GEOGRAPHICAL VARIATION IN CLUTCH SIZE AMONG PASSERINE BIRDS: ASHMOLE'S HYPOTHESIS

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ABSTRACT.—Ashmole (1961, 1963) suggested that clutch size should vary in direct proportion to the degree of seasonal fluctuation in the level of resources utilized by a population. He argued that populations are regulated during the winter months when resources are scarce; clutch size is determined by the resources available during the breeding season relative to population density. Hence, the greater the seasonal fluctuation in resources, the larger the average clutch size. Latitudinal variation in clutch size and the relative uniformity of clutch size among species within areas are consistent with Ashmole's hypothesis. The hypothesis is tested indirectly in this paper by relating clutch size to seasonal variation in actual evapotranspiration (AE), which is proportional to primary production. Clutch size is directly related to the ratio between summer AE and winter AE. In addition, clutch size is inversely related to winter AE, but it is independent of summer AE. These results are consistent with the hypothesis that the number of breeding individuals is regulated in winter and that population size exerts a density-dependent influence on resources available to each individual for reproduction. To demonstrate further the relation between population density and reproductive rate, clutch size is shown to be directly related to the ratio between summer productivity and the density of breeding adults. Moreover, clutch size is inversely related to population density, but it is not related to production during the breeding season. This analysis suggests that geographical trends in clutch size are caused primarily by factors that limit populations during the nonreproductive period rather than by the abundance of resources during the breeding season. *Received 26 February 1979, accepted 18 August 1979.*

VARIATION among populations of birds in the number of eggs per nest (clutch size) has preoccupied evolutionary ecologists since David Lack (1947, 1948) first discussed the subject in detail. Lack suggested that the characteristic clutch size of each species should correspond to the number of young that parents can nourish adequately. Within this constraint, birds should rear the largest number of young possible so as to maximize their individual fitness. Lack's ideas about food limitation and fitness have been elaborated by numerous refinements, including optimization of reproductive effort with respect to life expectancy (Williams 1966, Gadgil and Bossert 1970, Cody 1971, Charnov and Krebs 1974, Goodman 1974) and habitat stability (Cody 1966, MacArthur and Wilson 1967), adjustment of parental feeding effort in accordance with the level of clutch-size-dependent predation (Skutch 1949), antipredator adaptations (Ricklefs 1970), overlap of breeding and molting seasons (Foster 1974), variation among species in the energy requirements of young (Royama 1969), and the relationship of the breeding season to the spring flush of insects (Slagsvold 1975). But as yet, ecologists have not reached a concensus about the relative importance of these factors.

The single most striking pattern of variation in clutch size, by which all hypotheses about clutch size are ultimately tested, is the direct relation between clutch size and latitude. To account for this trend, Ashmole (1961, 1963) outlined a simple hypothesis based upon seasonality of resources. He suggested that reproductive rate should depend upon both resource level and population density during the breeding season. If populations were limited by resources during the nonbreeding season, the level of resources available in the breeding season relative to population density would depend upon the seasonality of resources. Clutch size accordingly would increase in direct proportion to seasonality, irrespective of the average resource level.

Ashmole stated his model in a few paragraphs but developed it no further. Lack and Moreau (1965) attempted to test the model by examining clutch size among equatorial species of passerines, comparing species inhabiting relatively less seasonal forests to those in more seasonal savannas. By restricting their survey to equatorial birds, Lack and Moreau avoided complicating influences associated with latitude. They found that clutch size was larger among savanna-dwelling species, by about one-half egg on average. Differences in clutch size between one habitat and the other were therefore consistent with Ashmole's hypothesis. For additional support, they cited Marchant's (1959, 1960) study of passerine birds inhabiting the arid Santa Elena Peninsula of Ecuador, which lay larger clutches than do species of humid zones at the same latitude.

In spite of Lack and Moreau's confirmation, little attention has been paid to Ashmole's hypothesis. Lack (1968: 167 *ff*) reiterated the hypothesis and the Lack-Moreau data in his synthesis, *Ecological Adaptations for Breeding in Birds*. But to explain the latitudinal trend in clutch size, he clearly preferred his own hypothesis (Lack 1947), that longer days at high latitudes enable birds to gather more food for their young, and he considered Ashmole's idea only as an important modification. Klomp (1970) mentioned Ashmole's hypothesis without special emphasis in his thorough review of clutch size. Hussell (1972) also remarked upon the idea but felt the evidence to be inconclusive and instead favored hypotheses based on demographic optimization of reproductive effort with respect to life expectancy.

