

LIFE HISTORY FACTORS AFFECTING THE INTRINSIC RATE OF NATURAL INCREASE OF BIRDS OF THE DECIDUOUS FOREST BIOME

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The intrinsic rate of natural increase, r_m , is an important population trait indicating the capacity of a population for growing (Lotka 1925). It is, specifically, the rate of increase per head when the population is suffering no adverse effects from crowding (see Caughley and Birch 1971 for a more complete definition and Cole 1954 and Andrewartha and Birch 1954 for discussion of the concept). A high r_m results from many offspring (in birds, large clutches and multiple broods), low mortality through the reproductive ages, especially through the first reproduction, reproduction at an early age, and a long reproductive life.

MacArthur and Wilson (1967) used the terms r and K selection to designate, respectively, selection occurring in populations living in an uncrowded environment and selection in populations at their carrying capacity (that is, at K). One important contribution of the discussions of r and K selection (Cody 1966; MacArthur 1960; Pianka 1970, 1972; Southwood et al. 1974) was the realization that, contrary to the traditional view, natural selection will not necessarily tend to maximize r_m in populations which are generally at their carrying capacity.

In a series of field studies of the organization of avian communities and life histories of the constituent organisms (such as Brewer 1967 and Robins 1971) differences between communities in life history traits influencing r_m became evident. The purpose of this study was to examine, by a literature survey, life history features bearing on r_m for characteristic birds of different communities of the deciduous forest biome of eastern North America. More specifically, the purpose was to determine whether species of successional communities tended to have traits favoring a high r_m in comparison with species of presumably more stable communities, such as the climax forest.

METHODS

Three basic vegetation types, forest, forest edge, and grassland-marsh, were subdivided as follows: forest into wet, mesic, and dry; forest edge into thicket, trees-shrubs, and open trees; and grassland-marsh into grassland and marsh. Thicket is dense, low, woody growth, generally set in herbaceous vegetation; tree-shrubs is an interspersed growth of low, woody growth with some trees and usually patches of herbaceous vegetation; open trees is a parkland category with good-sized trees numerous but not forming a closed canopy. After preparation of lists of characteristic native species for each community, life history information was collected. Seventy-five species were used. Several other species breeding

in the biome were omitted because we could not locate minimal satisfactory life history information for them. Studies from the part of the biome between about 38° and 44° N latitude were favored; findings obtained elsewhere were ignored unless there seemed reason to believe they were applicable to the middle area of the biome. Features considered were clutch size, number of broods per year, age at first reproduction, presence of non-breeding individuals, and nesting, hatching, and fledging success. For most species included we failed to locate satisfactory information on one or more topics. In cases of conflicting statements we exercised judgment, often based on our own experience with the species, to reject aberrant reports.

The species used, by community, are listed in Appendix I. A complete listing of sources of life history information has not been provided because most are the same as those cited in the various volumes of Life Histories of North American birds by A. C. Bent and in the compilations by Kendeigh (1952), Verner and Willson (1966), and Ricklefs (1969).

Most data were assembled so that significance of differences in a particular trait could be tested between communities using χ^2 . In the subsequent text, stated differences are significant at the 5% level. To save space we have not included χ^2 values but the data are presented in such a way that the reader can readily calculate them for himself.

CLUTCH SIZE

Modal clutch size was determined for each species for which satisfactory data were available. For double-brooded species, the first clutch was used. When 2 clutch sizes seemed equally prevalent, the species was counted as half in one category and half in the other.

Modal clutch size in the deciduous forest biome overall is clearly 4 (Table 1) but differences existed among the communities. Confining our attention to open-nesting passerine species (to eliminate 2 obvious additional sources of variation in clutch size), number of eggs is largest in grassland where there are as many species with clutches of 5 as of 4 and smallest in mesic forest where modal size is but 3.

Comparing related birds in different communities tends to confirm the trend of smaller clutches in forest, particularly mesic forest. The 4 species of mesic forest having clutches of 3 are Red-eyed Vireo (Southern 1958), Eastern Wood Pewee (Bendire 1895, Mengel 1965), Acadian Flycatcher (Mumford 1964), and Hooded Warbler (Mengel 1965). Most vireos (Bent 1950) and small flycatchers (Walkinshaw 1966a, b) in other communities of the biome have 4-egg clutches. Other warblers of the biome have 4- or 5-egg clutches (Bent 1953).

Good comparisons within families are fewer for grassland-marsh versus other habitats. The grassland sparrows, nevertheless, seem to have 5 eggs more frequently than do sparrows of forest edge; the Bobolink (Raim 1975) and Eastern Meadowlark (Roseberry and Klimstra, 1970) have 5 eggs whereas the Northern Oriole has 4 (Bendire 1895); and the marsh wrens have larger

TABLE 1
NUMBERS OF SPECIES HAVING A GIVEN MODAL CLUTCH SIZE BY HABITAT (ALL SPECIES
AND, SECOND LINE IN EACH HABITAT, OPEN-NESTING PASSERINES)

Habitat	Modal Clutch Size ¹										
	2	3	4	5	6	7	8	9	10	11	15
Mesic forest		4	2.5	2.5	1	1					
		4	2		1						
Wet forest	2		4	2						1	
			4								
Dry forest	2		4	1			1				
			3	1							
All forest	4	4	10.5	5.5	1	1	1			1	
		4	9	1	1						
Grassland		1	3.5	3.5		1					
		1	3.5	3.5		1					
Marsh		1	3	2	1		1	1	1		
			2	1							
Grassland-marsh		2	6.5	5.5	1	1	1	1	1		
		1	5.5	4.5		1					
Thicket			4								1
			4								
Trees-shrubs	1	4	6	4							
		3	6	3							
Open trees		1	4	1	2						
			4								
All forest edge	1	5	14	5	2						1
		3	14	3							
Total, all habitats	5	11	31	16	4	2	2	1	1	1	1
		8	28.5	8.5	1	1					

¹ No species had modal clutch sizes of 1, 12, 13, or 14.

clutches than do House or Carolina wrens (Bent 1948), even though the latter pair are hole-nesters.

