COMPONENTS OF AVIAN BREEDING PRODUCTIVITY

ROBERT E. RICKLEFS AND GEORGE BLOOM

ABSTRACT.—Numbers of nestlings fledged per pair per season were calculated for 35 species of passerine birds in four localities from data on length of breeding season, clutch size, nesting mortality, and length of nest cycle. Mean numbers of nestlings fledged was 6.42 for 12 woodland and edge species in Kansas, 4.33 for 8 species in lower Sonoran desert habitat in Arizona, 2.36 for 6 species in humid forest and second-growth habitats in Costa Rica, and 4.80 for 9 species in a desert scrub habitat in Ecuador. The data were analyzed by multiple correlation and stepwise multiple regression to determine the contribution of the variables to variation in the number of young fledged from one species to another in each locality. Variations in season length, clutch size, and breeding success were important components in variation in numbers of young fledged in Kansas, but length of nest cycle, being positively correlated with both clutch size and nest success, had the strongest correlation with the number of young fledged. In Arizona and Costa Rica, variation in breeding success held the key to predicting variation in number of young fledged, whereas in Ecuador season length and clutch size were the critical variables. The analyses suggest that data on production of young and the factors that cause production to vary from one species to another would add immensely to our understanding of the population ecology of birds.—*Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19174.* Accepted 1 July 1975.

Ornithologists have pondered the significance of clutch size in birds for nearly three decades without fully resolving the factors responsible for its variation among species and regions. Although Skutch (1949) linked the evolution of clutch size to adult mortality and population turnover rate, population biologists have only recently placed clutch size in a demographic context. For example, not until 1961 did Drury point out that the production of young by a pair of birds during a breeding season depends on the number of broods raised as well as clutch size. Cody (1971) and Ricklefs (1973) treated avian demography more fully and demonstrated the use of life table analyses to compare species.

Although breeding biology and mortality have been investigated in scores of detailed field studies, complete life tables have been constructed for only a handful of species. Of the statistics required to complete a life table, the annual production of young is one of the most difficult to obtain. Observation of individually marked birds yields relatively few data per hour of effort (for example see Nice 1937, Snow 1958). Furthermore, estimates of mean annual productivity obtained from direct observation have large probable errors (wide confidence limits) owing to the great variation between individuals. Annual productivity can be calculated indirectly from clutch size, breeding success, nest cycle length, and length of breeding season (Ricklefs 1970). These data are more readily obtained than direct measures of breeding productivity. Furthermore, data from different studies may be combined to calculate the annual production of a species.

In this paper we calculate annual production (fledglings per pair of adults) for various passerine birds in two temperate and two tropical localities. The data are analyzed to determine the factors responsible for differences between species in annual production. Productivity is calculated by the equation:

$$\text{productivity} = \text{clutch size} \cdot \text{nesting success} \cdot \text{number of clutches laid per year.}$$

The number of clutches a female lays each year depends on the length of the nest cycle (from egg to egg) and the length of the season during which clutches are initiated. The length of the nest cycle is the average of both failures and successful nestings. Breeding season length is adjusted for peak periods of egg laying. These calculations are discussed in detail below.

MATERIALS AND METHODS

Life history data were compiled for passerine birds in four regions, mesic temperate habitats in Kansas, Sonoran desert near Tucson, Arizona, wet tropical forest and second-growth habitats in Costa Rica, and arid coastal habitat on the Santa Elena Peninsula, Ecuador. Clutch size and length of breeding season for species in Kansas were obtained from Johnston (1964); nest success and nest cycle length are from various studies within the eastern United States (Ricklefs 1969a, 1969b). Most of the data in the Kansas sample are means of several years' observations. All data from Arizona were generously provided from an unpublished 2-year study by George T. Austin. The Costa Rican data are from Skutch's extensive observations on tropical birds (1954, 1960, 1966). Marchant's (1959, 1960) detailed 4-year study served as the sole source of data for Ecuador.

The number of species used in the analyses for each area was limited by the availability of suitable data, particularly nesting success. In addition, the period between nest termination (whether by fledging or by failure) and the following clutch is not known for most species. For many species, these were represented by averages for local avifaunas (Ricklefs 1969a, MS).