Many ecologists interpret the relationship between clutch size and latitude as an expression of variation in optimum reproductive effort, as it is influenced by predation on the nest (Skutch 1949, 1966; Snow 1970; and others), by adult mortality not related to reproduction (Cody 1971, Hussell 1972, Goodman 1974), and by tradeoffs with so-called "K-selected" traits (Cody 1966, 1971). I have used a modeling approach to evaluate the influence of predation and optimization of reproductive effort on clutch size (Ricklefs 1977a, 1977b). According to these models, variation in rate of predation on nests and rate of adult mortality together account for no more than a quarter of the variation in clutch size with latitude, and probably much less. These results have led me to reconsider hypotheses relating clutch size directly to food availability, especially Ashmole' hypothesis. Following Ashmole's reasoning, I suggest that density-dependent adult mortality during the nonbreeding season influences reproductive rate by limiting population size during the breeding season. Accordingly, seasonality of resources determines the density of breeding birds relative to breeding season resource levels. I demonstrate here that clutch size is directly related to seasonality of production, as Ashmole predicted, rather than to absolute level of production. Thus, the density-dependent influence of adult population size on resource availability during the breeding season appears to be the major cause of variation in reproductive rate.

PATTERNS IN CLUTCH SIZE

In this analysis I consider only passerine birds. Passerines have relatively uniform morphology and parental care; all passerines feed their young (or impose upon foster parents) until the young are nearly fully grown. I shall further restrict this analysis

TABLE 1. Average clutch size, breeding season, and maximum and minimum actual evapotranspiration of selected localities.

Locality and source	Latitude	Principal habitat	Number of species[a]	Distribution of clutch sizes[b]										Clutch size		Breeding season[c]	Actual evapotranspiration[d]	
				2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5+	$\bar{x}$	SD		Min.	Max.
1. Cape Thompson, Alaska (Williamson et al. 1966)	67 N	Tundra	7						29	43	29			5.0	0.38	1.5	0	170
2. Southern Finland (Haartman 1969)	61 N	Mixed forest	32					16	14	27	19	14	11	5.2	0.78	2.5	0	254
3. Kansas (Johnston 1964)	38 N	Prairie-forest	48			8	29	40	10	10	2			4.0	0.57	3.8	0	353
4. Arizona (G. T. Austin and S. M. Russell MS)	32 N	Desert scrub	12			33	50	17						3.4	0.35	4.5	30	70
5. Oaxaca, Mexico (Rowley 1966)	17 N	Thorn forest	35	37	11	34	9	9						2.7	0.66	—	57	287
6. South Africa (Moreau 1944)	25–35 S	Varied	118	16	14	42	16	3	9					3.0	0.69	—	104	200
7. Central American highlands (Skutch 1967)	10–15 N	Wet forest	24	54	34	13	4							2.4	0.42	5.7	156	264
8. Costa Rica (Skutch 1954, 1960, 1969, 1972)	10 N	Lowland forest	99	59	15	20	1	3		2				2.4	0.63	6.6	255	389
9. Equatorial Africa (Moreau 1944)	0	Varied	160	66	8	14	4	2	5					2.4	0.70	6.7	229	262
10. Ancon, Ecuador (Marchant 1960)	3 S	Desert scrub	21	14	24	33	5	19			5			3.1	0.85	3.8	—	—
11. West Java (Sody 1930)	8 S	Wet tropical	51	43	12	20	10	6	8	2				2.8	0.87	9.9	351	400
12. East Java (Sody 1930)	8 S	Wet tropical	31	32	10	16	19	10	3	10				3.1	0.98	7.6	277	423
13. Borneo (Coomans de Ruiter)	0	Wet tropical	14	50		36	7	7						2.6	0.66	6.4	377	420

[a] Number of species for which clutch size data were provided.

[b] Percentages of the number of species; half-egg categories tend to be under-represented, because clutch sizes are frequently reported as, or rounded off to, whole eggs.