NUMBER OF BROODS PER YEAR

The difference between forest and other habitats in the tendency toward multiple broods is striking (Table 2). Forest birds are single-brooded; the regular exceptions are the Wood Thrush (Brackbill 1958), Carolina Wren (Laskey 1948), and Acadian Flycatcher (Walkinshaw 1966c). A high proportion of grassland-marsh and forest-edge birds—probably well over half in both categories—regularly have multiple broods.

TABLE 2
NUMBER OF SPECIES WITH SINGLE OR MULTIPLE BROODS BY HABITAT¹

Habitat	1 brood	1 brood, sometimes 2	1 brood + 1, sometimes 2	2 or more broods
Mesic forest	3	6	9	2
	2	4	6	2
Wet forest	4	2	6	1
	0	2	2	1
Dry forest	2	3	5	0
	1	2	3	0
All forest	9	11	20	3
	3	8	11	3
Grassland	1	2	3	5
	0	1	1	3
Marsh	1	4	5	3
	0	0	0	0
Grassland-marsh	2	6	8	8
	0	1	1	3
Thicket	0	1	1	4
	0	1	1	3
Trees-shrubs	3	4	7	5
	1	1	2	1
Open trees	2	0	2	4
	0	0	0	4
All forest edge	5	5	10	13
	1	2	3	8
Total, all habitats	16	22	38	24
	4	11	15	14

¹ The category "1 brood, sometimes 2" includes species in which second broods have been reported but are rare and species said to have one brood in the north and two in the south. The first line in each habitat includes all species, the second, species on which information is based on banded populations.

Most species in a family are consistent in being single- or multiple-brooded regardless of habitat; differences between communities, consequently, are mainly the result of differences in the distribution of families among the various communities. Differences within families, when they occur, generally are in the expected direction: although most warblers have only one brood, the Common Yellowthroat (thicket) has 2 (Stewart 1953); most fringillids raise more than one brood but the Rose-breasted Grosbeak (dry forest) raises only one (Forbush 1929 but cf. Rothstein 1973).

NON-BREEDING BIRDS

As Cole (1954) and Lewontin (1965) have demonstrated, the age at which reproduction begins is an extremely influential determinant of r . Although some birds are known to delay reproduction until they are 2 or more years old (Lack 1968:295–305), with a consequent low value for r , most of the birds considered here probably breed as yearlings.

The existence of “surplus” or non-breeding birds is known for several species, including birds of forest, forest edge, grassland, and marsh (e.g., Stewart and Aldrich 1951, Offutt 1965, Ficken 1962, Zimmerman 1963, 1966, Hardy 1961, Kendeigh 1941). Reliable information is not available for enough species to draw conclusions as to differences among the various habitats. Most of the surplus birds detected are males and in a few of the species considered here (such as the Red-winged Blackbird) some or most males regularly delay breeding until their second year. The failure of males to breed would not lower r_m if all females were mated. The failure of females to breed would lower r_m , and markedly if the birds which did not breed were yearlings. Although the percentages of birds of various ages which do not breed is difficult to determine, the topic is one to which more life history studies should address themselves.

For a few species, mostly not those of habitats considered here, age at first breeding is clearly density dependent, being earlier when populations are low (Lack 1968:298). For these species r_m is higher than it would appear to be when based on the age of first reproduction in stable populations.

MATING SYSTEMS

Monogamy is the rule among species of the deciduous forest biome (Table 3). Our compilations agree with Verner and Willson (1966) that regular polygyny is a feature primarily of grassland and marsh.

The influence of polygyny on r_m is not completely obvious. We may consider the situation in which a number of birds greater than the carrying capacity is available to occupy a particular area. If, as often happens, males which fail to gain a mate derive less of their food from the area than those that do (for example, by failing to maintain a territory through the whole breeding season; Ficken 1962), then polygyny will increase r_m by substituting females for males as members of the population existing on the limited resources.

