀♀LB	116 (32)	54 (15)	103 (28)	6 (1)	5 (1)	7 (2)	76 (21)
U♂♂SB	89 (26)	36 (10)	53 (15)	30 (9)	19 (6)	11 (3)	107 (31)
U♀♀SB	118 (50)	7 (3)	21 (9)	14 (6)	6 (3)	0 (0)	69 (29)

	Intergroup Comparisons[4]		
Paired vs Paired	P♂♂LB vs P♀♀LB** P♂♂LB vs P♂♂SB P♂♂SB vs P♀♀SB P♀♀LB vs P♀♀SB***	Paired ♂♂ vs Unpaired ♂♂	P♂♂LB vs U♂♂LB** P♂♂LB vs U♂♂SB*** P♂♂SB vs U♂♂LB*** P♂♂SB vs U♂♂SB***
Unpaired vs Unpaired	U♂♂LB vs U♀♀LB*** U♂♂LB vs U♂♂SB*** U♂♂SB vs U♀♀SB*** U♀♀LB vs U♀♀SB**	Paired ♀♀ vs Unpaired ♀♀	P♀♀LB vs U♀♀LB*** P♀♀LB vs U♀♀SB*** P♀♀SB vs U♀♀LB*** P♀♀SB vs U♀♀SB***

[1] P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.

[2] UL = utility line; SP = small plant.

[3] Number (%).

[4] Differences between groups non-significant unless noted; ** = $p < 0.01$; *** = $p < 0.001$. Differences based on 2 × 3 tables, i.e., two groups of birds vs three clusters of staging points: high perches, low perches, and aerial positions. High perches = use of trees + utility lines + fences. Low perches = use of small plants + rocks + ground positions.

and small broods. Paired males with small broods hawked less frequently than unpaired males with large broods but flycaught more frequently. Paired females with large broods hover-foraged more frequently than unpaired females with large broods and flycaught more frequently than unpaired females with small broods. Unpaired females at both brood sizes hover-foraged more frequently than paired females with small broods.

Various differences occurred among the groups of Experiment II in use of staging points. Some of these had no functional significance because they represented between-territory differences in presence or absence of such perch types as utility lines and trees. To minimize the importance of between-territory differences, the seven types of staging points are reduced here to three: high perches, low perches, and aerial positions. High perches include trees, utility lines, and fences; low perches include small plants, rocks, and ground positions; aerial positions are the same as in previous analyses. Even though analysis was based on only three categories, the use of all seven is displayed in Table 17. Comparative use of aerial staging points is illustrated in Figure 5 and described below along with the use of other staging points.

Among groups of paired birds, females with large broods used aerial positions significantly more often than their mates (Table 17, Fig. 5). There were no intersexual differences between birds with small broods and no interbrood differences for males. Paired females with large broods used both aerial positions and low perches (particularly rocks) more frequently than paired females with small broods. Among groups of unpaired birds, females with large broods used high perches more than males with large broods. With small broods, females used high

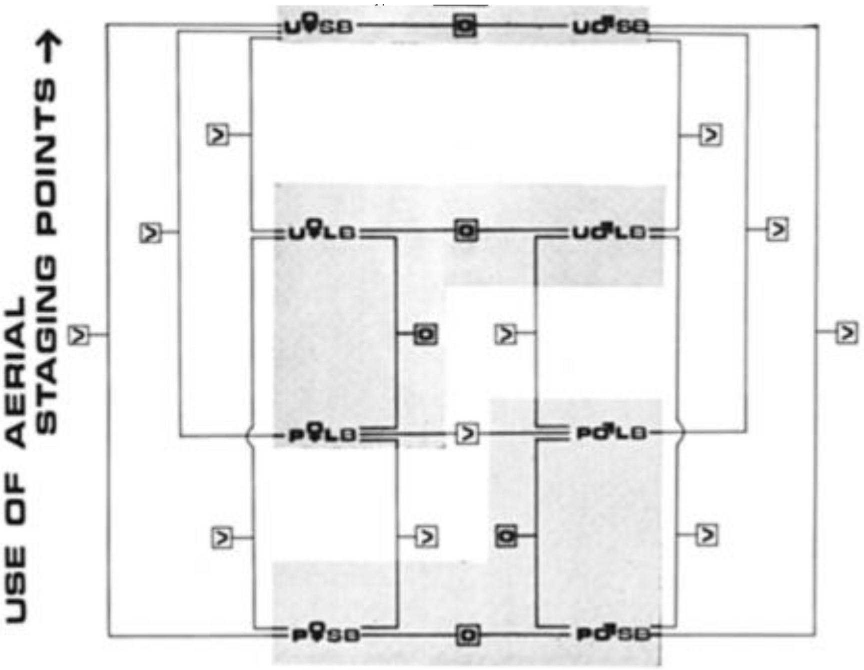


Fig. 5. Wiring diagram of statistical comparisons of the use of aerial staging points by groups in work load Experiment II. The 8 experimental groups reduce to 3 sets because only some between groups differences were statistically significant. The 3 sets are blocked by stippling. Between group comparisons are shown by lines connecting pairs. Statistically significant differences are shown by a carat (>) symbol attached to a line, statistically insignificant differences by a zero (0). P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.

perches more than males. Between broods, unpaired birds with small broods used aerial positions significantly more often than unpaired birds of the same sex with large broods. Unpaired females with small broods also used low perches significantly more often than unpaired females with large broods. Without exception, unpaired males at both brood sizes used aerial positions significantly more often than paired males at both brood sizes. Single males at both brood sizes also used low perches (particularly rocks) more often than paired males with small broods. Paired females with large boods used low perches more than unpaired females with large broods. Unpaired females with large broods used aerial positions more often than paired females with small broods. Unpaired females with small broods used aerial positions more frequently than either class of paired female; they also used low perches more often than paired females with small broods.

Paired males with small broods used taller vegetation significantly more often than their mates (Table 18, Fig. 6). Unpaired females with large broods foraged in taller vegetation significantly more often than either unpaired males with large broods or unpaired females with small broods. Unpaired males with large broods used taller vegetation more often ($p < 0.06$) than unpaired males with small broods; I consider this difference significant on the basis of subjective field experience. Unpaired males and females with small broods used taller vegetation about equally often. Unpaired males with large broods used taller vegetation

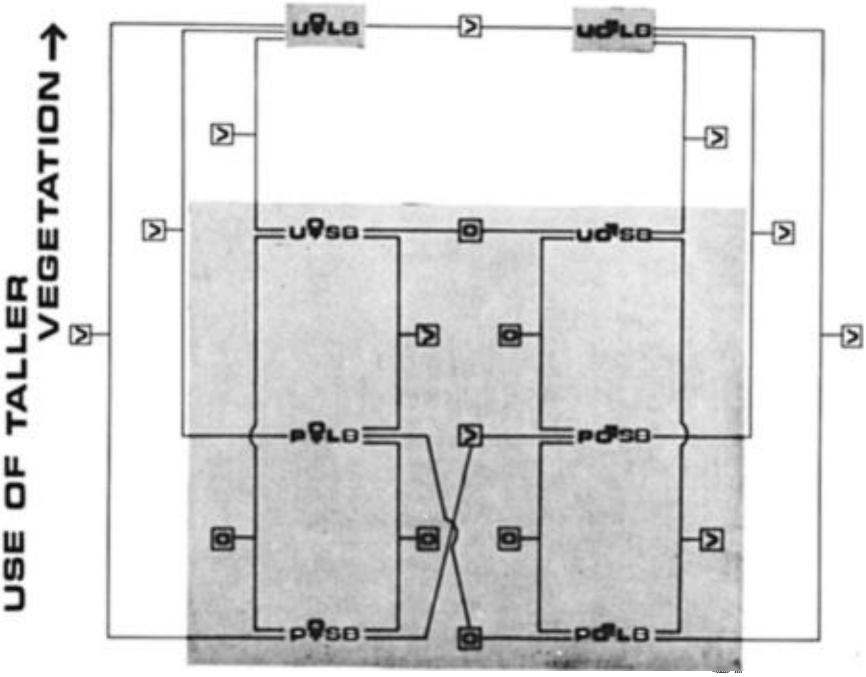


Fig. 6. Wiring diagram of statistical comparisons of the use of taller vegetation by groups in work load Experiment II. The 8 experimental groups reduce to 3 sets because most intergroup differences were statistically insignificant. The 3 sets are blocked by stippling. Between group comparisons are shown by lines connecting pairs. Statistically significant differences are shown by a carat (>) symbol attached to a line, statistically insignificant differences by a zero (0). P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.

significantly more often than paired males with either large or small broods. Unpaired males with small broods foraged significantly more often in taller vegetation than paired males with large broods but not more often than paired males with small broods. Unpaired females with large broods used taller vegetation significantly more often than paired females with either large or small broods. Unpaired females with small broods used vegetation height classes about the same as paired females with small broods but used taller vegetation more often than paired females with large broods.

High Cost Score

Figure 5 shows that the 8 groups of birds in Table 17 reduce to 3 groups in terms of significant differences in the use of aerial staging points. Thus, the members of these groups can be assigned values of 3, 2, and 1, respectively, for use of aerial staging points. Figure 6 shows that the 8 groups also reduce to 3 in terms of significant differences in the use of taller vegetation although the composition of these groups is different from those in Figure 5. The members of the 3 groups of Figure 6 are assigned values of 3, 2, and 1, respectively, for use of taller vegetation. High cost score is obtained by adding values across both parameters for each treatment group:

Group	Values	Score
P ♂♂ LB	1 + 1	2
P ♀♀ LB	2 + 1	3
P ♂♂ SB	1 + 1	2
P ♀♀ SB	1 + 1	2
U ♂♂ LB	2 + 2	4
U ♀♀ LB	2 + 3	5
U ♂♂ SB	3 + 1	4
U ♀♀ SB	3 + 1	4

These scores are plotted in Figure 7 against the four potential proximate factors of work load.

CONCLUSIONS

Figures 7A–B show that number of adults per territory and number of birds per territory are unrelated to work output by foraging birds. Figure 7C shows a very weak relationship between work output and number of young per nest. Figure 7D shows a strong and statistically significant correlation ($r_s = 0.838$, $p < 0.01$) between work output and number of young per attendant adult. Therefore, number of young per attendant adult was accepted as the operative factor of work load driving work output in foraging behavior.

The hypothesis of intersexual food competition was rejected as an ultimate factor because unpaired birds worked harder than paired birds (Fig. 7A), exactly opposite of expectation because intersexual competition was only possible with paired birds.