[c] Breeding season in months averaged over species from Ricklefs (1966) calculated by the formula: Season = $\exp(-\Sigma p_i \log_e p_i)$, where p_i is the proportion of nests started in the ith month.

[d] Calculated from monthly mean temperature and precipitation according to the method of Thornthwaite and Mather (1957) and expressed in millimeters. Weather data were chosen from stations as close to the study locality as possible.

to species that build open, cup-shaped nests; species nesting in natural or excavated cavities tend to lay more eggs than open-nesting species (Haartman 1957).

Clutch sizes of open-nesting passerine birds presented in Table 1 illustrate geographical variation. The most common number of eggs per clutch is 2 or 3 in the tropics and 4 to 6 in temperate and arctic regions; birds in dry tropical areas (Ancon, Ecuador) lay larger clutches than relatives in the humid, lowland tropics; birds in wet, highland regions in the tropics (Central American highlands) do not. Trends in the Eastern Hemisphere parallel those in the New World egg for egg, indicating the generality of these clutch-size patterns.

Table 1 also illustrates the similarity of clutch size among species inhabiting the same region, regardless of the nature of their food resources or the manner in which they feed. For the localities in Table 1, the mean clutch sizes of 48–88% of the species in each locality fall within a range of one egg. Although this uniformity has received little comment, it seems remarkable that clutch sizes vary no more than between 2 and 3, or between 4 and 5, among species as different as aerial feeders, bark probers, leaf gleaners, and ground scratchers, among species that feed by sallying after flying insects, hawking insects from foliage, deliberately searching the vegetation and litter, or sitting and waiting for the passing prey individual, or among species that consume insects, fruits, and seeds in varying proportions. Uniformity of clutch size within a region is predicted by Ashmole's hypothesis, as we shall see below.

ASHMOLE'S HYPOTHESIS

All populations, even in the humid tropics, have distinct breeding seasons separated by periods without reproductive activity (Lack 1950, Skutch 1950, Snow and Snow 1964). According to Ashmole's hypothesis, resources limit population size during the period of greatest scarcity, presumably the period between one breeding season and the next (Fig. 1). The number of young that each adult can feed, and hence clutch size, is related directly to the resources available during the breeding season and inversely to the density of the population. That is, clutch size is predicted to vary according to the ratio of the highest level of resources to the lowest level and it is independent of absolute amount. Ashmole's model therefore predicts uniformity of clutch sizes among co-occurring species utilizing different resources, so long as the degree of seasonal variation in their resources is similar. As shown in Fig. 1, clutch size is determined by the ratio of the food supply to its demand by the population of breeding adults. The supply depends largely upon the production of the habitat during the breeding season, while the demand is regulated by density-dependent factors acting upon the population during the nonbreeding season.

The model in Fig. 1 may be elaborated upon in several ways. By storing resources, switching to more abundant food types, and migrating to regions of greater productivity during the nonbreeding period, populations might achieve larger size, and thereby restrict the access of each individual to resources during the breeding season. Influx of migrants to an area during the nonbreeding season might reduce populations of residents through interspecific competition (Chipley 1976) and thereby increase the access of resident individuals to resources during the breeding season. Between the winter period of severe limitation and the onset of the breeding season, the number of individuals in the population declines as adults die. The higher mortality rates of temperate species compared to their tropical counterparts (Ricklefs