This implies that polygyny might raise r_m for birds living at K but would be unlikely to do so for birds under uncrowded conditions. It has been suggested (Verner 1964, Orians 1969) that selection for polygyny occurs where resources important for nesting are patchily distributed such that polygamous

TABLE 3
NUMBER OF MONOGAMOUS AND POLYGYNOUS SPECIES BY HABITAT¹

Habitat	Monogamous	Monogamous with exceptions	Monogamous + monogamous with exceptions	Polygynous
Mesic forest	7	2	9	0
Wet forest	3	3	6	0
Dry forest	4	1	5	0
All forest	14	6	20	0
Grassland	4	0	4	4
Marsh	1	0	1	3
Grassland-marsh	5	0	5	7
Thicket	2	2	4	0
Trees-shrubs	12	0	12	1
Open trees	3	3	6	1
All forest edge	17	5	22	2
Total, all habitats	36	11	47	9

¹ The category "Monogamous with exceptions" includes normally monogamous species for which any incident of polygyny has been reported.

females on good territories are more successful than monogamous ones on poor territories. This hypothesis of the evolution of polygyny depends on local populations being at K ; at population sizes which were low relative to K , sufficient favorable habitat would be available that all males could establish themselves in suitable sites and monogamous females presumably would be more successful than polygamous ones (because of the greater participation of the male in nest building, feeding young, etc., Martin 1974).

OTHER FACTORS INFLUENCING r_m

For 2 species otherwise similar, the one producing more eggs in its first year has a higher r_m and this is true even if the other species later has an increased number of eggs so that the lifetime egg production is the same (Lewontin 1965). Some changes in number of eggs laid with age occur (Ricklefs 1973:368, van Balen 1973) but how important they are and whether there is a difference among habitats are unknown.

The pattern of survivorship of birds under uncrowded conditions is another trait influential in determining r_m but poorly known. Survival to the first breeding season is, of course, particularly important. Information on survival to fledging is available for many species and some comments on this time

period are given beyond; however, the period from fledging to first nesting is difficult to study owing to its being the main time of dispersal in birds. Also, differential mortality in this period is probably of importance in population limitation; consequently, the mortality figures for stable populations will be higher than under uncrowded conditions and will be of little value for comparisons designed to evaluate r_m .

ESTIMATES OF r_m

It is worth dealing with some numerical examples to help visualize the effects of some of these life history features on r_m . Uncrowded survivorship/maternity data for a real calculation of r_m do not exist for any bird as far as we know. For the following calculations we tried to use mortality values that would be realistic for a small altricial bird in an uncrowded environment. The assumed mortality rates were 15.5% from egg-laying to hatching (15 days), 7.5% for the nestling period (10 days), 40% per annum from fledging to the age of 12 months, and 35% per annum past this age. Potential natural longevity was assumed to be 10 years.

The same survivorship schedule was used throughout. The maternity schedule was varied to include clutch sizes of 1–8 eggs and 1–3 broods per year. Egg laying was assumed to begin at 12 months of age for all birds in single-brooded species and for birds of first broods in multiple-brooded species but at 11 months for birds produced in second broods and at 10 months for third broods. Also, a one-year delay (first breeding at 24 months for single-brooded species) was examined for several clutch-brood combinations. Calculation of r was iterative, using the formula (Lotka 1925)

$$1 = \sum_{x=0}^{\infty} l_x m_x e^{-r_m x}$$

where l_x is survival rate at age x , m_x is natality rate at age x , and e is the base of natural logarithms (see Birch 1948 for additional details of calculations).

Although we believe that the survivorship-natality model and the values used are realistic, some simplifications are involved (Ricklefs 1973:394–396). We think that these do not impair the model's usefulness for examining the relative effects on r_m of the various maternity schedules.

The results (Fig. 1) suggest that r_m for mesic forest species (if represented by 1 clutch of 3 eggs per year) may be only about $\frac{1}{4}$ that of grassland species (if represented by 3 clutches of 4 eggs per year). The importance of this difference for population growth is more easily grasped when translated into population figures. If a male and a female of 2 species arrive on an island of favorable habitat and one species undergoes population growth such that