Sexual dichromatism was not shown to be a cause of sexual foraging differences because no males were preyed upon; I had predicted predation of males foraging like females provided the experimental manipulations controlled predator behav-

TABLE 18

USE OF VEGETATION OF DIFFERENT HEIGHTS IN EXPERIMENT II

Group[1]	Short[2]	Tall[3]	Group	Short	Tall
P♂♂LB	70 (78)[4]	20 (22)	U♂♂LB	84 (50)	84 (50)
P♀♀LB	33 (70)	14 (30)	U♀♀LB	34 (33)	68 (67)
P♂♂SB	49 (71)	20 (29)	U♂♂SB	74 (62)	45 (38)
P♀♀SB	50 (81)	12 (19)	U♀♀SB	58 (59)	41 (41)
		Intergroup Comparisons[5]			
Paired vs Paired	P♂♂LB vs P♀♀LB P♂♂LB vs P♂♂SB P♂♂SB vs P♀♀SB*** P♀♀LB vs P♀♀SB		Paired ♂♂ vs Unpaired ♂♂	P♂♂LB vs U♂♂LB*** P♂♂LB vs U♂♂SB* P♂♂SB vs U♂♂LB** P♂♂SB vs U♂♂SB	
Unpaired vs Unpaired	U♂♂LB vs U♀♀LB* U♂♂LB vs U♂♂SB† U♂♂SB vs U♀♀SB U♀♀LB vs U♀♀SB***		Paired ♀♀ vs Unpaired ♀♀	P♀♀LB vs U♀♀LB*** P♀♀LB vs U♀♀SB*** P♀♀SB vs U♀♀LB*** P♀♀SB vs U♀♀SB	

[1] P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.

[2] "Short" combines data from columns "Bare" and "Rock" in Table 46, and column "G ≤ T" in Table 47 of Power (1974).

[3] "Tall" combines data from columns "T < G ≤ S," "S < G ≤ H," and "H < G" in Table 47 of Power (1974).

[4] Number (%).

[5] Differences between groups non-significant unless noted; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; † = $p < 0.06$.

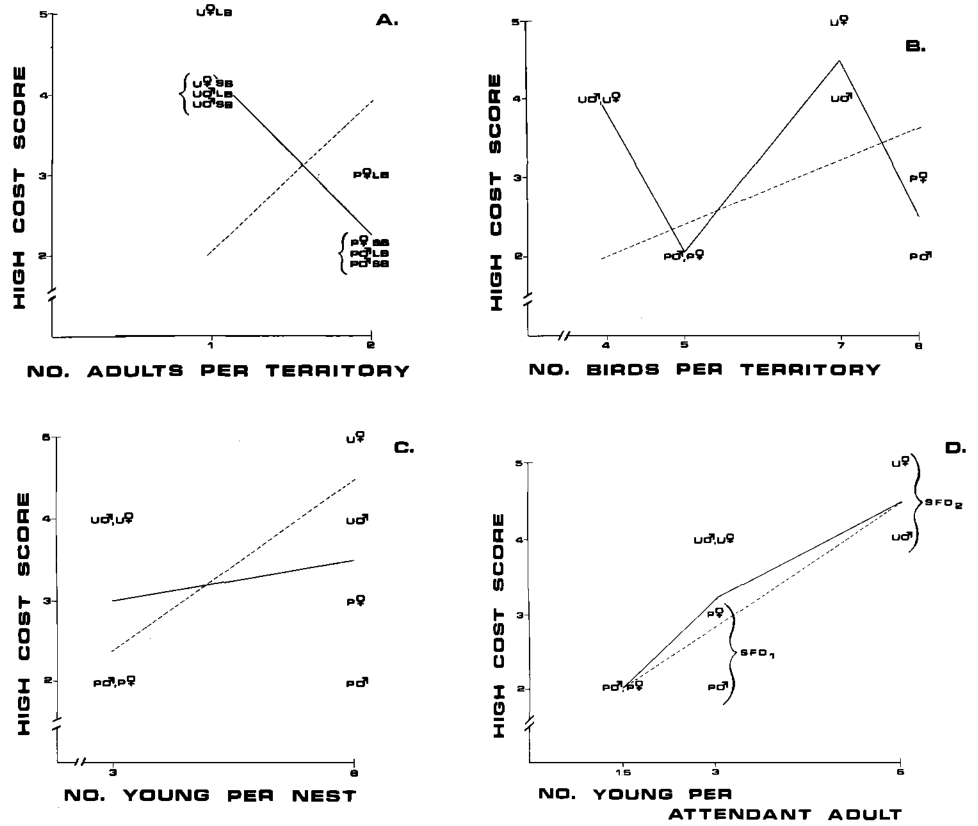


Fig. 7. High cost score in relation to several factors in work load Experiment II. Each figure compares an expected relationship (dashed line) to an observed relationship (solid line). P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.

A. High cost score in relation to number of adults per territory. The expected relationship is based on the hypothesis that more adults per territory forces foragers to use costly behaviors more frequently.

B. High cost score in relation to number of birds per territory (adults plus young). The expected relationship is based on the hypothesis that more birds per territory forces foragers to use costly behaviors more frequently.

C. High cost score in relation to number of young per nest. The expected relationship is based on the hypothesis that more young per nest forces foragers to use costly behaviors more frequently.

D. High cost score in relation to number of young per attendant adult (brood size divided by number of adults at a nest). The expected relationship is based on the hypothesis that more young per attendant adult forces foragers to use costly behaviors more frequently. SFD = sexual foraging difference.

ior as well as bluebird behavior. However, the hypothesis that sexual dichromatism leads to differential predation on males and females was not rejected on the basis of absence of predation because it was not possible to assess the experiment's effect on predators. Moreover, the persistence of sexual dimorphism in behavior at even the highest number of young per attendant adult (Fig. 7D) is consistent with the interpretation (given in "Non-experimental Observations") that males are more reluctant to work as hard as females or to accept as much cost; differential predation thus remains a potential source of male reluctance. That males with six young to care for did not work as hard as unpaired females with six young does not contradict the interpretation (also given in "Non-experimental Observations") that males are fully as capable of foraging away-from-large-perches as females by means of hover-foraging and hawking. This is true because (1) unpaired males with large and small broods used aerial positions as often as unpaired females with large and small broods, respectively; (2) both groups of unpaired males used aerial positions equally or more often than paired females with large broods; (3) unpaired males with small broods used aerial positions more frequently than any other group albeit not significantly more than unpaired females with small broods. Evidence of male reluctance combined with evidence of male ability suggest sex differential costs in foraging; predation risk could be such a cost.

The hypothesis of male exploitation was not shown to be a cause of sexual foraging differences because only three of the four relationships needed to demonstrate male coercion were found and the fourth relationship was contrary to prediction. The relevant groups for these comparisons were those with 3 young per attendant adult in Figure 7D because they were the only groups of paired and unpaired males and females where the average work load was equal. As predicted, (1) unpaired males and females with the same work load worked equally hard, (2) paired males worked less than unpaired males with the same average work load, and (3) paired females worked harder than their mates. Contrary to prediction, (4) unpaired females worked harder than paired females. The hypothesis was not rejected, however, because unpaired females may have worked harder than paired females for reasons unrelated to male coercion of paired females (e.g., possible differences between paired and unpaired females in territory quality, brood thermal efficiency, etc.).

That females designated to lose their mates had only five young each before brood reduction and mate loss whereas females designated to retain their mates had six young each suggests that the territories of the former may have been inferior in prey content by about 17%, and, thus, unpaired females had to work harder to find a given amount of prey. However, the broods of unpaired females were reduced 40% prior to observation of foraging behavior which should have compensated for any differences in territory quality.

Differences in thermal efficiency between large and small broods may have affected the foraging behavior of paired and unpaired females. Small broods have higher caloric demands per individual because of greater heat loss owing to the higher surface to volume ratio (Royama 1966). But, differences in brood size thermal efficiency were probably relatively low during the second experiment (nestling days 13–14) because young were mostly feathered and tended to clump less than when younger, thus reducing effective brood size differences in surface to volume ratio. Moreover, unpaired females did not feed more often than paired females (Table 13), leaving open the possibility that their young did not have higher individual caloric needs.

Because territory quality and brood thermal efficiency may not have been important differences between unpaired and paired females with the same average work load, the contradiction of prediction (4) may argue against the reality of male coercion and, thus, of male exploitation. To clarify the importance of male exploitation, I performed a follow-up experiment in 1977 (see p. 60).

The second experiment provided a basis for (1) rejecting three hypotheses of factors of work load, (2) accepting the hypothesis that number of young per attendant adult is the driving work load factor, and (3) rejecting one hypothesis of cause of sexual foraging differences. It also provided supporting evidence for the sexual dichromatism and male exploitation hypotheses but failed to provide critical evidence for or against either.

CHAPTER 7

EXPERIMENT III: MATE LOSS

The third experiment was designed to determine the effects of mate loss on foraging behavior. This was accomplished by comparing the behavior of birds before and after mate loss while controlling for differences in habitat between territories. Birds had the same territories before and after mate loss. The data for the "before" parts of comparisons are presented with this section. The data for the "after" parts were the results of the second experiment. All groups of birds will be referred to by the names they bore in the second experiment. Thus, "paired" birds did not suffer mate loss while "unpaired" birds did.

PARENTAL CARE

Groups of paired birds did not significantly alter their frequency of box visits or fecal sac removals following manipulation (Tables 19, 20). All groups of unpaired birds significantly increased their frequency of box visits after mate loss but not their rate of fecal sac removals.

FORAGING BEHAVIOR

All groups of paired birds significantly reduced their frequency of use of the area away-from-large-perches after manipulation (Table 21). Unpaired males with large broods slightly reduced their use of that area, whereas other groups of unpaired birds increased their foraging effort away-from-large-perches although that increase was statistically significant only for unpaired males with small broods. The increase might have been significant for unpaired females with small broods had my sample of their behavior before mate loss been larger.

Paired birds with large broods significantly reduced their hover-foraging after manipulation, but paired birds with small broods did not change in that regard (Table 22). All groups of paired birds significantly increased their flycatching activity after the day 12 manipulations, but the impact on resource use of this apparently opportunistic change is obscure. Unpaired birds greatly reduced their frequency of ground-foraging after mate loss except for unpaired females with small broods. Unpaired birds with small broods tremendously increased their rate of hover-foraging after mate loss. Unpaired birds with large broods significantly reduced their relative frequency of hover-foraging after mate loss (ca. 21% before to ca. 12% after), but their actual number of hover-foragings did not decrease (29 per group before to 28.5 per group after; compare Tables 16 and 22). What actually happened was that unpaired birds with large broods greatly increased their amount of perch-foraging and hawking after mate loss; other groups of birds also did this, but to a much lesser extent.

Paired birds reduced their use of aerial staging points after day 12 but increased their use of high perches (Table 23). Unpaired birds with large broods increased their use of high perches after mate loss and decreased their relative use of aerial positions (ca. 21% before to 20% after). However, they increased their actual use of aerial positions from an average of 53 per group before to 78 per group after (compare Tables 17 and 23). Unpaired birds with small broods increased their use of aerial staging points in all respects after mate loss while decreasing their use of high perches.