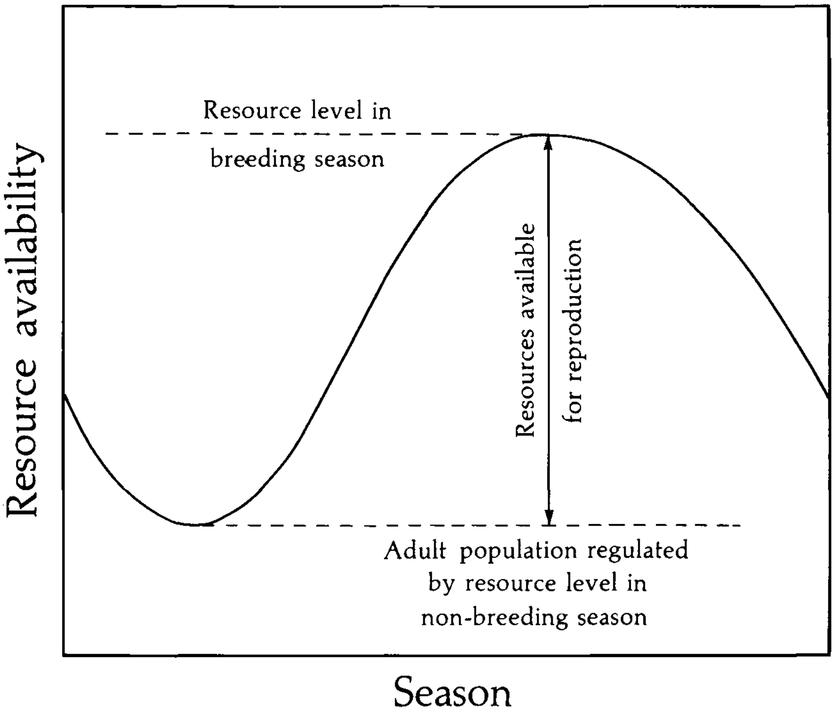

Fig. 1. Graphical model of Ashmole's hypothesis. Adult population level is limited by resource availability during low point of seasonal cycle. Resources available to the population for reproduction are the difference between the high point of the seasonal cycle and adult requirements. Clutch size is proportional to the ratio of the breeding season surplus to the adult population.

1973) might result in larger clutches in temperate latitudes relative to tropical regions. If temperate and arctic homeotherms required more resources in winter than in summer, the difference between clutch sizes within tropical and temperate latitudes might be increased. Additional factors include the efficiency with which birds convert resources into offspring. Tropical species grow more slowly than temperate species and may have lower food requirements (White 1974, Ricklefs 1976); temperature regulation by nestlings and by brooding adults also may be less costly in the tropics. High probability of nest failure among tropical species (Lack 1954, Nice 1957, Skutch 1966, Ricklefs 1969) may reduce the resource demand of a population, giving successful breeders increased access to resources. Although it is not possible to account for the influence of these factors in the absence of detailed studies, we may nonetheless be justified in determining whether Ashmole's hypothesis is consistent with patterns of seasonality as they are currently understood.

THE SEASONALITY OF RESOURCES

To test Ashmole's hypothesis adequately, one would have to measure the annual course of resources available to and required by each species. Resources are undoubtedly more seasonal in temperate regions than in the tropics, but resource fluctuations are never likely to be measured directly, owing to seasonal variation in foods and competitors and to migration.

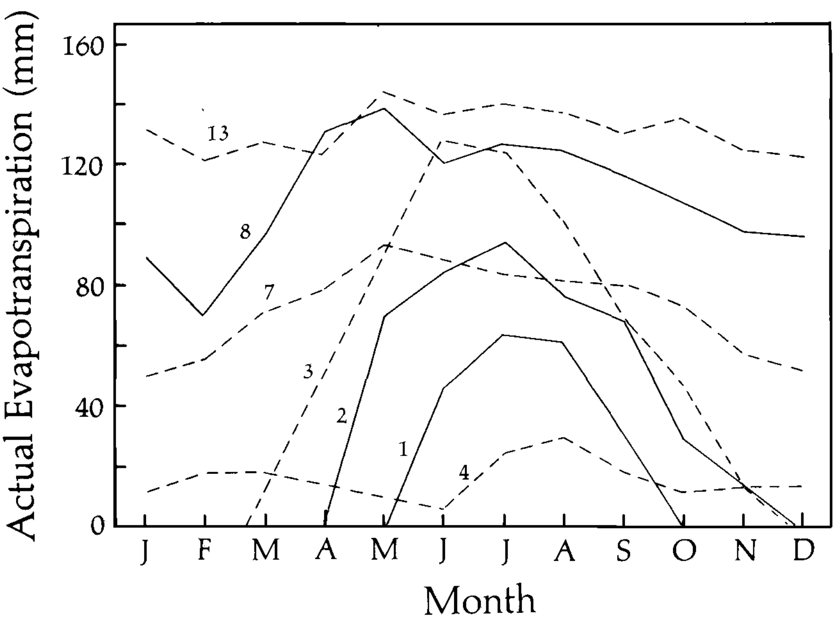

Fig. 2. Representative seasonal courses in actual evapotranspiration for localities considered in this study. Numbers key localities listed in Table 1: 1 = Cape Thompson, Alaska; 2 = Southern Finland; 3 = Kansas; 4 = Arizona; 7 = Central American highlands; 8 = Costa Rica; 13 = Borneo.