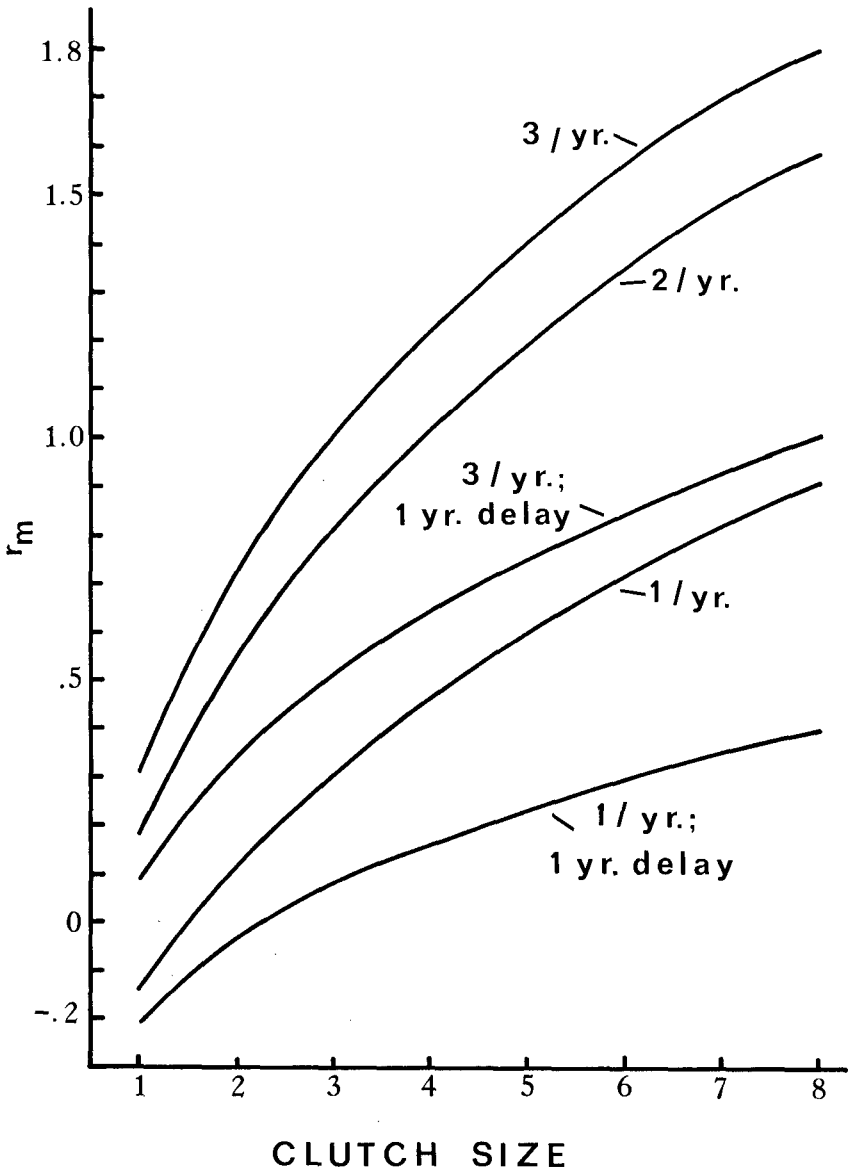


FIG. 1. Values of r_m (per head per year) for birds having clutch sizes of 1 to 8 and 1-3 broods per year (mortality schedules as described in text).

r is .3 per head per year and the other such that r is 1.2 (Fig. 1), the population size at the end of some period (t) during which the environment remains uncrowded is given by the expression for exponential population growth

$$N_t = N_0 e^{rt}$$

If we take t as 3 years, then the population of the species with the r of .3 is, at the end of 3 years, 3 or 4 birds. The population of the species with the r of 1.2 is over 70 birds.

Certain other features in Fig. 1 are worth pointing out. As has been mentioned, age at first breeding is extremely important. A bird which lays a clutch of 8 eggs but delays breeding until 2 years of age has an r_m well below that of a bird which lays a clutch of 4 eggs but begins breeding at age 1 (Fig. 1). Delaying reproduction by a year reduces r_m proportionately less for small clutches than for large but only birds with considerably lower mortality than that assumed in the model could adopt a life history of delayed breeding if their clutch size was 1 or 2; r_m in both these situations is negative. Finally, the assumed survival rates are not high enough to allow a bird such as the Passenger Pigeon (which was, of course, a mesic forest species) to exist; r_m is negative for a bird laying a single 1-egg clutch per year.

If, as we believe, the estimates of r_m in Fig. 1 are in the right neighborhood, they indicate that r_m for birds is low in relation to other animals of comparable size (e.g., Leslie and Ransom 1940, Leslie 1945). The main reason is the periodic nature of avian reproduction. Birds of temperate regions have little opportunity for raising r_m by lowering age of first reproduction below one year; the opportunity does exist for some tropical species and a few have taken it (Cody 1971:468). Most tropical birds, however, breed at about one year, have some sort of annual cycle of reproduction (Immelmann 1971) and, owing particularly to their small clutches (Ricklefs 1973), probably have low values of r_m .

DISCUSSION

It has been postulated that r selection should occur in organisms of temporary or unstable ecosystems; species would be fitted to such environments if they could "(1) discover the habitat quickly, (2) reproduce rapidly to use up the resources before other, competing species could exploit the habitat, and (3) disperse in search of other new habitats as the existing one began to grow unfavorable" (Wilson and Bossert 1971:110). In stable environments (Wilson and Bossert mention climax forest, coral reefs, and caves) "no longer is it very advantageous to have a high r . It is more important for genotypes to confer competitive ability, in particular the capacity to seize and to hold a piece of the environment and to extract the energy produced by it."

TABLE 4
SUMMARY OF LIFE HISTORY TRAITS AFFECTING r_m BY HABITAT

Trait	Habitat			
	Mesic forest	Other forest	Grassland marsh	Forest edge
Clutch size	low	medium	high¹	medium
Number of broods	single	single	multiple	multiple
Mating systems	monogamy	monogamy	polygyny frequent	polygyny infrequent
Non-breeding females, uncrowded changes in clutch size or number of broods with age	?	?	?	?

¹ Traits favoring a high r_m are shown in boldface.

Our compilations indicate that birds of forest, especially mesic forest which is generally climax, tend to have life history traits favoring a low r_m (Table 4). Birds of forest edge and, especially, grassland and marsh tend to have traits favoring a high r_m . We address, first, the question of whether forest represents a K-selecting environment and grassland, marsh, and edge, r-selecting environments and, later, the question of whether the low r_m of forest birds is, or is not, maximal.

Are breeding-bird populations at carrying capacity?—By the Clementsian criterion of potential replaceability (Clements 1916) all of the ecosystems discussed except mesic forest are successional and, in this sense, temporary. The actual period of existence of a particular stand may vary from a few years for some pioneer herbaceous communities to thousands of years for some marshes and forests. For some kinds of organisms some of these habitats may be uncrowded for a significant period after establishment but we think this is not true for birds. We know of no studies of newly created grassland showing population growth curves for any bird species unrelated to successional changes in vegetation. In studying a new alfalfa field Harrison (1974) found the same species in almost the same numbers in the first full year of its existence (following planting the preceding year) as in its second. The high dispersal powers of birds in conjunction with habitat selection presumably account for the virtually immediate occupancy at carrying capacity of newly created habitats.