TABLE 19
VISITS TO THE NEST BOX IN EXPERIMENT III[1]

Group[2]	No. observ.	Visits/hour	
		Mean	Range
P♂♂LB	47	5.3	0–10.9
P♀♀LB	66	7.3	3.1–14.5
P♂♂SB	18	3.0	0–8.9
P♀♀SB	20	3.2	1.2–5.0
U♂♂LB	29	4.2	0–10.9
U♀♀LB	35	5.2	0–12.0
U♂♂SB	28	3.5	1.3–9.5
U♀♀SB	12	4.9	0–15.0
Comparison of Visits Before and After Mate Loss[3]			
P♂♂LB	P♂♂SB	U♂♂LB***	U♂♂SB**
P♀♀LB	P♀♀SB	U♀♀LB*	U♀♀SB*

[1] The sum of box visits listed here is less than in Table 7 because the latter also includes visits by birds subsequently collected and not reported here. All tables for Experiment III omit data from birds that were collected.
[2] P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.
[3] Differences non-significant unless noted; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Paired birds increased their use of taller vegetation (more than tarsal height) after day 12, but this increase was not statistically significant (Table 24). By contrast, all but one group of unpaired birds greatly increased their use of taller vegetation after mate loss. Unpaired females with small broods were observed too infrequently before mate loss to determine their use of vegetation height classes then.

MATE LOSS

All groups of birds changed their behavior following the experimental manipulations at their nests on the twelfth day of nestling life. As expected from the doubling of the number of young per attendant adult, birds losing their mates changed their behavior more dramatically than birds not losing their mates. This was seen in both parental care and costly foraging behaviors. Paired birds did not change their frequency of parental care (Tables 19 and 20), whereas unpaired

TABLE 20
FECAL SAC REMOVALS IN EXPERIMENT III[1]

Group[2]	No. observ.	Removals/hour	
		Mean	Range
P♂♂LB	8	0.9	0–2.1
P♀♀LB	10	1.0	0–4.8
P♂♂SB	0	0	0–0
P♀♀SB	3	0.7	0–2.3
U♂♂LB	5	0.5	0–1.9
U♀♀LB	14	2.3	0–8.0
U♂♂SB	5	0.5	0–1.9
U♂♂SB	3	1.0	0–1.9

[1] All intergroup differences non-significant.
[2] P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.

TABLE 21

PROXIMITY OF FORAGING BIRDS TO LARGE PERCHES IN EXPERIMENT III

Group[1]	NLP[2]	AFLP
P♂♂LB	55 (64)[3]	31 (36)
P♀♀LB	35 (35)	65 (65)
P♂♂SB	37 (79)	10 (21)
P♀♀SB	56 (80)	14 (20)
U♂♂LB	115 (70)	49 (30)
U♀♀LB	106 (92)	10 (8)
U♂♂SB	119 (91)	12 (9)
U♀♀SB	12 (92)	1 (8)

Comparison of Behavior Before and After Mate Loss[4]

P♂♂LB***	P♂♂SB**	U♂♂LB	U♂♂SB***
P♀♀LB***	P♀♀SB***	U♀♀LB	U♀♀SB

[1] P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.

[2] NLP = near-large-perches; AFLP = away-from-large-perches.

[3] Number (%).

[4] Differences non-significant unless noted; ** = $p < 0.01$; *** = $p < 0.001$.

birds more than doubled their number of nest box visits and, thus (presumably), their frequency of feeding of young.

Changes in frequency of costly foraging behaviors are illustrated by a new quantity, the “change in costly behavior” score. A new quantity is required because the high cost scores of the first and second experiments cannot be compared directly as their minima ($=2$) are based on significantly different frequencies of aerial staging positions (Tables 17, 23). The procedure for calculating change in costly behavior score was to assign a “-1” to a group for a significant reduction in use of each costly behavior, a “0” for no change in behavior, and a “$+1$” for a significant increase in use of each costly behavior. Assigned values were then summed for both costly behaviors.

All groups of paired birds significantly reduced their use of aerial staging po-

TABLE 22

USE OF FORAGING PATTERNS IN EXPERIMENT III

Group[1]	PF[2]	PF/HF	GF	HF	Fly	Ha
P♂♂LB	62 (56)[3]	1 (1)	5 (5)	34 (31)	9 (7)	0 (0)
P♀♀LB	24 (25)	3 (3)	1 (1)	63 (64)	7 (7)	0 (0)
P♂♂SB	40 (73)	0 (0)	0 (0)	7 (13)	4 (7)	4 (7)
P♀♀SB	43 (61)	0 (0)	13 (18)	9 (13)	6 (8)	0 (0)
U♂♂LB	67 (40)	0 (0)	38 (23)	33 (20)	26 (16)	3 (1)
U♀♀LB	50 (42)	0 (0)	35 (29)	25 (21)	9 (7)	1 (1)
U♂♂SB	78 (57)	1 (1)	11 (8)	9 (7)	35 (25)	3 (2)
U♀♀SB	7 (54)	0 (0)	0 (0)	0 (0)	5 (38)	1 (8)

Comparison of Behavior Before and After Mate Loss[4]

P♂♂LB***	P♂♂SB**	U♂♂LB***	U♂♂SB***
P♀♀LB***	P♀♀SB	U♀♀LB***	U♀♀SB**

[1] P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.

[2] PF = perch foraging; HF = hover-foraging; GF = ground-foraging; Fly = flycatching; Ha = hawking.

[3] Number (%).

[4] Differences non-significant unless noted; ** = $p < 0.01$; *** = $p < 0.001$.

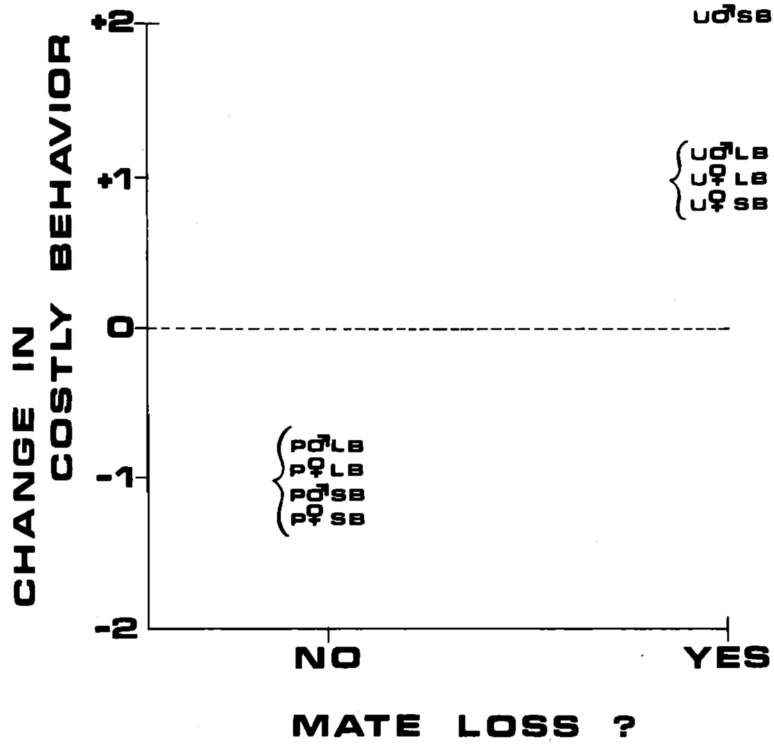


Fig. 8. Effects of mate loss on use of costly behaviors. Paired birds (P) did not lose their mates, unpaired birds (U) did. Only birds suffering mate loss increased their use of costly behaviors. LB = birds with large broods; SB = birds with small broods.

sitions (Table 23) and were assigned values of −1. Unpaired birds with large broods did not significantly alter their use of aerial positions and, thus, were assigned values of 0. Unpaired birds with small broods significantly increased their use of aerial positions and were accordingly assigned values of +1.

No group of paired birds changed its use of taller vegetation (Table 24); thus, each was assigned a value of 0. Unpaired males and females with large broods, and unpaired males with small broods significantly increased their use of taller vegetation and so were assigned values of +1. Unpaired females with small broods also probably increased their use of taller vegetation, but the number of observations of them before mate loss was too few to show this; thus, they were assigned a value of 0.

When values for both costly behaviors are summed, all groups of paired birds earn change in costly behavior scores of −1, both groups of unpaired birds with large broods earn scores of +1, unpaired males with small broods earn a score of +2, and unpaired females with small broods earn a score of +1 (Fig. 8). Thus, mate loss produced increases in frequency of costly behaviors, especially for unpaired males with small broods. Had behavior before mate loss been adequately sampled, unpaired females with small broods probably also would have shown as dramatic an increase in use of costly behaviors. That birds with small broods changed their behavior more than those with large broods

TABLE 23
USE OF STAGING POINTS IN EXPERIMENT III

Group[1]	Tree	UL[2]	Fence	SP[2]	Rock	Ground	Aerial
P♂♂LB	8 (4)[3]	2 (1)	98 (47)	12 (6)	5 (2)	14 (7)	68 (33)
P♀♀LB	19 (9)	1 (1)	47 (23)	10 (5)	3 (1)	8 (3)	120 (58)
P♂♂SB	7 (6)	19 (16)	44 (37)	16 (13)	3 (3)	3 (3)	26 (22)
P♀♀SB	18 (14)	42 (34)	20 (16)	12 (10)	4 (3)	14 (11)	15 (12)
U♂♂LB	32 (10)	56 (18)	75 (24)	12 (4)	11 (4)	61 (20)	63 (20)
U♀♀LB	21 (11)	24 (12)	70 (35)	3 (2)	0 (0)	38 (18)	43 (22)
U♂♂SB	36 (14)	21 (8)	93 (37)	8 (3)	23 (9)	37 (15)	33 (13)
U♀♀SB	11 (47)	5 (22)	5 (22)	0 (0)	0 (0)	0 (0)	2 (9)

Comparison of Behavior Before and After Mate Loss[4]

P♂♂LB***	P♂♂SB***	U♂♂LB***	U♂♂SB***
P♀♀LB***	P♀♀SB***	U♀♀LB***	U♀♀SB*

[1] P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.

[2] UL = utility line; SP = small plant.

[3] Number (%).

[4] Differences significant; * = $p < 0.05$; *** = $p < 0.001$. Differences based on 2 × 3 tables: before and after vs high perches (trees, utility lines and fences), low perches (small plants, rocks and ground positions), and aerial positions.

following mate loss suggests that birds with large broods were closer to some point of maximum output of costly behaviors before mate loss. This is a reasonable interpretation derived from Lack's (1968) hypothesis that birds tend to rear the maximum number of young they predictably can support. Thus, birds with large (normal) broods could be expected to have fewer opportunities to provide more food for their young through changes in foraging behavior than birds with broods experimentally reduced in size.