The annual production of fledglings by a pair of birds (P) was calculated by the equation

$$P = F \cdot B \tag{1}$$

where F = expected rate at which young are fledged in a large population (young fledged/pair·day) and B = length of breeding season (days).

The length of the breeding season is calculated from the number of nests initiated each month by an equation derived from information theory

$$B = 30 \exp(-\Sigma\, p_i \log_e p_i) \tag{2}$$

(MacArthur 1964, Ricklefs 1966), where e = base of natural logarithms, p_i = proportion of clutches laid by a population during month i. This expression for breeding season takes into account the fact that breeding is not equally intense in all months during which eggs are found. The number of months of clutch initiation (B) is multiplied by 30 to give the number of days during which clutches are initiated.

The rate at which the young are fledged (F) is calculated by

$$F = C \cdot S \cdot I \tag{3}$$

where C = clutch size, S = breeding success (proportion of individuals that fledge), I = rate of nest initiation (clutches/pair·day). Rate of nest initiation is calculated by an equation that takes into account rate of nest failure and interval between nestings,

$$I = \frac{m}{p_f + m\,(p_s r_s + p_f r_f)} \tag{4}$$

(Ricklefs 1970), where m = nest mortality rate (proportion of nests failing per day), p_s = probability that a nest successfully fledges at least one young, p_f = probability that a nest fails before fledging ($p_f = 1 - p_s$), r_s = delay before a new clutch is laid after successful fledging, r_f = delay before a new clutch is laid after nest failure. Nest success (p_s) is related to daily nest mortality rate (m) by the expression

$$p_s = e^{-mT} \tag{5}$$

where T = length of the nest cycle from clutch initiation to fledging (days). Rate of nest initiation (I) does not take into account the death of adult birds and consequent decrease in the breeding population during the breeding season. We feel that discrepancies caused by differences between localities in adult mortality rate are at least partly balanced by differences in the length of the breeding season. In the tropics, for example, low adult mortality rate is balanced by a long breeding season compared to that in temperate

TABLE 1

ANALYSIS OF THE SENSITIVITY OF PRODUCTION (P, EQUATIONS 1–5) TO VARIATION IN INDEPENDENT VARIABLES

Variable	Range	Sensitivity (b)	Constants			
			m	r_s	r_f	T
m	0.005–0.04	−0.15	—	10	10	30
T	24–36	−1.10	0.02	10	10	—
r_s	4–16	−0.15	0.02	—	10	30
r_s	5–50	−0.31	0.01	—	10	30
r_s	5–50	−0.26	0.02	—	10	30
r_s	5–50	−0.18	0.04	—	10	30
r_s	5–50	−0.12	0.06	—	10	30

[1] The measure of sensitivity (b) is the slope of the logarithmic relationship between production and the variable in question.

[2] m = daily mortality rate; r_s = interval between fledging and relaying (days); r_f = interval between nest failure and relaying (days); T = length of the nest cycle.

localities. The proportion of adults dying during the breeding season in tropical localities should be more similar to the proportion of adults dying in temperate localities than indicated by adult mortality rates in the two regions.

Values for annual production were related to the original variables used in the equation for production by stepwise multiple regression and partial correlation (programs BMD02R and BMD03R, UCLA biomedical computer programs). These regression analyses compute linear, or additive, relationships between variables, but the factors determining production bear factorial, or multiplicative, relationships to each other, as summarized by the expression

$$P \propto \frac{C \cdot B \cdot S}{T}. \tag{6}$$

Because in the logarithmic form of equation (6)

$$\log P \propto \log C + \log B + \log S - \log T \tag{7}$$

the relationships between variables are linear, we have used the logarithms of the variables in the multiple regression and correlation analyses.