We believe that the characteristic birds of all of these habitats tend to be near K. The existence of surplus birds in various life history studies and in the studies of Stewart and Aldrich (1951) and Hensley and Cope (1951)

suggest K conditions. Further, in those 2 studies, the re-establishment of most species in 1950 in about the same numbers as 1949, despite the almost complete annihilation of the 1949 resident population and the failure of the plot to produce any fledglings (3 species excepted) suggest that these numbers represent carrying capacities. Experiments in which nest-boxes have been added to habitats (cited in von Haartman 1971:401–404) have produced larger breeding populations of both migratory and sedentary species.

The studies mentioned in the preceding paragraph deal mostly with forest species but surplus birds are known in marsh and forest edge (e.g. Kendeigh 1941, Nero 1956). The correlation of numbers of Red-winged Blackbirds with breeding site favorability reported by Davis and Peek (1972) suggests K conditions. As we have already pointed out, polygyny, common only in grassland and marsh, is not an adaptation to uncrowded conditions.

In the next section we present evidence that grassland species frequently do not occupy every area that seems to be suitable habitat. This may seem contradictory to the conclusion just reached but local populations and regional (or whole-species) populations must be considered separately. Birds tend to be at or near K in examples of their optimal habitat because of their tendency to occupy habitats according to their suitability (Fretwell 1972). Even if some additional field, marsh, or forest exists which could support the species, the slightly suboptimal habitat tends not to be occupied (disregarding the effects of site tenacity and sociability which are complicating factors for some species) if the regional population of the species is low (cf. Svårdson 1949, Brown 1969).

Consequences of low habitat stability in grassland and marsh.—We suggest that a feature important in selection for life history traits affecting r_m by which forest and grassland-marsh differ is stability (cf. Wilbur et al. 1974). Grasslands and marshes may show drastic differences from year to year, or even within years, even though successional changes are occurring slowly, if at all. The classic study of vegetational fluctuation (sensu Hanson and Churchill 1961) is of the Nebraska grasslands during the great drought of the 1930's (e.g. Weaver 1961). Such fluctuations presumably affect K for the bird populations, both by altering the structure of the vegetation and by changing the kinds and amounts of food. Changes of similar magnitude occur in marshes (Weller and Spatcher 1965). Vegetational fluctuations have rarely been reported for forest. This is at least partly because of the buffering effect of the greater perennial biomass of forest and possibly also a greater capacity for integrating environmental fluctuations (e.g., by leaf production being based partly on energy stored in preceding years). Ricklefs (1969) has suggested that the high starvation component of nestling mortality of birds

of field and marsh indicates that the food supply in these habitats is more variable than in forest and edge.

Fluctuations in avian populations in marshes were studied by Weller and Spatcher (1965). Their study began with the marshes nearly dry and continued into a wet period in which much of the vegetation was inundated. Bird populations changed drastically; for example, Least Bittern nests at one marsh rose from 5 in 1958 to 62 in 1961 and dropped to 2 the following year (Weller and Spatcher 1965: Table 4).

Reports of fluctuations in density of grassland species are numerous. Wiens (1974:397), in a paper which develops the theme of instability in climax grassland, cited large population changes in bird numbers on a Texas grassland during drought. Most reports are not quantitative but consist of remarks about the "local and erratic" occurrence of the species, implying that not all seemingly suitable areas are occupied every year and that abundance at a given site varies greatly from year to year. Some typical citations are Barrows (1912), Pough (1946), Smith (1963), Bull (1964), and Mengel (1965) for the Dickcissel, Short-billed Marsh Wren, Grasshopper Sparrow, Henslow's Sparrow, and Lark Sparrow, respectively.

Our own observations on grassland birds and several accounts in the literature (Nero 1956, Smith 1963, Robins 1971, Potter 1972, Raim 1975) suggest a shifting pattern of occupancy, including shifts in territory locations and changes in population size, even within a breeding season. A forest-edge species for which large-scale territory shifts have been reported is the Gray Catbird (Darley et al. 1971). Comparable changes between breeding seasons and, especially, within the season are difficult to find in the literature for forest species. Populations of the more common species on a given area vary little from year to year (Brewer 1963). The whole breeding population apparently arrives within a few days and the arrival of a new male thereafter is a rare event (e.g., Hann 1937).

We suggest that grassland or marsh that remains stable tends to support populations around *K*. Because of habitat fluctuations altering *K*, populations fairly frequently find themselves overcrowded or undercrowded. The shifting pattern of occupancy of grassland birds can be best understood as movements into and out of areas as suitability changes. Areas which, in fact, show large swings in numbers with essentially no change in vegetational or other environmental conditions are usually suboptimal for the species in question, occupied mainly by the overflow, large, small, or none, from more nearly optimal areas (cf. Kluyver and Tinbergen 1953, Brewer 1963, 1967, Fretwell 1972).

We presume that the main source of additional birds, when grassland popu-

lations build up over the course of the breeding season, is from nearby areas abandoned as unsuitable; however, this may not be the only source. It is possible, for example, that some of these species have an unusually long period over which they return from winter quarters.