Curiously, birds not losing their mates decreased their use of costly behaviors (Fig. 8) by decreased use of aerial staging points (Table 23). This result suggests that either paired birds experienced a decrease in food demand or were so traumatized by banding of their young on day 12 that they reduced their foraging

TABLE 24
USE OF VEGETATION OF DIFFERENT HEIGHTS IN EXPERIMENT III

Group[1]	Short[2]	Tall[3]
P♂♂LB	58 (91)[4]	6 (9)
P♀♀LB	69 (88)	9 (12)
P♂♂SB	52 (83)	11 (17)
P♀♀SB	48 (87)	7 (13)
U♂♂LB	91 (78)	26 (22)
U♀♀LB	45 (58)	32 (42)
U♂♂SB	49 (77)	15 (23)
U♀♀SB	4 (57)	3 (43)

Comparison of Vegetation Use Before and After Mate Loss[5]

P♂♂LB	P♂♂SB	U♂♂LB*	U♂♂SB*
P♀♀LB	P♀♀SB	U♀♀LB*	U♀♀SB†

[1] P = paired birds; U = unpaired birds; LB = birds with large broods; SB = birds with small broods.

[2] "Short" includes data from columns "Bare" and "Rock" of Table 63, and column "G ≤ T" of Table 64 of Power (1974).

[3] "Tall" includes data from columns "T < G ≤ S," "S < G ≤ H," and "H < G" of Table 64 of Power (1974).

[4] Number (%).

[5] Differences non-significant unless noted; * = $p < 0.05$; † = too few data for comparison.

output in my presence. Decreased food demand seems unlikely because nestlings averaged 3+ days older in the second experiment than in the first, and, thus, increased appetites should be expected. However, it may be that nestlings do not need more food after unsheathing of flight feathers (about day 12) because their weight maximizes about that time (Power 1966, 1974) as it does in many species (Ricklefs 1968). [See Pinkowski (1975) for a demonstration of asymptotic approach to fledging weight about day 11–12 in the Eastern Bluebird, *S. sialis*.] The effect of traumatization, if any, is equally obscure. Alarm notes did not become more common after banding of young (Power 1974), but paired birds (although not unpaired ones) were less tolerant of me after day 12. I attempted to compensate for this by staying as far from birds as possible and in a vehicle. Moreover, mate loss did not so traumatize unpaired birds that they reduced their foraging effort. Thus, I can offer no satisfactory explanation for the reduction in use of aerial staging positions by paired birds after banding of their young.

CHAPTER 8

RELATIONSHIP OF FORAGING BEHAVIOR TO WORK LOAD

I present here the results of observations on foraging rates, distance from the nest at which foraging occurred, and type of vegetation in which birds hunted, none of which shows any clear relation to work load.

FORAGING RATES

I timed 1259 foraging patterns and 2184 uses of staging points during the first and second experiments of 1972 but found no consistent relationship between the rate of foraging (measured on a "foraging minute" basis, see General Methods), and either sex or work load (Power 1974: tables 12, 13, 37, 38). However, mate loss and foraging rate were weakly related. Some groups of unpaired birds foraged more rapidly than paired birds. I hypothesize that bluebirds respond to greater work load by increasing their rate of foraging on an hourly (but not a foraging minute) basis by reducing the intervals between bouts of active foraging.

DISTANCE TO NEST DURING FORAGING

I estimated the distance from the nest box at which birds foraged in 2241 cases in the first experiment and 1943 cases in the second but found no consistent relationship between foraging distance and either sex or work load (Power 1974: tables 26–31, 50–53, 65–66). Foraging distance was influenced by habitat features of territories and the tendency of birds to forage close to their nests.

The effect of habitat is illustrated by the foraging behavior of birds on four territories in 1972. Pairs 5 and 6 had nest boxes located in a field with hay about 0.5 m high and 300 m from the nearest suitable foraging habitat. This combination of features caused these pairs to effectively translocate the zero point of their foraging efforts 300 m from their nests. When these pairs were included in analysis of foraging distance, birds with small broods appeared to forage at greater distances than birds with large broods, but this was merely an artifact of the peculiar territories of pairs 5 and 6. Female 69 used two trees about 50 m from her nest as staging points for 28% of her foraging effort after mate loss. These trees commanded an area rich in prey, judging from her high rate of harvest, and also allowed her to keep her nest in constant view. Members of pair 47 frequently foraged close to their nest from fences and utility lines and caught a great deal of prey on the gravel surface of a nearby road. This pair never used trees as staging points because their territory contained none.

The foraging behavior of birds in each of these cases was clearly influenced by habitat features unique to their territories. Actually, all territories had unique features complicating all aspects of data analysis, particularly foraging distance. I therefore minimized the effect of idiosyncratic territory features by an appropriate statistical transformation. I plotted foraging distance against intensity of foraging effort on a log-log scale (Fig. 9). I define "intensity of foraging effort" to be the number of foraging efforts per square meter, i.e., uses of staging points (with or without exhibition of foraging patterns) in each square meter surrounding the nest. Thus, this plot measures the frequency of foraging over successive concentric annuli surrounding the nest. Birds foraged as close to their nests as the distribution of such habitat features as fences and scattered trees allowed

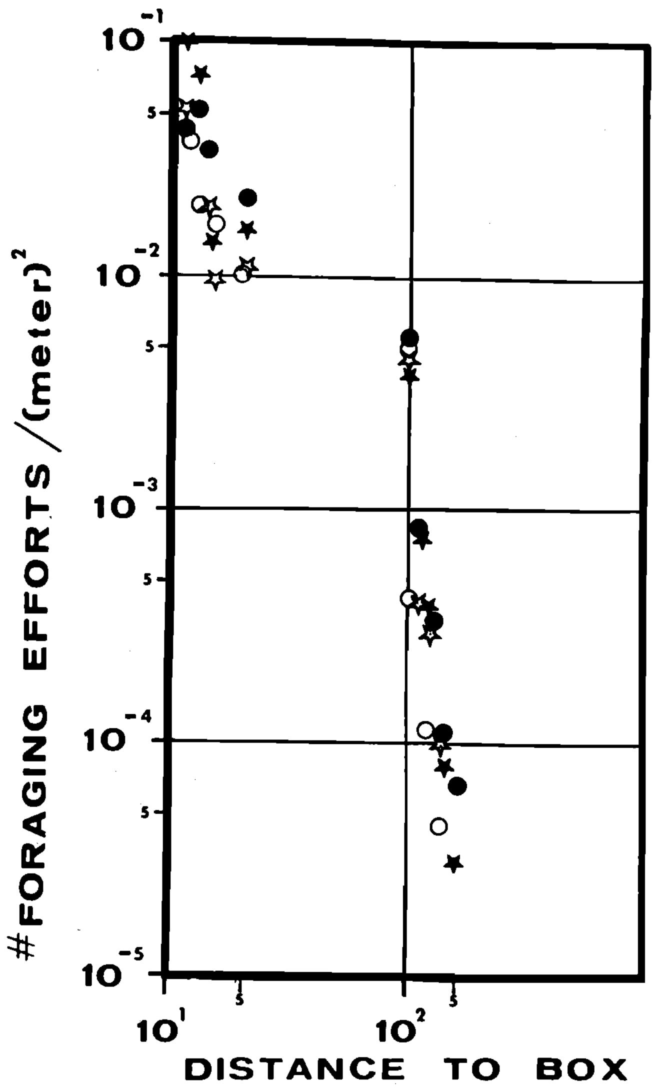


Fig. 9. Intensity of foraging effort in relation to distance from the nest site. The abscissa is distance from the nest box in meters plotted on a log scale. The ordinate is the number of foraging efforts (counted by number of uses of staging points) observed per square meter in concentric annuli around the nest box, also plotted on a log scale. Data are from observation of birds in the first work load experiment (Power 1974, Table 67). Solid stars indicate males with large broods; solid circles, females with large broods; open stars, males with small broods; open circles, females with small broods.

(Fig. 9). Foraging close to the nest minimized time and flight cost in carrying food to nestlings and returning to foraging locations. However, birds seldom foraged exactly at their nest sites; this might have led predators to their nests.

Type of Vegetation

I categorized the vegetation in which birds hunted into seven types (see General Methods) but found no consistent relationship between type and either sex or work load. Instead, statistically significant differences (Power 1974: tables 21, 46, 63) reflected the extremely patchy distribution of types across the study range and the small but significant correlation between vegetation type and height (cc = 0.28, $p < 0.001$, Power 1974: table 23). Some vegetation types were found on only a few territories, and not many territories contained all seven. Birds shifting between places of different vegetation height in many cases automatically shifted between vegetation types because types often had characteristic heights; e.g., two of the three hayfield types were always tall, and the third was always short. Thus, choice of type could not be expressed with equal freedom on all territories nor fully separated from choice of height. In combination with the results of the 1976 habitat alteration experiment and the findings of other studies on grassland birds (see section on Importance of Vegetation Height, below), these results suggest that vegetation type is not in itself an important factor influencing foraging behavior although it may have indirect influences through restriction of choice of foraging location.

CHAPTER 9

ADDITIONAL HYPOTHESES AND EXPERIMENTS

The results of the work load experiments suggested hypotheses about the role of territory in bluebird life, the impact of consorts on foraging behavior, the effect of experimental treatment on reproductive success, the effects of possible male exploitation on female well-being, and the importance of vegetation height on changes in foraging behavior. Development of some of these hypotheses called for additional experiments. The work load experiments also confirmed the existence of a sequence of two levels of foraging tactics, revealed a third level, and in combination with other results showed how the habitat peculiarities of individual territories influence switches between levels.

ROLE OF TERRITORY

That only number of young per attendant adult was a significant factor of work load suggested (1) that rate of food delivery to each nestling is a crucial factor in fledging young, (2) that the carrying capacity for nestlings is less than for adults, and (3) that bluebird territories are formed to encompass a sufficient biomass of readily available prey to guarantee a sufficient rate of food delivery under adverse hunting conditions.

(1) The importance of rate of food delivery follows from the correlation of greater frequency of box visits per hour and more frequent high cost foraging when adults responded to increased number of young per attendant adult. If rate of food delivery were not crucial, then adults would not have increased it with higher work load because increases in rate of delivery apparently can be achieved only by greater use of high cost foraging behavior. Therefore, increased rate of delivery would seem to promote fitness by improving nestling survivorship despite its attendant high cost.

(2) Limited nestling carrying capacity was implied by some nestling deaths from apparent starvation (Power 1974, unpubl. data) and by the importance of rate of food delivery. However, no adult carrying capacity was found because factors that should influence it (total number of birds per territory and number of adults per territory) had no measured effect on adult behavior. These results jointly imply that the carrying capacity for nestlings is less than for adults and, thus, that nestling carrying capacity is a limiting factor for bluebird populations.

This conclusion does not preclude the possibility that other factors may be as or more important in limiting bluebird populations over the course of an entire season or several seasons. Miller (1970) validated Power's (1966) findings on the importance of number of nest sites. Likewise, conditions on the wintering grounds may be crucial (Fretwell 1972; Darwin 1975:184–185), and single storms may severely depress populations for years (Forbush 1929:419–420; Wallace 1959). Finally, sex differential mortality may result in a relative scarcity of females (Brown 1969). The discovery that nestling carrying capacity limits populations in bluebirds parallels the results of research on marine birds (Ashmole 1963) and carnivorous mammals (Kruuk 1972; Schaller 1972). Thus, predator populations, be they of insectivores, piscivores, or carnivores, commonly may be regulated by the carrying capacity for young.