To determine the sensitivity of P to changes (or errors) in each of the independent variables, we constructed a hypothetical species for which we systematically altered each variable, calculating P by equations (1) through (5). We then related P to each variable (x) by a line, having the form $\log P = a + b \log x$, fitted by least squares to the data points generated for our hypothetical species. The slope b of the relationship between $\log P$ and $\log X$ is the percentage change in P as a proportion of the percentage change in X. If b were 0.1, for example, P would change only 10% as rapidly as X. Values of b are listed in Table 1. Fortunately, the variables most prone to measurement error, m and r_s, have the least influence on P. Errors of 30% are tolerable because they would cause less than 10% error in P. The influence of m on P is small because of the balancing effects of m on nesting success and rate of nest initiation. The influence of r_s on P is greatest for species with low m, hence with few nest failures. Slope b is less than -1.0 for varying T because increasing T reduces both number of nesting attempts and nesting success. B and C both enter the equation for P as simple factors, hence both yield a slope of 1.0.

RESULTS

Reproduction data for each species are tabulated in Table 2. Means, standard deviations (SD), and coefficients of variation (CV = SD × 100 divided by the mean) for each variable in each locality are presented in Table 3. The variables exhibit well-known trends. Breeding seasons in the tropical localities are longer than in the temperate localities. Clutch size and nesting success follow an opposite trend, being greater in temperate localities. Length of the nesting cycle (T) has little geographic variation. Young leave their nests somewhat sooner in Ecuador than elsewhere,

TABLE 2

COMPONENTS OF BREEDING PRODUCTIVITY FOR SELECTED PASSERINE BIRDS IN FOUR LOCALITIES

Species	Season length (months)	Clutch size (eggs)	Nest mortality[1]	Nest period (days)	Egg success[2]	Replacement lag		Young fledged[3]
						r_s (days)	r_f	
Kansas								
Eremophila alpestris	3.46	3.6	0.0213	24	0.451	6	6	6.80
Parus atricapillus	2.20	5.4	0.0090	37	0.716	10	10	6.15
Troglodytes aedon	2.77	5.8	0.0055	34.5	0.648	10	10	7.54
Turdus migratorius	3.14	3.6	0.0221	28.5	0.478	10	10	5.20
Sialia sialis	3.26	4.9	0.0103	34.5	0.602	10	10	7.39
Sturnus vulgaris	3.34	5.2	0.0068	39	0.768	6	6	9.94
Protonotaria citrea	1.93	4.5	0.0135	27	0.613	6	6	5.58
Dendroica petechia	1.99	4.2	0.0256	24	0.542	6	6	5.68
Agelaius phoeniceus	2.81	3.7	0.0365	25	0.416	6	6	5.79
Quiscalus quiscula	2.15	4.5	0.0208	26.5	0.499	10	10	4.77
Icterus spurius	2.22	4.1	0.0076	29	0.803	10	10	6.09
Spizella pusilla	2.96	4.1	0.0411	23.5	0.357	6	6	6.17
Ecuador								
Pyrocephalus rubinus	4.82	2.8	0.0248	28.5	0.384	10	10	5.11
Muscigralla brevicauda	4.12	4.0	0.0315	30	0.373	10	10	6.27
Euscarthmus meloryphus	2.32	2.0	0.0195	27	0.500	10	10	2.25
Mimus longicaudatus	5.36	3.9	0.0235	29	0.408	10	10	8.25
Polioptila plumbea	2.68	3.2	0.0166	28	0.441	10	10	3.50
Sporophila peruviana	3.76	2.7	0.0295	23.5	0.510	10	10	5.76
Sporophila telasco	2.50	2.6	0.0437	22.5	0.368	10	10	2.95
Rhodospingus cruentus	1.97	3.2	0.0209	21	0.591	10	10	4.14
Poospiza hispaniolensis	3.22	3.6	0.0321	23.5	0.377	10	10	4.95
Costa Rica								
Myiozetetes granadensis	3.09	2.5	0.0220	38	0.408	11	15	2.42
Elaenia flavogaster	4.14	2.0	0.0473	34	0.167	13	15	1.32
Turdus grayi	3.64	2.5	0.0478	29	0.161	19	14	1.42
Ramphocelus passerinii	4.51	2.0	0.0330	25	0.423	34	15	2.84
Thraupis episcopus	3.46	2.0	0.0250	32.5	0.440	12	15	2.54
Tiaris olivacea	5.93	2.5	0.0428	28.5	0.267	19	15	3.64
Arizona								
Auriparus flaviceps	2.53	3.0	0.0170	36	0.441	8	5	2.99
Campylorhynchus brunneicapillus	4.09	3.5	0.0248	38.5	0.478	6	5	6.80
Mimus polyglottos	1.92	3.5	0.0582	26.5	0.216	8	5	2.27
Toxostoma curvirostre	4.09	2.8	0.0441	32	0.242	13	5	3.45
Pipilo fuscus	2.49	3.0	0.0329	26	0.440	7	9	3.85
Amphispiza bilineata	2.57	3.0	0.0213	24	0.583	8	5	5.27
Aimophila carpalis	2.24	3.4	0.0401	23.5	0.420	4	5	4.84
Aimophila cassinii	1.80	4.0	0.0189	24	0.625	8	5	5.15