Although we suspect that grassland birds have evolved a more flexible system of habitat occupancy than forest birds, it is possible that forest birds if presented with habitat changes of comparable magnitude might also show a more shifting pattern. Kluyver (1951), for example, was able to cause adult Great Tits, *Parus major*, to abandon an area by plugging all the nest holes. When about half of a 10 ha spruce forest was blown down by hurricanes between breeding seasons (Cruickshank and Cadbury 1954, 1955) nesting Golden-crowned Kinglets, *Regulus satrapa*, decreased from 8 to 1; however, several spruce forest warblers showed no significant decline.

Wilson and Bossert (1971) mentioned the abilities to discover habitat quickly and to disperse in search of new areas as the existing one began to grow unfavorable as traits to be selected for in species of temporary habitats. These traits are related to a high r_m only to the degree that a high r_m favors greater or more effective dispersal. For most organisms, increasing offspring is a poor way of increasing distant dispersal. This is because the number of dispersing units, or disseminules, reaching a given distance tends to be directly proportional to the number produced (e.g., Kettle 1951, Andrewartha and Birch 1954:103). Consequently, committing the resources necessary to double production of offspring merely doubles whatever small fraction of an individual is expected to reach some distant site. Because an exponential relationship tends to exist between dispersal ability and the number of disseminules reaching a particular distance, increasing dispersal ability is a more efficient way of achieving increased dispersal.

For birds (and some other kinds of organisms; Johnston 1961, French 1971), the pattern of dispersal is complex, with more individuals reaching greater distances than would be expected. Birds as different as the Song Sparrow (Johnston 1956) and the Pied Flycatcher, *Ficedula hypoleuca*, (Berndt and Sternberg 1968) have a basically similar dispersal pattern. Murray (1967) showed that this pattern could be reproduced by a model making the assumptions that dispersal is by sub-adults, the adults returning to their previous breeding site where they are dominant to sub-adults; that the first sub-adult to reach an unoccupied site is dominant to subsequent arrivals; and, an important implicit assumption, that the environment is patchy such that individuals that leave the modeled habitat rarely settle on an immediately adjacent site but instead go some appreciable distance. These assumptions seem realistic for birds (Murray 1967; see also Pinowski 1965).

Murray further found that increasing survival of young to breeding age

from 23% to 62% increased the number of young settling near their natal site slightly but greatly increased the number of young leaving the area. It seems possible, then, that a high production of offspring, in fact, increases dispersal. The major affect is probably increased dispersal ability as a result of intra-specific antagonism.

Although this paper deals primarily with life history traits affecting r_m , this is just one aspect of the broader question of the adjustment of life histories to ecosystems. There are too few detailed studies to judge whether birds of different habitats differ in dispersal pattern. One behavioral feature, however, that could increase dispersal ability, including the ability to leave an unfavorable area for a favorable one in the middle of the summer, exists in at least 2 grassland birds. In the Bobolink (Raim 1975) males throughout the breeding season take long flights in which they leave the breeding area; often they fly out of sight and may be gone for many minutes. Suitable areas could be found on such flights, either for switching locations in the same breeding season or for possible occupancy in a later one. Similar "distant flights" also occur in the Dickcissel (Schartz and Zimmerman 1971).

The foregoing discussion would suggest that site tenacity (except on optimal sites) ought to be low in grassland and marsh and this seems often to be the case; however, males of one of the most characteristic marsh species, the Red-winged Blackbird, are known to show strong site tenacity (Nero 1956). Davis and Peek (1972) described a situation in which the number of territorial males (apparently not individually marked) varied in one marsh only between 17 and 21 during an 8-year period that included a drought. The number of females in the same period varied from 7 to 42. Surplus females are rare or absent in the species (Orians 1969) so many of the females presumably shifted to other areas where males were occupying more favorable habitat. This suggests that polygyny is, in effect, an exceedingly flexible method of maintaining a high r_m where short-term fluctuations are common. The evolution of such a system is explainable by individual selection: females having the ability to shift would probably leave more offspring than if they remained in a deteriorating habitat; males, on the other hand, might well contribute more to the next generation if they stayed put rather than trying to establish themselves in a strange area, often in competition with other, already-established, males. These disadvantages may help to explain the higher site tenacity of male birds generally; however, except in polygynous species, the result of some males occupying territories unacceptable to females might be to leave some females unmated, lowering r_m .

Does the low r_m of forest birds represent K selection?—The alternative to K selection, in explaining the low r_m of forest birds, is that, low or not, it is the best they can do. The most common version of this idea is Lack's view of

the evolution of clutch size (or what might be called the "I can scarce maintain two" hypothesis after the ancient nursery rhyme that goes [Opie and Opie 1951]: The dove says coo coo, what shall I do?/ I can scarce maintain two. pooh, pooh, says the wren, I have got ten,/ and keep them all like gentlemen). In its simplest form, this hypothesis states that "in species in which parents feed their young, clutch size corresponds to that brood-size from which the parents can, on average, raise most young, the limit being set by the amount of food which they can collect for them" (Lack 1968:307). Following Lack's line of reasoning for number of broods per season would suggest that every bird raises as many broods as it can; the single brood of forest birds results from the period in which the food supply is sufficient for raising young being too short for another brood.