Here I estimate the fluctuation of resources indirectly by the seasonal course of actual evapotranspiration (AE), which varies in direct proportion to primary plant production (Rosenzweig 1968) and presumably to resource production more generally. Values of AE were calculated from monthly temperature and precipitation using tables in Thornthwaite and Mather (1957). The annual course of AE for representative localities discussed in this paper is shown in Fig. 2. To estimate breeding season (summer) resources, I added the three highest contiguous values for AE. To estimate resources during the nonbreeding (winter) period, I added the three lowest values. The "summer" values (S) varied between 170 and 423 mm AE per 3-month period in moist localities. Tropical and moist temperate localities differed little, while Finland (254 mm) and Alaska (170 mm) occupied the low end of the distribution. Desert scrub habitat in Arizona had considerably lower summer AE than all other localities (70 mm). During the nonreproductive or "winter" season (W), AE varied from 0 mm in three temperate-zone localities to 30–104 mm in subtropical regions and 156–377 mm in the wet tropics.

According to Ashmole's hypothesis, clutch size should vary in constant proportion to the ratio between resources during the breeding and nonbreeding periods. Using estimates of actual evapotranspiration, we may express this relationship by

$$\text{clutch size } (C) = aS/W \tag{1}$$

where a is an arbitrary constant. To test whether the data in Table 1 conformed to this model, I calculated the Spearman rank correlation (r_s) between clutch size (C) and the ratio (S/W). The data were analyzed two ways: first, including all localities listed in Table 1; second, excluding data from the East Indies (localities 11–13). Birds of the East Indies lay more eggs per clutch than do birds of other humid

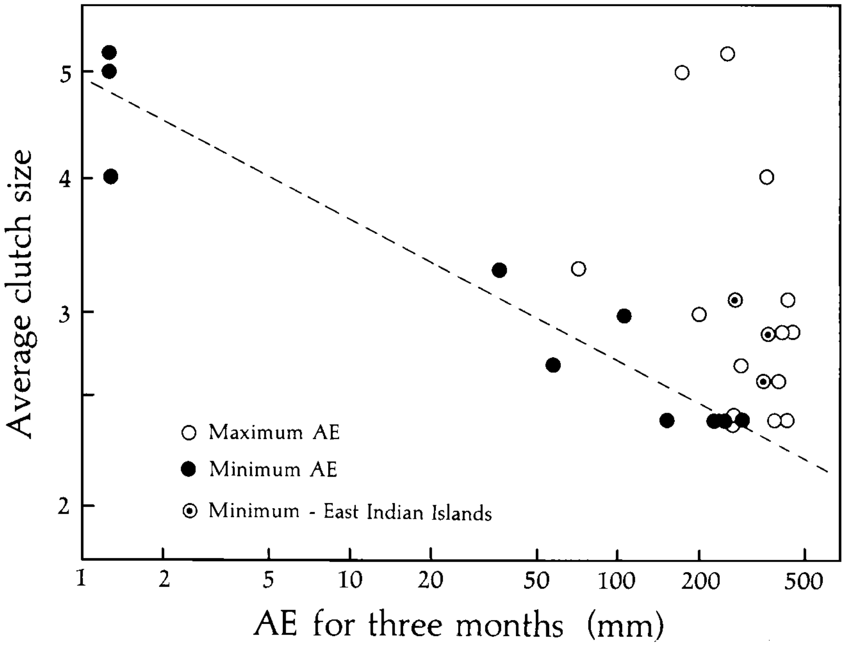

Fig. 3. Relationship of average clutch size to maximum and minimum values for actual evapotranspiration. Data are from Table 1.

tropical regions. I suggest below that migrants from Asia may depress the populations of resident species and thereby increase the ratio of resource supply to demand during the breeding season. Because of their peculiar geographical position, the East Indian localities were excluded from one set of analyses. For all localities, $r_s = 0.65$ ($P \leq 0.05$). Excluding the East Indies (localities 11–13), $r_s = 0.98$ ($P \leq 0.01$).