(3) I have frequently seen the weather on my mountain study area change in

less than a day from warm and sunny with very high insect activity to cold and snowy with insect activity so low that I could not find even a single active insect. Mass reproductive failure has sometimes resulted from severe weather. This experience, combined with knowledge of the importance of rate of food delivery to young, the population limiting effect of nestling carrying capacity, and the vital role of the space immediately surrounding the nest site in providing food for young (Fig. 9), led me to hypothesize that bluebirds try to form their territories to encompass that amount of readily available prey necessary to insure a sufficient rate of food delivery to nestlings during *bad weather* conditions. A corollary to this hypothesis is that prey may be far more abundant on good weather days (perhaps by several orders of magnitude) than is required to feed nestlings because the amount of prey available on bad weather days is only a fraction of that.

Williams (1966:242) credits this idea in more general form to Tinbergen (1957), and Tinbergen (1957) credits it to Howard (1935). No matter who first developed this "critical supply" hypothesis, it has long been overlooked [e.g., Brown (1969), Wilson (1975), and Verner (1977) do not mention it, but see Wolf and Wolf (1976)], and attention has focused on the less precise idea that a Type A territory provides sufficient food for young under unspecified environmental conditions. Lack of specification of environmental conditions has made this less precise food hypothesis difficult to test because it does not imply what results can be used to disprove it. This has led to a tediously anecdotal literature that I shall not attempt to review. Efforts to test this less precise food hypothesis have been confounded especially by an apparent paradox: if birds stake-out Type A territories primarily to sequester the food they require during nesting, why is food usually superabundant within territories? Why is it not just equal to that required? This apparent paradox is not at all real; it is an artifact of sampling prey and watching foraging on *good weather* days. Sampling prey and watching foraging on *bad weather* days would show that food at that time is not superabundant. Thus, neglect of the critical supply hypothesis has been unfortunate because it accounts for the superabundance of food during good weather.

Belief in the superabundance of food within territories has led to the conclusion that territory is an adaptation to limit population size evolved through group selection (Wynne-Edwards 1962; Ardrey 1966), and no amount of argument (see Brown 1969) seems able to eradicate this hypothesis from the minds of the naive. Moreover, this same belief in the superabundance of food within territories has led Verner (1977) to hypothesize that territoriality is a form of what Hamilton (1970) called "spiteful behavior" and that it is favored because territory holders promote the relative frequency of their genes by depriving others of the resources to breed. I cannot accept Verner's (1977) hypothesis because such spiteful behavior would cause selection to operate more intensely on those without territories than on those with them, and that would inevitably lead to the collapse (or non-evolution) of territoriality itself. Selection would operate more powerfully on non-territorial individuals because failure to obtain and hold territories would lead to their extinction (a 100% genetic loss), whereas territory holders could gain no more than a fraction of a percent in genetic representation by excluding a few individuals in a population. Moreover, territory holders would lose little by occasional defeats and loss of part of their territory with its superabundant food supply so long as they retained a portion with sufficient food resources to enable successful reproduction. Thus, Verner's (1977) hypothesis implies an enormous asymmetry in costs and benefits between territorial and non-territorial individuals. With such great asymmetry, non-territorial individuals would be strongly favored for refusing to acknowledge the conventions of territoriality (e.g., boundaries, displays, retreat from territory holders), and territoriality, thus, would vanish (or fail to evolve) as territory holders died or lost their territories in savage fights with non-territorial individuals favored for non-stop aggression.

By contrast, the critical supply hypothesis does not require among the players of the territorial game so great an inherent genetic imbalance that it would guarantee the elimination (or non-evolution) of territoriality. Territory holders are just as threatened as non-territorial individuals under the critical supply hypothesis because loss of territory means loss of the critical supply of food that is required for young (and perhaps adults) during bad weather. Moreover, under conditions of the critical supply hypothesis, non-territorial individuals can be favored for adhering to the conventions of territoriality and waiting until a territory becomes available (even if this means losing a breeding season) rather than for fighting without restraint at each territorial encounter. They will always have a chance (no matter how small) of breeding in the future because there is no *de facto* "plot" to drive them to extinction as is implicit in Verner's (1977) hypothesis. [Tullock (1979) has published a critique of Verner's (1977) hypothesis from a different perspective. He has shown that the benefits of excluding some birds from breeding would be distributed among all territory holders but that the costs of this exclusion would be borne solely by territory holders having larger than necessary territories. Thus, Tullock also concludes that exclusion of competitors *per se* could not persist as the basis for territoriality.]

In addition to explaining the evolution of the conventions of territorial behavior and dissipating the phantom of superabundant food and its attendant theoretical wraiths, the critical supply hypothesis is important as both a lemma and a corollary to Lack's (1968) keystone hypothesis that clutch size ultimately is controlled by food. I therefore take this opportunity to re-introduce the critical supply hypothesis with this formal statement: "Birds stake-out Type A territories to encompass the amount of prey that must be obtained by breeding adults for themselves and/or their young under the worst probable hunting conditions."

"Worst conditions" must be contextually defined for each species. For example, rain makes hunting more difficult for birds largely preying on xerophilic insects, but easier for birds like Robins (*Turdus migratorius*) that prey on earthworms (*Lumbricus*) driven to the surface by flooding of their burrows. Chill factor is probably a robust measure of hostile conditions for most species. "Worst probable" tentatively can be defined as the 95th percentile of hostile conditions although experience may show selection is actually more potent at some other percentile. The percentile of worst hostile conditions may have to be defined differently in different environments.

The critical supply hypothesis will be disproven if these predictions are found to be false: (a) under the worst probable hunting conditions, territorial birds will find that amount of food that just meets their needs and those of their dependents, and (b) territories within species will increase in size as the variance in hostile conditions increases. The first prediction can be tested by sampling for prey across all weather conditions and by determining whether an inverse correlation exists between birds' rate of harvest and deteriorating environmental conditions, e.g., increasing chill factor. The second can be tested by comparing territory sizes with the frequency and magnitude of negative departures from environmental means in different localities occupied by the same species. Wolf (pers. comm.) has suggested that a fairly large sample of birds and territories will be required to test both predictions because birds should be favored for holding territories containing somewhat more than the critical food supply as a buffer against uncertain conditions. Thus, not every territory may meet the predictions.

The critical supply hypothesis disagrees with the view that territory generally depresses bird populations. In fact, territory defense may secondarily result in larger bird populations than would obtain if birds were non-territorial because Type A territories lower the nest failure rate by exclusion of most adult birds from the hunting grounds supporting breeding birds and their dependents. Acceptance of this latter view neither precludes the possibility that territory holders may be favored for more than one reason nor denies that Type A territories restrict the density of breeding birds. Although territorial exclusion limits breeding bird density by definition, it does not inevitably limit population size or growth rate. To the contrary, restriction of breeding bird density can restrict offspring density with the beneficial effect that improved offspring nutrition and its consequent higher offspring survivorship can more than compensate for reduced offspring density, or, in Williams' (1966:163) words, "Low mortality rates are a result of low fecundity." However, increased population size and growth rate do not necessarily result from higher offspring survivorship because other factors may limit populations as soon as offspring survivorship improves, or offspring survivorship may not improve sufficiently to overcompensate for the reduction of breeding bird density.

CONSORTS AND THE FORAGING BEHAVIOR OF UNPAIRED BIRDS

Several unpaired birds in the second experiment were courted by prospective replacement mates after loss of their original mates. I called these courting birds consorts because there was no evidence of a pair bond. No copulation was observed, consorts largely ignored the young of their would-be mates, and the original adults seemed only to tolerate the presence of consorts. Eventually, some consorts became true pair partners and successfully nested (Power 1975, 1976a, b).

The arrival of consorts on some territories posed the question of whether the possibility of intersexual competition was really eliminated by mate loss. Had consorts arrived on all territories immediately following mate loss, intersexual competition would have been as possible as if mate loss had not occurred, and my experimental design would not have adequately tested for intersexual competition. However, only six of a potential 25 consorts appeared within the first two days following collection when data were taken for the second experiment, only four of these occurred on the first day after collection, and all of those occurring during the first two days were males (Power 1975). Therefore, the foraging behavior of unpaired males could not have been influenced by consorts during the data collection period, only half the females could have been influenced at all, and only one-third of the females could have been influenced on both days of the data collection period. Moreover, the presence of consorts on some females' territories would not explain the overall greater use of high cost behaviors by unpaired females relative to paired females, i.e., how could a few consort males have generated more intersexual competition than the original male mates?

Nevertheless, the arrival of consorts does show that testing for intersexual competition must be performed quickly after mate loss. Observation of foraging behavior from mate loss to fledging could become increasingly biased by the arrival of more and more consorts until it would no longer be correct to assume an absence of intersexual competition on the territories of mate-deprived birds. By taking data on only the first two days after mate collection, I believe I controlled for this potential bias and adequately tested the hypothesis of intersexual competition.

REPRODUCTIVE SUCCESS AND EXPERIMENTAL TREATMENT

In another publication I will detail reproductive success at Calvert for 1970–77. Here I only mention the relation between experimental treatment and reproductive success. Birds in all groups successfully fledged all their young except for those that fledged prematurely after banding. Eight nests had 18 prematurely fledging young, all of which probably died. Thirty nests successfully fledged all young. Young from 34 nests in which fledging dates were known within two days of occurrence fledged in an average time of 20 days without differences between experimental groups. Fledging weights are unknown because behavioral observations precluded weighing nestlings. Except for the possibility of differential fledging weights, neither brood size nor mate loss seemed to affect reproductive success in 1972, the year of the experiments.

If birds adjust clutch size to the probable number of young they can fledge (Lack 1968), brood size would not affect fledging success in these experiments because large broods were of normal size. But mate loss might reduce success by halving the work force anticipated for rearing young. That mate loss apparently did not reduce success in 1972 introduces the possibility that both parents are not normally necessary to rear full clutches, but this possibility was belied by mass reproductive failure in 1974–76 when not even both parents could prevent nestling starvation. Thus, the success of 1972 does not indicate broods are smaller than those that normally can be reared.