There is no reason, for birds living generally under carrying capacity conditions, that clutch size or number of broods must be selected for in this way (although under *r*-selecting conditions they should be). Neither, however, is selection against a high r_m under *K*-selecting conditions inevitable. For the genotype with fewer eggs or fewer broods to have the advantage over ones with more, the first must use savings of time or energy from the decreased birthrate to enhance its changes for recruitment into the breeding population above those of the second (cf. Cody 1966; Fretwell 1969). Some of the ways in which this might be achieved would be by improved parental care that brought a larger fraction of the young through the vulnerable egg-nestling stage, by increased ability to locate appropriate territorial sites and to establish and defend territories, and by increased ability to escape death from predation, parasitism, and disease. If the low r_m of forest birds represents *K* selection the saving of time or energy, or its result, should be detectable in comparisons with related species of different habitats.

In comparisons not presented here we examined, first, various measures of nesting success. Nesting success is clearly higher in forest than in grassland-marsh (see Ricklefs 1969: Table 5); however, nesting success of forest-edge species is at least as good as forest species. Consequently, it is difficult to conclude that the higher success of forest species vs. grassland-marsh is the result of diversion of resources which would otherwise have been used in maintaining a high r_m .

We also compared birds of the various habitats as to egg size (relative to body size) and length of incubation and nestling periods. We detected no consistent differences in forest birds compared with their non-forest relatives. It is, however, true that differences need not be consistent from one species to another: the savings of time or energy might be used differently by different species. For example, most members of the Tyrannidae in eastern North America delay molting until they reach the wintering grounds, unlike most

passerines which molt prior to fall migration. A lack of time or energy or both may tend to preclude molt prior to migration (Morehouse and Brewer 1968). We suggest that the ability of the Great Crested and Acadian flycatchers to molt prior to migration is related to their inhabiting mesic forest. (We note, further, that the other North American tyrannid which molts before migration, the Eastern Phoebe, *Sayornis phoebe*, is probably K-selected. Although it occurs in a variety of habitats, it depended for nesting, under primeval conditions, largely on rock ledges which were probably stable in terms of appearance and disappearance.)

Historical factors.—Many forest-edge species appear to have high values of r_m yet forest-edge habitats do not show obvious vegetational fluctuations and may be long-lived (Niering and Egler 1955). The forest-edge group is, of course, heterogeneous. Particular species may have life history features favoring either a high or a low r_m (e.g., Am. Goldfinch vs. Eastern Kingbird). Probably finer habitat subdivisions leading, ultimately, to a consideration of the different circumstances of every species would help to reconcile these differences (as would be true also for forest, grassland and marsh).

Additionally, historical factors may be important. The deciduous forest biome has undergone many changes during the Quaternary (Kendeigh 1974: 303–310); however, the period from around 8000 years ago until the arrival of European man was one of relative stability. In this period many forest birds must have been common and many grassland and forest-edge birds rare. Much of the habitat for forest-edge species may have been along rivers which, owing to flooding, probably was unstable. Many other suitable sites, such as areas of wind-thrown trees, must have been isolated and transient. Such conditions might have favored a high r_m .

The period from around 1650 to 1850 and a little later, in which man altered the landscape on a large scale, must have seen populations of forest-edge and grassland birds increase enormously. Whether or not local breeding populations were at K, the increasing amounts of habitat could have provided r-selecting conditions for many forest-edge and grassland species during this period. At some point, winter limitation of the size of the species populations might have become important (Fretwell 1972). It is conceivable that at least a part of the failure of some grassland species to occupy all seemingly suitable breeding sites results from limitation of total population size on the wintering grounds. At the same time total populations of forest species must have shrunk greatly. Unless large changes in competitive relations occurred, it seems unlikely that most migratory forest species have been winter-limited. This situation may, of course, be changing with the heavy destruction of natural habitats that has recently occurred in the American tropics.

SUMMARY

Forest birds, especially those of mesic forest, have life history traits favoring a lower intrinsic rate of natural increase (r_m) than do birds of grassland, marsh, or forest edge. Specifically, forest birds tend to have smaller clutches than birds of grassland or marsh; several mesic forest species typically have clutches of only three eggs. Almost no forest species are regularly double-brooded but a high percentage of grassland, marsh, and forest-edge species have two or more broods per season.

Forests can probably be thought of as K-selecting environments. Grassland and marsh probably are not, specifically because vegetational fluctuations make particular areas unpredictably uncrowded or overcrowded. Probably because of these fluctuations (and consequent changes of K) grassland birds show a more flexible pattern of occupancy, even within a breeding season, than do forest birds. Polygyny may be a particularly powerful method of maintaining a high r_m where short-term fluctuations are common.

Probably one advantage of a high production of young in unstable environments is enhanced dispersal. The main effect seems to be through increased dispersal ability because of increased intraspecific antagonism.

The low r_m of forest birds may be partly the result of natural selection diverting resources from reproduction to other traits more advantageous for organisms living continually around their carrying capacity; however, a conclusion to this effect should await a demonstration of what activities that time or energy otherwise used in reproduction is being diverted to. This demonstration may be difficult because the diversion may be to different activities in different species. The alternative explanation, that r_m in the various habitats is a reflection of the amount of available energy and the time over which it is available, deserves continued attention.