[1] Nest mortality = proportion of nests failing each day (see Ricklefs 1969b).

[2] Proportion of eggs laid that eventually leave the nest as fledged young.

[3] Young fledged = number per pair per season calculated from the other breeding parameters by the equations presented in the text.

which is perhaps attributable to the absence from the sample of hole-nesting species with long nest periods. Number of young fledged per season is greatest in Kansas (6.42), intermediate in Arizona (4.33) and Ecuador (4.80), and least in wet, tropical Costa Rica (2.36).

How typical are the small samples presented in Table 3 of the localities from which they were taken and of the regions they represent? In Kansas the average season length in our sample (2.69) is similar to that in a sample of 58 species (2.70 months) reported on by Johnston (1964); clutch size and nest length are similar to mean values reported elsewhere for temperate regions. The 57% egg success of the Kansas birds is reasonable for a temperate sample having one-third hole-nesting species (Nice 1957,

TABLE 3
SUMMARY OF BREEDING PRODUCTIVITY DATA FOR FOUR LOCALITIES

Locality	Number of species	Variable[1]	Mean	SD[2]	CV[2]
Kansas	12	Season	2.69	0.56	22
		Clutch	4.47	0.73	16
		Period	29.38	5.47	19
		Success	0.57	0.14	25
		Fledged	6.42	1.38	21
Arizona	8	Season	2.72	0.89	33
		Clutch	3.28	0.40	12
		Period	28.81	5.90	20
		Success	0.43	0.14	33
		Fledged	4.33	1.46	34
Costa Rica	6	Season	4.13	1.02	25
		Clutch	2.25	0.27	12
		Period	31.17	4.61	15
		Success	0.31	0.13	42
		Fledged	2.36	0.88	37
Ecuador	9	Season	3.42	1.18	34
		Clutch	3.11	0.65	21
		Period	25.89	3.28	13
		Success	0.44	0.08	18
		Fledged	4.80	1.84	38

[1] Season = length of the egg-laying period, adjusted for unequal distribution of clutches, in months (equation 2); clutch = number of eggs per set; period = time between first egg of a clutch and fledging, in days; success = proportion of eggs that eventually produce fledglings; fledged = number of young raised to the time of nest-leaving per pair per season.

[2] SD = standard deviation; CV = coefficient of variation = (SD/mean)·100.

Lack 1954). It should be remembered that nest success data used in the calculations for Kansas were taken widely from studies in the eastern United States, and that hole-nesting species, which lay large clutches and have high nesting success, are disproportionately represented.

So little comparative information is available for birds from arid temperate habitats that we cannot assess the validity of the Arizona sample. The data were collected in a small study area of uniform habitat over a 2-year period. Clutch size and nest cycle length are undoubtedly reasonable because these measures are usually uniform within species.