MALE EXPLOITATION

The second work load experiment provided data consistent with an interpretation of male coercion but insufficient to demand acceptance of that interpretation. As stated in the Introduction, male exploitation implies both male coercion (with beneficial results to the male) and damage to females. The second experiment included no direct measure of damage. Therefore, I sought an independent means of testing the hypothesis of male exploitation. At the end of the 1976 breeding season, I attached nest boxes to specially constructed observation booths that allowed me to weigh birds as they entered their nests (Power, unpubl. data). In 1977 I weighed 14 pair partners a total of 52 times during the nestling stage to determine whether they showed progressive weight changes. I hypothesized that male exploitation would be indicated by progressive female weight loss (a measure of damage) coincident with either no male weight loss or a slower rate of male weight loss. I partitioned the data into early, middle, and late weights

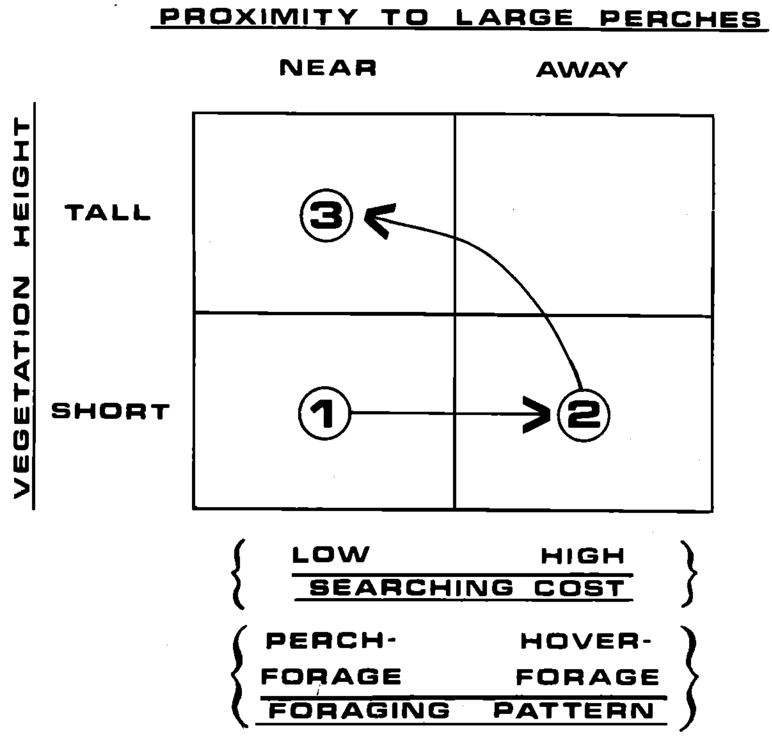


Fig. 10. Foraging tactics in relation to searching cost per foraging pattern, and vegetation height of foraging location. When tactic 1 does not provide enough food to satisfy their work load, birds increase their searching cost per pattern (tactic 2) before they increase their use of tall vegetation (tactic 3).

corresponding to days 1–4, 5–9, and 10–20 of the nestling period. Data were analyzed by the Mann-Whitney U Test.

I found no evidence of difference in male and female weights or of progressive weight change by either sex ($p > 0.15$ in all cases). Thus, because the second work load experiment failed to reveal unequivocal evidence of male coercion and because the subsequent weighings of birds during the nestling stage did not produce evidence of damage to females, I reject the hypothesis of male exploitation with regard to Mountain Bluebird foraging behavior. I admit, however, that weight loss is not the only possible indicator of damage nor, perhaps, even the best.

IMPORTANCE OF VEGETATION HEIGHT AND THE HABITAT ALTERATION EXPERIMENT

In the second experiment, only unpaired birds with large broods intensively sought prey in tall vegetation, and they did this by more frequently perch-foraging (Tables 17, 19, Fig. 10). Birds with lighter work loads used a variety of behaviors including more frequent hover-foraging in short vegetation and bare places away-from-large-perches. This suggests that bluebirds would rather hover-forage in short (or no) vegetation than perch-forage in tall vegetation even though hover-foraging is several times as expensive calorically as perch-foraging. This, in turn, suggests that vegetation height constrains foraging behavior more than the caloric cost of foraging. I found this suggestion curious because most models of foraging tactics (reviewed in Pyke et al. 1977) emphasize the importance of caloric cost. Therefore, in 1976 I performed an experiment to determine whether vegetation height really does constrain foraging behavior more than caloric cost or whether birds were responding to different prey types or densities in places of different vegetation height or to some unknown factor(s).

Prior to manipulation at each territory in the nestling stage, I noted the geographic distribution of foraging effort for the two hours following sunrise (the period of most rapid foraging) and collected arthropods with a sweep net at those places that I intended to use as control and experimental plots. I manipulated the habitat by making available a fresh area of short vegetation; I cut a 1 m wide swath through tall vegetation outward from the nest box for a distance of 10 m along one side of either a preexisting fence or one that I built for the experiment. This procedure allowed birds to choose between short or tall vegetation within 10 m of their nests while foraging from fences and, thereby, eliminated the need for birds to employ foraging patterns of different caloric cost (hover-foraging vs perch-foraging) while hunting in short and tall vegetation. After manipulation, I again noted the geographic distribution of foraging effort for the two hours following sunrise and collected arthropods by sweep netting in adjacent control (uncut) and experimental (cut) plots.

Analysis of the arthropod collection showed that prey types and abundance were greater in tall than short vegetation and decreased when tall vegetation was cut short. In particular, the caterpillars and grasshoppers that closed circuit television had shown to be so important in the nestling diet were less than 25% as common in short as in tall vegetation ($N = 29$ plots; $U = 24$; $p < 0.001$).

Despite these results of insect sampling, the behavioral results of the habitat alteration experiment were consistent with the hypothesis that vegetation height is a critical and more important factor in foraging than the caloric cost of foraging. When given a choice between short and tall vegetation on opposite sides of the same fence and within 10 m of their nests, birds always foraged more frequently (usually exclusively) in short vegetation ($N = 7$; $X = 0$; $p = 0.008$; Sign Test). This shows that birds prefer short vegetation despite its far lower prey abundance. When only tall vegetation was available adjacent to fences within 10 m of nests (before cutting) and birds had to fly some distance (up to 700 m in one case) to reach short vegetation, birds still preferred to forage in short vegetation even when it was not adjacent to a fence or other large perch ($\chi^2 = 66$; $p < 0.001$; McNemar Test). This shows that birds hunt in short vegetation even when it requires the expenditure of many more calories in searching and transportation; it implies that the distribution of short vegetation has a greater influence on foraging behavior than the caloric cost of foraging.

Given the reasonable assumption that bluebird foraging behavior is adaptive, bluebirds' preference for hunting in bare places and short vegetation implies that there is an advantage to foraging in those places that surmounts their lower prey abundances relative to tall vegetation. Bluebirds probably can achieve a higher rate of capture for themselves and a higher rate of food delivery to their nestlings when hunting in places of short (or no) vegetation because insects are probably less concealed. Moreover, birds on the ground in short vegetation and bare places

TABLE 25

LEVELS AND TACTICS OF FORAGING BEHAVIOR

Level	Tactics per level	Total cost per level[1]
I	1	Low
II	1 + 2	High
III	1 + 2 + 3	Highest

	Foraging tactics[2]		
	1	2	3
Characteristic foraging pattern of tactic[3]	PF	HF	PF + (Ha)[4]
Proximity to large perches	NLP	AFLP	NLP
Vegetation height	Short	Short	Tall
Searching cost per tactic[5]	Low	High	Low

[1] Total cost increases with the sequence of levels because each successive level adds a new tactic with its own searching cost to the tactic(s) of the preceding level(s) and its (their) attendant searching cost(s).

[2] PF = perch-foraging; HF = hover-foraging; Ha = hawking; NLP = near-large-perches; AFLP = away-from-large-perches.

[3] All 6 foraging patterns and their attendant staging points are used by birds on all levels, but only 1 pattern is most characteristic of the tactic initiated with each level.

[4] Although birds on level 3 hawk after flying insects more frequently than birds on other levels, hawking is an unimportant diagnostic character of tactic 3 compared to perch-foraging.

[5] In calories.

are probably less impeded by vegetation that is often wet and sticky, more likely to avoid ambush by concealed predators, and better able to view their larger surroundings, including their nests, mates, unwanted conspecifics, and approaching predators.

Bluebirds are not the only bird species foraging in grassland whose behavior is constrained by vegetation structure. Wiens (1969, 1973) and Cody (1968) found that grassland physiognomy was more important in the distribution, abundance, and resource use of grassland birds than either geographic location or floristic composition. Wiens' (1973) observations on the effect of grazing on species distribution are particularly relevant. He found that some species (e.g., Horned Larks, *Eremophila alpestris*) were especially common in heavily grazed places, while others (e.g., Western Meadowlarks, *Sturnella neglecta*) were more common in ungrazed places. It would appear that grazing is important in bluebird resource use because it generates places of short vegetation, keeps them short, and speeds the succession of woody plants that provide large perches and potential sites in which woodpeckers may excavate nest holes. It might, therefore, be true that any impetus for the cattle industry of the West that promotes grazing is also an impetus for Mountain Bluebird populations *provided* that it does not result in grazing so heavy that grassland is destroyed.

FORAGING LEVELS AND TACTICS

Non-experimental observations revealed a three step sequence of foraging behavior in response to increasing work load. I find it convenient to call each of these steps "levels" (defined in Table 25). A level consists of a foraging tactic initiated with it plus the foraging tactic(s) of the preceding level. Thus, Level II succeeds Level I by addition of tactic 2 to tactic 1, and Level III succeeds Level II by addition of tactic 3 to tactics 1 and 2. Tactics are the clusters of foraging behaviors and locations most characteristic of each level; e.g., tactic 1 consists of perch-foraging near-large-perches into short vegetation or bare places. An important feature of the sequence of foraging levels is its additive nature.

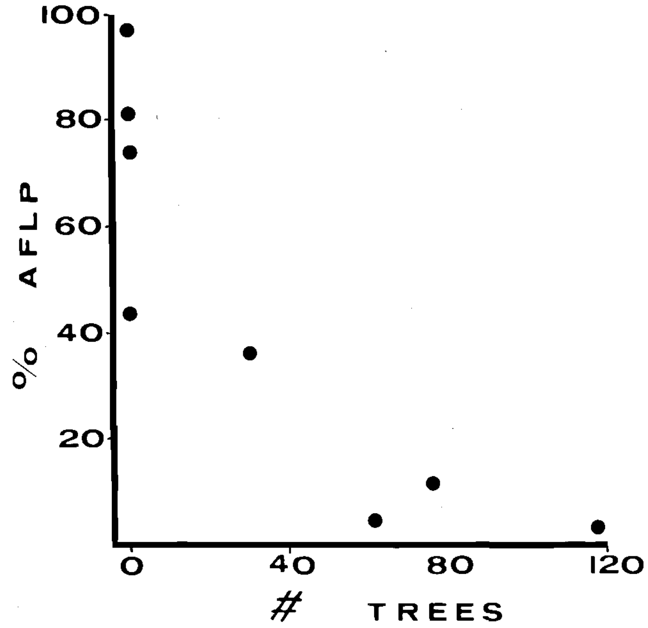


Fig. 11. The effect of scattered trees on use of the area away-from-large-perches (AFLP). Each point represents the use of the area away-from-large-perches by a female whose territorial boundaries were known in 1970.

Bluebirds responded to light work loads by using the Level I behavior of perch-foraging near-large-perches. They responded to heavier loads by also using the Level II behavior of hover-foraging away-from-large-perches. The work load experiments also showed the existence of Level I and II responses and tied them to vegetation height: whether near or away-from-large-perches, birds usually foraged on bare substrate or in short vegetation. The work load experiments also revealed a Level III response stimulated by very heavy work loads, i.e., more frequent perch-foraging into tall vegetation near-large-perches, and to a much lesser extent, more frequent hawking after flying insects.