ACKNOWLEDGMENTS

Some of the ideas developed in this paper arose from field studies of various species and communities by Brewer, Ted Gottshall, Arlo Raim, J. D. Robins, and J. D. Wenger. Helpful conversation on community organization with the last four is acknowledged. Stephen Fretwell, Robert Ricklefs, John Wiens, and John Zimmerman commented constructively on earlier drafts of the manuscript. Some of the field work was done while Brewer held Faculty Research fellowships and grants from Western Michigan University. Computer time was provided by the Western Michigan University Computer Center.

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APPENDIX I

Bird species assigned to each habitat:

Mesic Forest: *Melanerpes carolinus*, Red-bellied Woodpecker; *Picoides pubescens*, Downy Woodpecker; *Myiarchus crinitus*, Great Crested Flycatcher; *Empidonax virescens*, Acadian Flycatcher; *Contopus virens*, Eastern Wood Pewee; *Parus atricapillus*, Black-capped Chickadee; *Parus bicolor*, Tufted Titmouse; *Hylocichla mustelina*, Wood Thrush; *Vireo olivaceus*, Red-eyed Vireo; *Dendroica cerulea*, Cerulean Warbler; *Wilsonia citrina*, Hooded Warbler.

Wet Forest: *Aix sponsa*, Wood Duck; *Strix varia*, Barred Owl; *Caprimulgus carolinensis*, Chuck-will's-widow; *Thryothorus ludovicianus*, Carolina Wren; *Catharus fuscescens*, Veery; *Poliophtila caerulea*, Blue-gray Gnatcatcher; *Parula americana*, Northern Parula; *Protonotaria citrea*, Prothonotary Warbler; *Setophaga ruticilla*, American Redstart.

Dry Forest: *Bubo virginianus*, Great Horned Owl; *Caprimulgus vociferus*, Whip-poor-will; *Picoides villosus*, Hairy Woodpecker; *Sitta carolinensis*, White-breasted Nuthatch; *Mniotilta varia*, Black-and-white Warbler; *Seiurus aurocapillus*, Ovenbird; *Piranga olivacea*, Scarlet Tanager; *Pheucticus ludovicianus*, Rose-breasted Grosbeak.

Grassland: *Eremophila alpestris*, Horned Lark; *Cistothorus platensis*, Short-billed Marsh Wren; *Dolichonyx oryzivorus*, Bobolink; *Sturnella magna*, Eastern Meadowlark; *Spiza americana*, Dickcissel; *Passerculus sandwichensis*, Savannah Sparrow; *Ammodramus savannarum*, Grasshopper Sparrow; *Ammodramus henslowii*, Henslow's Sparrow; *Pooecetes gramineus*, Vesper Sparrow.

Marsh: *Podilymbus podiceps*, Pied-billed Grebe; *Ixobrychus exilis*, Least Bittern; *Botaurus lentiginosus*, American Bittern; *Anas platyrhynchos*, Mallard; *Rallus limicola*, Virginia Rail; *Porzana carolina*, Sora; *Chilidonias niger*, Black Tern; *Telmatodytes palustris*, Long-billed Marsh Wren; *Agelaius phoeniceus*, Red-winged Blackbird; *Melospiza georgiana*, Swamp Sparrow.

Thicket: *Colinus virginianus*, Bobwhite; *Dumetella carolinensis*, Gray Catbird; *Geothlypis trichas*, Common Yellowthroat; *Spizella pusilla*, Field Sparrow; *Melospiza melodia*, Song Sparrow.

Trees-shrubs: *Butorides striatus*, Green Heron; *Zenaida macroura*, Mourning Dove; *Coccyzus americanus*, Yellow-billed Cuckoo; *Tyrannus tyrannus*, Eastern Kingbird; *Empidonax traillii*, Willow Flycatcher; *Cyanocitta cristata*, Blue Jay; *Toxostoma rufum*, Brown Thrasher; *Vireo griseus*, White-eyed Vireo; *Vermivora pinus*, Blue-winged Warbler; *Den-*

droica petechia, Yellow Warbler; *Dendroica pensylvanica*, Chestnut-sided Warbler; *Cardinalis cardinalis*, Cardinal; *Passerina cyanea*, Indigo Bunting; *Carduelis tristis*, American Goldfinch; *Pipilo erythrophthalmus*, Rufous-sided Towhee.

Open trees: *Coccyzus erythrophthalmus*, Black-billed Cuckoo; *Colaptes auratus*, Common Flicker; *Troglodytes aedon*, House Wren; *Turdus migratorius*, American Robin; *Sialia sialis*, Eastern Bluebird; *Vireo gilvus*, Warbling Vireo; *Icterus galbula*, Northern Oriole; *Spizella passerina*, Chipping Sparrow.

NEW LIFE MEMBER



Mr. William W. Cole, Jr. is a new life member of the Wilson Ornithological Society. Professionally Mr. Cole has been a management consultant in the materials control field, although presently he is processing manager for a centrifugal pump manufacturer. He has been an amateur ornithologist since youth and has quite an extensive library of both books and periodicals. Mr. Cole conducts an ornithological thematic stamp business on the side and for the past year and one-half has been involved in preparing the rough draft of a comprehensive catalog of bird topical stamps of the world. He is married with twin daughters and in addition to his work and catalog project he enjoys tennis and classical music.