Mean values for season length, clutch size, nest cycle length, and egg success in the Costa Rican sample resemble means for larger samples taken more broadly from Skutch's work. But the average length of the breeding season, even in a larger sample of 37 Costa Rican species (4.53 months, Ricklefs 1966), is shorter than that reported for other tropical localities (5.3–7.8 months). This factor by itself suggests that in most tropical localities the number of young fledged per pair per season would be 20–75% greater than our estimate for the Costa Rican sample, assuming clutch size, nest mortality rate, and interval between broods were similar. This would bring the productivity of tropical birds into the range calculated for birds in Arizona and Ecuador, but it would still be below the productivity of birds in Kansas.

The sample from Ecuador reported on here includes most of the species for which Marchant (1959, 1960) had gathered data, and it thus cannot be compared more broadly.

Variation within the samples is difficult to compare statistically between one locality and another because each variable has a different mean in each locality. Coefficients of variation (SD, expressed as a percent of the mean) do, however, suggest some interesting patterns. Breeding season length varies more from one species to

TABLE 4

CORRELATION COEFFICIENTS AMONG LOGARITHMS OF INDEPENDENT VARIABLES THAT CONTRIBUTE TO ANNUAL BREEDING PRODUCTIVITY[1]

		Variable				
		Clutch	Period	Success	Fledge	Fledge[4]
Season	Kansas	−0.15	0.18	−0.27	0.57	(0.88[3])
	Arizona	−0.52	0.72[2]	−0.29	0.29	(0.99[3])
	Costa Rica	0.03	−0.64	−0.18	0.45	(0.97[3])
	Ecuador	0.47	0.64	−0.54	0.78[2]	(0.98[3])
Clutch	Kansas		0.80[3]	0.64	0.51[2]	(0.73[3])
	Arizona		−0.26	0.29	0.29	(0.99[3])
	Costa Rica		0.16	−0.22	0.13	(0.93[3])
	Ecuador		0.24	−0.36	0.78[2]	(0.95[3])
Period	Kansas			0.77[3]	0.64[2]	(−0.61[2])
	Arizona			−0.18	−0.01	(−0.93[3])
	Costa Rica			0.01	−0.30	(0.31)
	Ecuador			−0.44	0.30	(−0.93[3])
Success	Kansas				0.44	(0.74[3])
	Arizona				0.75[2]	(0.96[3])
	Costa Rica				0.74	(0.99[3])
	Ecuador				−0.25	(0.98[3])

[1] Number of species (*n*) are 12, 8, 6, and 9 for Kansas, Arizona, Costa Rica, and Ecuador, respectively. Degrees of freedom for statistical tests of correlation coefficients = n − 2.

[2] $P < 0.05$.

[3] $P < 0.01$.

[4] Values in parentheses are partial correlation coefficients obtained with Biomedical Computer Program BMD 03R.

another in dry localities than in wet localities. In both Arizona and Ecuador variation in breeding season length is increased by groups of species with relatively short breeding seasons in which reproduction is restricted to brief periods of abundant food following irregular and highly seasonal rains. Clutch size exhibits little variation within any locality. Its coefficient of variation is greatest in Ecuador probably because species that are resident in the arid coastal lowlands have larger clutches than species that migrate into the region seasonally to breed. Ranked in order of increasing variability of egg success, the localities are: Ecuador, Kansas, Arizona, and Costa Rica. Variation in nesting success is likely related to variation in nest construction and placement. A comparison of these factors in New York and the Panama Canal Zone revealed that the tropical sample was the more variable (Ricklefs 1969b).

To examine the relationships among the independent variables (season length, clutch size, nest cycle length, and egg success) and their individual contribution to variation in number of young fledged per season, we converted variables to logarithms and calculated correlation coefficients for each pair of variables at each locality (Table 4 and Fig. 1). The correlation between two variables indicates the degree to which the value for one can be predicted by the corresponding value for the other. Clutch size and season length are not significantly correlated in any of the four localities; egg success and season length are inversely, but insignificantly, related in all localities. Relationships between other pairs of variables follow no obvious patterns. Among independent variables, statistically significant correlations occur between season length and nest cycle length in Arizona and Ecuador. Nest cycle length, clutch size, and egg success are positively correlated with each other in Kansas, but not elsewhere. The well-known association of large clutches, long nestling periods, and high nest success among hole-nesting species (see Table 2) probably underlies these significant correlations in Kansas. (Hole-nesting species are not included in the