The other four foraging patterns and their attendant staging points were used by birds on all three levels with no particular relation to work load. They were related to short-lived opportunities (e.g., flycatching after temporarily abundant flying insects) and to habitat peculiarities of territories (e.g., frequent ground foraging on the fallow fields of territory 43, and perch-foraging/hover-foraging by birds with utility lines on their territories).

Vegetation height constrains movement between levels more than does the caloric cost of foraging (Fig. 10). Thus, birds preferred to hunt in short rather than tall vegetation even though hunting in short vegetation away-from-large-perches is most often done by hover-foraging, a pattern that is far more expensive calorically than the perch-foraging usually employed near-large-perches. However, this rule does not imply that the caloric cost of hunting is in itself unimportant, only that it is less important than vegetation height. The intrinsic importance of caloric cost is implied by the relationship of Levels I and II; birds

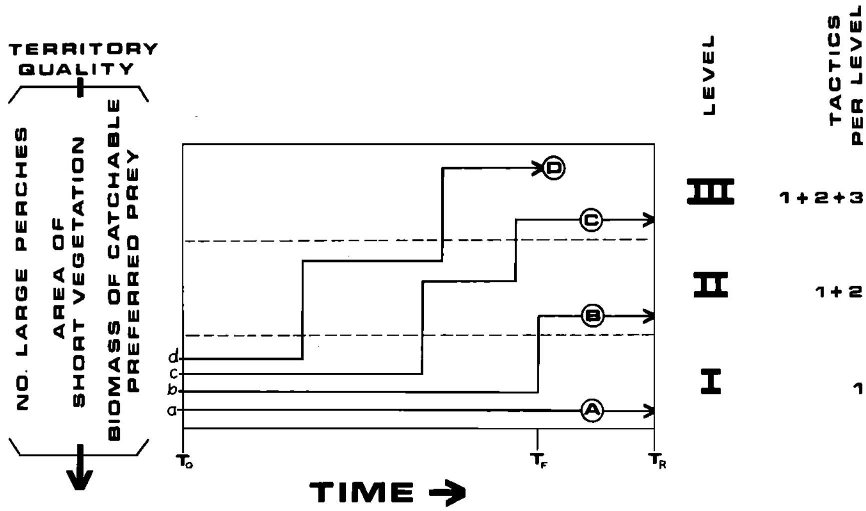


Fig. 12. How differences in quality of territories produce variation among birds in use of foraging levels. Levels have one to three foraging tactics each (see Table 25). Birds go from one level to the next when the tactics of the preceding level do not provide enough food to satisfy their work load. A–D are the individual paths of response of theoretical birds A–D. All birds have their own territories where they are confronted by the same work load. T_0 is the origin of an interval of response to work load. T_R is the time at which A–C reach a goal of reproduction such as fledging of their young. T_F is the time at which D fails in its attempt to reach its goal. Territory quality is fixed for birds A–D at values a–d, respectively; it is determined by the number of large perches, the area of short (or no) vegetation, and the biomass of catchable, preferred prey per territory. All scaling is purely ordinal.

A's territory is so good it can achieve the rate of food delivery required by its work load (and thus reach its goal) by using only the tactic of Level I. B and C have progressively poorer territories and therefore must use the tactics of Levels II and III, respectively, before they can reach their goals. D's territory is so poor it cannot reach its goal despite use of the tactics of all 3 levels.

hunt in short vegetation by perch-foraging near-large-perches before they hover-forage away-from-large-perches.

There is great individual variation in movement between levels. If there were not, only three points would appear in Figure 7D relating work load to high cost score (1 point for each level) because birds' behavior would be completely determined by their work load. However, examination of the results of this study repeatedly shows that the habitat idiosyncracies of territories strongly influence foraging behavior. For example, in Chapter 8 I showed how habitat affected the distance at which some birds foraged from their nests during the work load experiments of 1972. Likewise, Figure 11 shows how the number of scattered trees per territory is reciprocally related to use of the area away-from-large-perches. Realizing the influence of habitat features on foraging behavior, one can expect birds to initiate the new tactics of successively higher foraging levels in accordance with the opportunities afforded by the habitat peculiarities of their individual territories. This principle is illustrated in Figure 12 which shows that birds with the same work load deploy the tactics of the three foraging levels at different times (or not at all) because they possess territories of different qualities.

CHAPTER 10

CONCLUSIONS AND SUMMARY

Sexual foraging differences are differences between the sexes in prey exploitation. They may originate from sexual selection, intersexual competition, division of labor, differences in foraging efficiency, or intersexual exploitation. Although experimentation is probably necessary in most cases to determine the origins of sexual foraging differences, sexual selection always is involved irrespective of other forces because it is the only form of selection acting on the sexes *per se*. Thus, it is the only form of selection producing incipient sexual foraging differences. Other forms of selection can only exaggerate pre-existing sexual differences.

Despite the importance of sexual selection, I detected in the literature a tendency to overlook its significance even when its presence was recognized. In order to bring greater rigor to the study of the evolution and ecological expression of sexual foraging differences than had been previously employed, I observed and experimented on Mountain Bluebirds in the Little Belt Mountains, Cascade County, Montana. The pattern of foraging behavior throughout the breeding season was observed in 1970 and 1971. Three complete block design experiments based on the inferences of earlier observations were run in 1972. In these work load experiments, brood size and number of adults per territory were independently varied to provide a mix of potential factors of work load and causes of sexual foraging differences. Supplementary observations on foraging behavior and follow-up experiments testing hypotheses derived from the results of the work load experiments were performed from 1974 through 1977. The major conclusions of this study are:

(1) *Both sexes are governed in their foraging behavior by certain common factors.* Mountain Bluebirds stage several distinct foraging patterns from a variety of locations and physical objects in order to exploit a range of insect prey in several grassland-forest ecotone microhabitats. Their foraging behavior is driven by their need to feed themselves and their dependents but constrained by (a) the distribution and amount of short vegetation and bare places, (b) the distribution and number of large perches, (c) the caloric cost of foraging, and (d) the distance of foraging sites to the nest.

(a) The 1972 work load and 1976 habitat alteration experiments showed that birds prefer foraging in short vegetation (less than tarsal length in height) and bare places to foraging in tall vegetation (more than tarsal length in height). They also showed that the distribution of short vegetation and bare places more strongly influences foraging location and behavior than factors (b–d). Bluebirds foraged as if they sought to exploit all prey in short vegetation and bare places before exploiting any prey in tall vegetation. The advantage of foraging in short (or no) vegetation is not fully understood because the habitat alteration experiment also revealed that prey density is generally lower in short than tall vegetation. However, elements of that advantage probably include a higher rate of harvest due to poorer concealment of insect prey, less impeded movement, easier ability to detect predators, and more opportunity to monitor the nest and mate while foraging.

(b) Observation and experimentation showed that birds prefer to search for prey from large perches, such as scattered trees and fences, as opposed to other staging points, especially when that allows harvesting prey from short vegetation and bare places. Searching from large perches permits birds to use several foraging patterns, primarily the calorically inexpensive perch-foraging that in many ways typifies bluebird foraging behavior. Searching from large perches also allows birds to observe their mates, nests, and approaching conspecifics and predators, all at a distance. Thus, searching from large perches should reduce the risks of predation of adults and nest contents, loss or degradation of territory, and cuckoldry or mate loss.

(c) The pattern of use of aerial staging points through the breeding season and the work load experiments implied that bluebirds use calorically expensive foraging behaviors only when compelled to by hunger or work load. Use of aerial staging points in hover-foraging and hawking allows prey to be taken from short vegetation and bare places away-from-large-perches.

(d) The first work load experiment showed that birds prefer to forage as close to their nests as the distribution of short vegetation, bare places, large perches, and probably prey, allows. Birds almost always foraged within 500 m of their nests, and usually within 100 m. This preference for foraging close to the nest seems to be constant as it was not influenced by work load in the 1972 experiments. Foraging close to the nest reduces the time and cost of transporting food to the nest and returning to foraging sites.

(2) *Both sexes use the same foraging tactics in successive levels of foraging efforts.* Bluebirds successively use three levels of foraging effort in response to greater hunger and work loads by adding foraging tactics rather than by substituting them. Adding tactics enables birds to use more and more of the foraging locations around their nests instead of roaming farther and farther from them. Foraging near their nests allows birds to minimize their transportation costs while maximizing their rate of food delivery to their young and to quickly perceive and intercept conspecifics and predators approaching their nests. The three levels are:

Level I. Birds satisfy their individual food requirements and respond to light work loads (e.g., small broods) by using tactic 1: perch-foraging into short vegetation and bare places near-large-perches.

Level II. Birds employ Level II tactics when Level I does not allow them to satisfy their hunger and/or food demands of their dependents. This occurs with paired birds rearing large broods and mate-less birds rearing small broods. Level II adds tactic 2 to tactic 1. Tactic 2 consists of frequent hover-foraging away-from-large-perches into short vegetation and bare places. Thus, birds using Level II tactics exploit virtually all the places of short (or no) vegetation near their nests.

Level III. Birds use Level III tactics when even the tactics of Level II are insufficient to satisfy their needs. This occurs at very high work loads and, thus, was exhibited only by mate-less birds rearing large broods in the work load experiments of 1972. Level III adds tactic 3 to tactics 1 and 2. Tactic 3 consists of frequent perch-foraging into tall vegetation near-large-perches and, to a lesser extent, of hawking after flying insects. Thus, birds using Level III tactics intensively exploit all the foraging locations near their nests except tall vegetation away-from-large-perches. Level III produces greater total energy expenditure than Levels I and II because Level III incorporates those prior levels, but tactic 3 requires less energy than tactic 2 because most searching is done from large perches rather than from hovering positions. The hesitancy of birds to use tactic 3 suggests that it produces greater risks than tactic 2, probably the risks of ambush by concealed predators and reduced ability to see other predators, conspecifics, and the nest at a distance.

Use of each level is dependent not only upon the food demand experienced by the individual bird but also upon the features of its territory. Thus, birds with a high number of large perches near their nests switch to Level II later than birds with the same work load but fewer large perches near their nests. Birds with much short vegetation and many bare places near their nests switch to Level III later than birds with the same work load but less short vegetation and fewer bare places near their nests.

Birds use those foraging patterns, staging points, and foraging locations not listed above at all levels of foraging effort depending upon opportunity (e.g., flycatching on a day of high abundance of flying insects) or the idiosyncratic features of territories (e.g., frequent ground-foraging on a territory with few large perches).

(3) *Number of young per attendant adult is the work load factor to which both sexes respond in switching between the three levels of foraging effort.* Number of young per attendant adult is calculated by dividing the number of young in a nest by the number of adults attending that nest. The greater the number of young per attendant adult, the higher the level of foraging effort, other things being equal.

That number of young per attendant adult is the important factor in work load implies that:

(a) Mate loss affects foraging behavior by doubling the number of young per attendant adult.