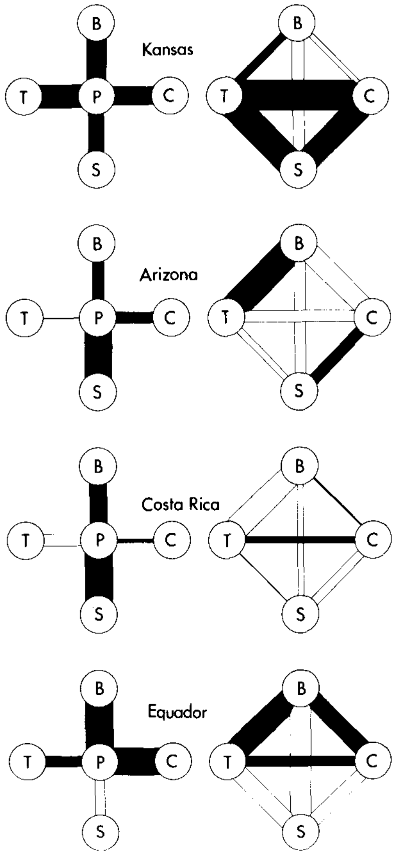

Fig. 1. Left: correlation coefficients of logarithms of independent variables with the logarithm of number of young fledged per pair per season. Thickness of bars indicates correlation coefficient (0 to 1), which is proportional to the contribution of the independent variable to variation in number of young fledged. Solid bars indicate positive coefficients, open bars negative coefficients. Right: coefficients of correlation between independent variables, portrayed in the same manner as the left portion of the figure. B = season length, C = clutch size, S = egg success, T = nest period, P = number of young fledged.

other samples, largely because they are absent from arid habitats without trees, and they are difficult to observe in the tropics.)

Factors correlated with interspecific variation in number of young fledged differ from one locality to the next. In both Arizona and Costa Rica egg success is the only factor whose variation among species is significantly correlated with variation in number of young fledged. In both localities egg success is the most variable factor in the sample. In Ecuador season length and clutch size are equally and highly correlated with variation in breeding productivity. As the two independent variables are not strongly correlated with each other, they must affect the number of offspring produced in different ways. Again, season length and clutch size are the most variable factors.

In Kansas the number of young fledged is most highly correlated with length of nest cycle. If this relationship reflected the direct effect of nest cycle length on breeding productivity, we would expect the correlation to be negative, but it is positive because nest cycle length is strongly related to both clutch size and nesting success (Table 4 and Fig. 1). Nest cycle length apparently represents some combination of the two that is more closely related to breeding productivity than is either clutch size or nesting success alone. Season length contributes independently to variation in number of young fledged in the Kansas sample.

To avoid the confusion caused by correlations among independent variables, we calculated partial correlation coefficients between the number of young fledged and each independent variable (Table 4). The partial correlation coefficient indicates the relationship between two variables when all other variables are held constant, thus revealing their true relationship. As all independent variables contribute to the calculation of production, their partial correlation coefficients with production are all highly significant, as we would expect, with the exception of nest cycle length in Costa Rica. In the last case, variation in period length is inversely related to the interval between a brood and the following clutch. Because interval between broods was not included in the partial correlation analysis, its relationship to nest cycle length would confound the latter's correlation with production.

A stepwise multiple linear regression analysis was performed for each locality using logarithms of the original data. This analysis was intended to provide a complete descriptive equation of the form

$$P \propto \frac{aC^{w}B^{x}S^{y}}{T^{z}} \tag{8}$$

where a is a constant and w, x, y, and z are exponents of variables C (clutch size), B (breeding season length), S (egg success), and T (nest cycle length). Because clutch size and breeding season length enter into the equation for number of young fledged as simple multiplying factors, we would expect exponents w and x to be 1. Nest cycle length and egg success enter the equation for number of young in a more complicated manner because the average length of a nest cycle depends on the time to failure, replacement delay, and proportion of nests lost. The exponents y and z therefore should differ from 1 (see Materials and Methods).