(b) Rate of food delivery is crucial in fledging nestlings. The higher the rate, the higher the probability of fledging.

(c) The carrying capacity of each territory is less for nestlings than for adults.

(d) Bluebird territories are formed to encompass enough readily available prey to ensure a sufficient rate of food delivery to nestlings even under adverse hunting conditions. Consequently, food will appear to be superabundant under good hunting conditions. Other species with Type A territories probably also form them to meet the minimum food requirements of their young under adverse conditions.

Three other possible work load factors (number of birds per territory, number of adults per territory, and number of young per nest) were tested but found not to affect foraging behavior.

(4) *Males have a higher threshold for use of at least the second of the three levels of foraging effort.* This sexual difference in response threshold generates an important quantitative difference in resource use during the nestling stages. At that time females make far greater use of the area away-from-large-perches than males, particularly by hover-foraging into short vegetation and bare places, thus generating an incomplete micro-allopatry of the sexes on most territories. Thus, the cause(s) of sexual difference in response threshold is the cause(s) of sexual difference in foraging behavior. Several possible causes were investigated:

(a) Males are not less able to hover-forage or exploit the area away-from-large-perches than females. Capture success, morphological measurements, and the second and third work load experiments showed that males can use the same tactics as females with the same success in capturing prey and fledging young.

(b) Males and females do not compete to obtain food for themselves when sexual foraging differences occur. Unpaired males incurred more costs in foraging for young than paired males in the second work load experiment, directly contrary to the intersexual competition hypothesis.

(c) Males probably do not exploit females. The hypothesis of male exploitation was only equivocally supported in the second work load experiment, i.e., three of four expected results occurred but one was contrary to expectation. Moreover, that hypothesis was further weakened in application to bluebirds by a later experiment that showed no evidence of weight loss by females despite their more frequent use of costly behaviors.

(d) The hypothesis that males' brighter color exposes them to a higher risk of predation while using high cost foraging behaviors and, therefore, that males are more reluctant to use high cost behaviors was supported but not fully corroborated. The hypothesis was supported by the occurrence of a sexual difference in response threshold in spite of the proven equal foraging abilities of males and females; it was particularly supported by the sex role reversal of mate-less males in the work load experiments. These males successfully foraged like females. The hypothesis was not corroborated, however, because no predation of males occurred when they foraged like females in the work load experiments. But, predators were not directly built into the design of the work load experiments.

Mountain Bluebird sexual foraging differences may reflect a peculiar kind of division of labor. The first criterion for inferring that selection for division of labor is the cause of bluebird sexual foraging differences appears to be met, i.e., the differences appear to be based on sexual dimorphism in plumage. The third criterion is certainly met, i.e., there is a common effort by males and females to feed nestlings when important sexual foraging differences occur. The second criterion is not so obviously met; males and females do not appear to differ in efficiency of use of different foraging tactics in the sense of caloric efficiency, but they may differ in the sense of efficiency of avoiding predation. Thus, insofar as bluebird sexual foraging differences are a division of labor, they are of a more indirect kind than such obvious reflections of sexual selection as sexual differences in foraging height in warblers or sexual differences in foraging substrate in woodpeckers, which are unencumbered by any difficult-to-measure intermediate variables like differential predation.

(5) *Sexual foraging differences besides those occurring when adults feed young in the nest do not produce different uses of resources by males and females and are divisions of labor directly reflecting sexual selection.* This is exemplified by females foraging more rapidly than males during females' brief periods off the nest in the incubation stages, reflecting their care of eggs.

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LITERATURE CITED

Alexander, R. D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst. 5:325–383.

Ardrey, R. 1966. The Territorial Imperative. Atheneum, New York.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103b:458–476.

Bateman, A. J. 1948. Intrasexual selection in Drosophilla. Heredity 2:349–368.

Bock, C. E. 1970. The ecology and behavior of the Lewis Woodpecker (*Asyndesmus lewis*). Univ. California Publ. Zool. 92:1–100.

Brown, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81:293–329.

Cody, M. L. 1968. On the methods of resource division in grassland bird communities. Am. Nat. 102:107–147.

Darwin, C. R. 1871. The descent of man, and selection in relation to sex. John Murray, London.

Darwin, C. R. 1975. Natural selection. Edited by R. C. Stauffer from an 1856–58 manuscript. Cambridge University Press, Cambridge, England.

Dawson, W. R., and F. C. Evans. 1960. Relation of growth and development to temperature regulation in nestling Vesper Sparrows. Condor 62:329–340.

Forbush, E. H. 1929. Birds of Massachusetts and other New England states. Part III. Mass. Dept. Agric., Boston.

Ford, E. B. 1965. Ecological genetics, second edition. Methuen and Co., London.

Fretwell, S. 1972. Populations in a seasonal environment. Monogr. Popul. Biol. 5:1–217.

GRIFFIN, D. R., AND C. D. HOPKINS. 1974. Sounds audible to migrating birds. Anim. Behav. 22:672–678.

HAMILTON, T. H. 1961. The adaptive significance of intraspecific trends of variation in wing length and body size among bird species. Evolution 15:180–195.

HAMILTON, W. D. 1964. The genetical evolution of social behavior. J. Theoret. Biol. 7:1–52.

HAMILTON, W. D. 1970. Selfish and spiteful behaviour in an evolutionary model. Nature 228:1218–1220.

HARTSHORNE, J. M. 1962. Behavior of the Eastern Bluebird at the nest. Living Bird 1:131–149.

HOWARD, H. E. 1935. Territory and food. Brit. Birds 28:285–287.

HUTCHINSON, G. E. 1965. The ecological theater and the evolutionary play. Yale Univ. Press, New Haven, CN.

KILHAM, L. 1970. Feeding behavior of Downy Woodpeckers, part 1. Preference for paper birches and sexual differences. Auk 87:544–556.

KRUUK, H. 1972. The Spotted Hyena: a study of predation and social behavior. Univ. Chicago Press, Chicago, IL.

KÜCHLER, A. W. 1964. Potential natural vegetation of the conterminous United States. Spec. Publ. No. 36. Am. Geog. Soc. N.Y.

LACK, D. 1968. Ecological adaptations for breeding in birds. Chapman and Hall, London.

LASIEWSKI, R. C. 1963. Oxygen consumption of torpid, resting, active, and flying hummingbirds. Physiol. Zool. 36:122–140.

LIGON, J. D. 1968. Observations on Strickland's Woodpecker, *Dendrocopos stricklandi.* Condor 70:83–84.

LIGON, J. D. 1973. Foraging behavior of the White-headed Woodpecker in Idaho. Auk 90:862–869.

MILLER, W. 1970. Factors influencing the status of Eastern and Mountain Bluebirds in southwestern Manitoba. Blue Jay 29:38–46.

MORSE, D. H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. Ecology 49:779–784.

PINKOWSKI, B. C. 1975. Growth and development of Eastern Bluebirds. Bird-Banding 46:273–289.

POWER, H. W. 1966. Biology of the Mountain Bluebird in Montana. Condor 68:351–371.

POWER, H. W. 1974. The Mountain Bluebird: sex and the evolution of foraging behavior. Unpubl. Ph.D. dissert. Univ. of Michigan, Ann Arbor.

POWER, H. W. 1975. Mountain Bluebirds: experimental evidence against altruism. Science 189:142–143.

POWER, H. W. 1976a. Altruism in Mountain Bluebirds? (Reply). Science 191:809–810.

POWER, H. W. 1976b. Altruism: methodological and definitional issues. (Reply). Science 194:562–563.

POWER, H. W. 1980. Predation on females at the nest cavity and male escorting in Mountain Bluebirds. Wilson Bull., in press.

POWER, H. W., AND C. G. P. DONER. 1980. Experiments on cuckoldry in the Mountain Bluebird. Am. Nat., in press.

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

RAND, A. L. 1952. Secondary sexual characteristics and ecological competition. Fieldiana-Zoology 34:65–70.

RICKLEFS, R. 1968. Patterns of growth in birds. Ibis 110:419–451.

ROBINS, J. D. 1971. Differential niche utilization in a grassland sparrow. Ecology 52:1065–1070.

ROBINSON, M. H. 1969. Defenses against visually hunting predators. Evol. Biol. 3:225–259.

ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits *Parus major.* Ibis 108:313–347.

ROYAMA, T. 1970. Factors governing the hunting behavior and selection of food by the Great Tit (*Parus major* L.). J. Anim. Ecol. 39:619–668.

SCHALLER, G. B. 1972. The Serengeti lion: a study of predator-prey relations. Univ. Chicago Press, Chicago, IL.

SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68:113–151.

SELANDER, R. K. 1972. Sexual selection and dimorphism in birds. Pp. 180–230 *in* B. Campbell (ed.), Sexual selection and the descent of man, 1871–1971. Aldine, Chicago, IL.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry: the principles and practice of statistics in biological research. W. H. Freeman, San Francisco, CA.

STORER, R. W. 1966. Sexual dimorphism and food habits in three North American Accipiters. Auk 83:423–436.

TINBERGEN, N. 1957. The functions of territory. Bird Study 4:14–27.

TRIVERS, R. L. 1971. The evolution of reciprocal altruism. Quart. Rev. Biol. 46:35–57.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 *in* B. Campbell (ed.), Sexual selection and the descent of man, 1871–1971. Aldine, Chicago, IL.

TULLOCK, G. 1979. On the adaptive significance of territoriality: comment. Am. Nat. 113:772–775.

VAN VALEN, L. 1965. Morphological variation and width of ecological niche. Am. Nat. 99:377–390.

VAUGHAN, T. A. 1959. Functional morphology of three bats: *Eumops, Myotis, Macrotus*. Univ. Kansas Publ. Mus. Nat. Hist. 12:1–153.

VERNER, J. 1977. On the adaptive significance of territoriality. Am. Nat. 111:769–775.

VERNER, J., AND M. F. WILLSON. 1969. Mating systems, sexual dimorphism, and the role of male North American passerine birds in the nesting cycle. Ornithol. Monogr. 9:1–76.

WALLACE, G. J. 1959. The plight of the bluebird in Michigan. Wilson Bull. 71:192–193.

WALLACE, R. A. 1974. Ecological and social implications of sexual dimorphism in five melanerpine woodpeckers. Condor 76:238–248.

WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8:1–93.

WIENS, J. A. 1973. Pattern and process in grassland bird communities. Ecol. Monogr. 43:237–270.

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton Univ. Press, Princeton, NJ.

WILLIAMSON, P. 1971. Feeding ecology of the Red-eyed Vireo (*Vireo olivaceous*) and associated foliage-gleaning birds. Ecol. Monogr. 41:129–152.

WILSON, E. O. 1975. Sociobiology. Harvard Univ. Press, Cambridge, MA.

WOLF, L. L., AND F. R. HAINSWORTH. 1971. Time and energy budgets of territorial hummingbirds. Ecology 52:980–988.

WOLF, L. L., AND J. S. WOLF. 1976. Mating system and reproductive biology of Malachite Sunbirds. Condor 78:27–39.

WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, London.

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