Results of the stepwise regression analysis are presented in Table 5, where we have listed the step at which each variable was entered into the regression, its contribution to the residual variance, and its regression coefficient (exponent in equation 8). The order in which the independent variables entered the regression and magnitude of exponents in the equation for productivity do not exhibit any noticeable geographic pattern. Where the exponents of season length and clutch size differ from 1.0, these deviations are caused by correlations of clutch size and season length with other independent variables. The coefficient for egg success varies between 0.6 and 0.8 because nesting losses are partly compensated by the ability of the birds to renest quickly after nest failure. The constant of regression presented for each locality in Table 4 is the natural logarithm of the constant a in equation 8. These constants correspond to values of a of 21.9 in Kansas, 8.4 in Arizona, 0.36 in Costa Rica, and 12.0 in Ecuador.

DISCUSSION

Comparisons of breeding productivity presented in this paper indicate that despite the longer breeding season available to tropical species, small clutches, poor nesting success, and relatively long breeding cycles reduce their annual breeding productivity below that of temperate passerines. Even in tropical localities with long breeding

TABLE 5

SUMMARY OF A STEPWISE MULTIPLE REGRESSION ANALYSIS OF FACTORS CONTRIBUTING TO BREEDING PRODUCTIVITY

		Variable				
	Constant[1]	Season	Clutch	Period	Success	Total r^2[2]
Kansas						
Step entered[3]		2	4	1	3	
Increase in r^2[2]		0.22	0.16	0.41	0.08	0.87
Coefficient[4]	3.08	1.01	1.00	−0.98	0.70	
Ecuador						
Step entered		1	2	4	3	
Increase in r^2		0.66	0.21	0.04	0.09	0.99
Coefficient	2.48	1.05	0.98	−0.83	0.73	
Costa Rica						
Step entered		2	3	4	1	
Increase in r^2		0.35	0.10	0.00	0.54	0.99
Coefficient	−1.03	1.10	1.01	0.13	0.79	
Arizona						
Step entered		2	3	4	1	
Increase in r^2		0.19	0.12	0.12	0.56	0.98
Coefficient	2.12	1.21	1.52	−0.92	0.64	

[1] Logarithm of the constant a of equation 8.

[2] The value of r^2 (the square of the correlation coefficient) represents the amount of variation in number of young fledged accounted for by including the variable in question in the regression.

[3] The order (decreasing) in which the variables contribute to variation in number of young fledged.

[4] With regard to the independent variables, the coefficients represent the exponents w, x, y, and z in equation 8.

seasons, an average productivity of four young fledged per pair is a reasonable maximum. This value approaches the productivity of species in arid localities, in both temperate and tropical regions (4.3 for Arizona, 4.8 for Ecuador), but it falls short of the 6.4 young per pair calculated for a sample of passerines in Kansas.

Latitudinal variation in breeding productivity represents a shift in the balance between opposing factors. On one hand clutch size and nesting season increase and nest cycle length decreases as latitude increases, tending to increase production; on the other hand season length decreases as latitude increases, tending to reduce production. The latitudinal increase in breeding productivity may not, perhaps, continue into arctic regions. If we consider a typical arctic species as having a breeding season too short for more than one successful brood, and a clutch size of six, the maximum possible productivity is somewhat less than that calculated for the Kansas sample. A peak in annual production of young in temperate latitudes arises from the fact that decrease in the logarithm of breeding season length as latitude increases is most pronounced north of temperate regions whereas increases in the logarithm of clutch size and nesting success as latitude increases occur primarily south of temperate regions (Fig. 2). As the logarithm of productivity is approximately the sum of the logarithms of clutch size, breeding season length, and nesting success, a maximum is obtained in temperate regions.

Whereas variation in annual production between one region and another can be related to geographic trends in factors that influence reproduction, variation within regions is not so readily explained. The factor or factors contributing most to variation in production are generally the most variable factors within the sample: nesting success in Arizona and Costa Rica, and season length and clutch size in Ecuador. In Kansas variation in both productivity and the variables determining productivity is relatively low.

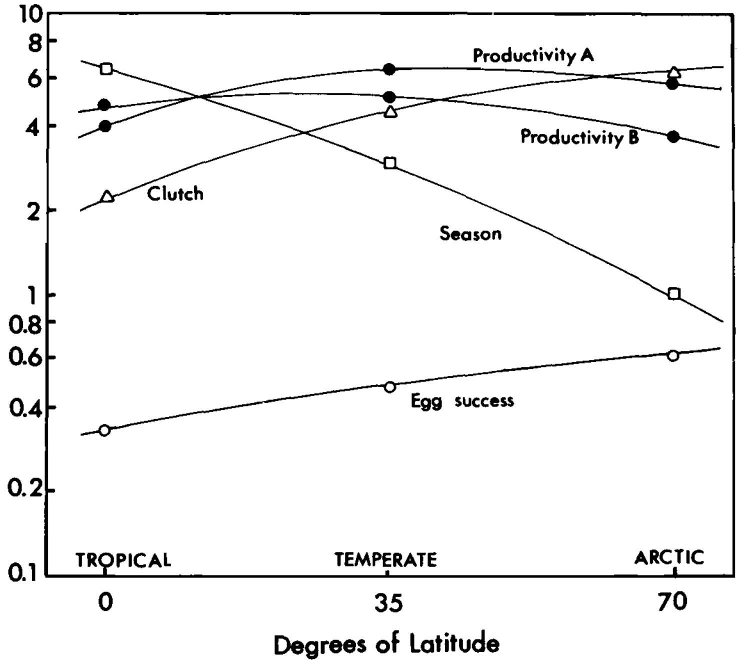

Fig. 2. Latitudinal variation in breeding productivity and its components. Reasonable values were estimated for each latitudinal belt (see text). Productivity was calculated by equations (1) to (7) (A) and by summing the logarithms of clutch size, season length, and egg success (B).

We cannot judge to what extent the analyses presented in this paper reflect important aspects of the environment for breeding birds. But our results suggest that in the Arizona and Costa Rican localities components of the environment that affect nesting success—whether related to diversity of predators or nesting sites—are more heterogeneous than components of the environment that determine clutch size and season length. In Ecuador food resource, expressed in both season length and clutch size, appears to be the most variable component of the environment of breeding birds. No single factor predominates in its contribution to variation in reproductive output in Kansas. Direct measurements in different localities of variation among species in nest site and food resource would be extremely interesting in comparison with these analyses.

Knowing the number of young fledged per pair each year and annual adult mortality, we can calculate the survival of young birds from fledging to the onset of reproduction. We must assume (a) that population size and age structure remain constant, (b) that young breed in their first year, and (c) that half the fledglings are females. Because, under these conditions, first-year birds must replace adult losses, mortality between fledging and reproduction must reduce the size of the cohort of potential recruits to the number of adults lost from the population each year. For example, if passerines in Kansas suffer 50% annual adult mortality (Lack 1954, Farner 1955) and produce 6.4 young per pair per year (3.2 young per individual), 3.2 fledglings must be reduced to 0.5 adults if population size is to remain constant. A survivorship of 15.7% (0.5/3.2) from fledging to reproduction is thus required to balance the population.

Annual adult survivorship in the tropics is poorly known, but available studies suggest mortality rates of 10–30% per year, with 20% being a reasonable average in the absence of more extensive data (Snow 1962, Ricklefs 1973, Snow and Lill 1974). If 1.5 young fledged per adult, a survivorship of 13% (0.2/1.5) during the first year would be required to balance the population.

The calculations presented in this paper border on demographic speculation, but we have pointed out likely trends in production and population turnover rates as a function of latitude. These trends must be verified by direct observation of annual adult survival, age at first reproduction, and annual reproductive performance in different localities, particularly in the tropics and arctic. Population and life table information of this kind is needed for the development and testing of models of demographic adaptations, particularly models pertaining to the evolution of reproductive effort (Williams 1966, Gadgil and Bossert 1970, Cody 1971).

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