The expected inverse relationship between clutch size (C) and minimum actual evapotranspiration (W) has a rank correlation (r_s) of -0.45 ($P \geq 0.05$) when all localities are considered and of -0.95 ($P \leq 0.01$) when the three East Indian sites are excluded. The expected direct relationship between C and maximum actual evapotranspiration (S) is not significant for either set of localities. These results show, first, that the data are consistent with the model (equation 1), and second, that variation in clutch size is more closely linked to variation in winter AE levels than to variation in breeding season AE.

To identify the separate relationships of clutch size to breeding season AE and nonbreeding season AE, I transformed equation (1) to a generalized logarithmic form,

$$\log C = \log a + b \log S - c \log W \tag{2}$$

and applied a multiple regression-partial correlation analysis (UCLA Biomedical Computer Program BMD03R). For temperate and arctic localities, I set values of W arbitrarily at 1 ($\log W = 0$) for this analysis, but higher or lower values would give similar results. The data are graphed in Fig. 3. The multiple regression had an F-value of 27.2 (2, 11 df, $P \leq 0.001$) and a multiple coefficient of determination (R^2) of 0.83. The partial correlation coefficient relating $\log C$ to $\log W$ was -0.90 ($P \leq 0.001$) and that relating $\log C$ to $\log S$ was -0.09 ($P \geq 0.05$). The results

TABLE 2. Distribution of clutch sizes among species of passerine birds with open nests in the West Indies (data from Bond 1971).[a]

		Clutch size						
	n	1.5	2.0	2.5	3.0	3.5	4.0	4.5
Lesser Antilles	25		40	40	16	4		
Greater Antilles	54	4	17	20	30	19	9	2

[a] For a Chi-square test, species were lumped into clutch-size categories of ≤ 2.0, 2.5, 3.0, and ≥ 3.5. The resulting value was $\chi_3^2 = 11.4$ ($P < 0.01$).

show that variation in clutch size is inversely related to winter AE and unrelated to summer AE. Therefore, if Ashmole's hypothesis were correct, geographical patterns in clutch size would be determined primarily by variation in the density of breeding adults. Breeding season production is too uniform geographically to cause major trends in clutch size.

Birds of the East Indian islands of Java and Borneo lay larger clutches than one would expect from either their tropical location or the seasonality of actual evapotranspiration. In the multiple regression, their residuals (0.44 and 0.56 eggs) exceeded those of all other localities. This discrepancy may be related to the influx of winter migrants from Asia, which filter into a rather small land area of the tropics in southeast Asia (e.g. Nisbet and Medway 1972, McClure 1974). If migrants reduced populations of resident species through competition for winter resources, each surviving resident individual would have access to more resources during the breeding season. The association of large clutches and presence of abundant winter migrants is evident also in the West Indies. The Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico) lie due south of the eastern United States and Canada and support large numbers of wintering migrants; the Lesser Antilles (Guadeloupe, Martinique, Dominica, etc) lie farther to the east and have fewer migrants (Lack 1976). Both island groups lie within the tropics, and their climates are generally similar. According to Ashmole's hypothesis, if migrants depressed populations of residents through competition, clutches should be larger on the Greater Antilles than on the Lesser Antilles. This is confirmed in Table 2.

TABLE 3. Relationship between breeding population density, production of the habitat during the breeding season, and clutch size in five localities.

Locality	Maximum actual evapotranspiration (mm)	Population density (pairs/100 acres)	$\frac{\text{AE}}{\text{Density}}$	Clutch size	Source for densities
Costa Rica (humid forest)	389	1,060	0.37	2.4	Skutch (1966)
Puerto Rico (humid forest)	342	392	0.87	2.8	Kepler and Kepler (1970)
Arizona (desert scrub)	70	88	0.80	3.3	G. T. Austin and S. M. Russell (MS)
Kansas (prairie-forest)	353	200	1.77	4.0	Breeding Bird Censuses, various
Alaska (tundra)	170	67	2.54	5.0	Williamson et al. (1966)

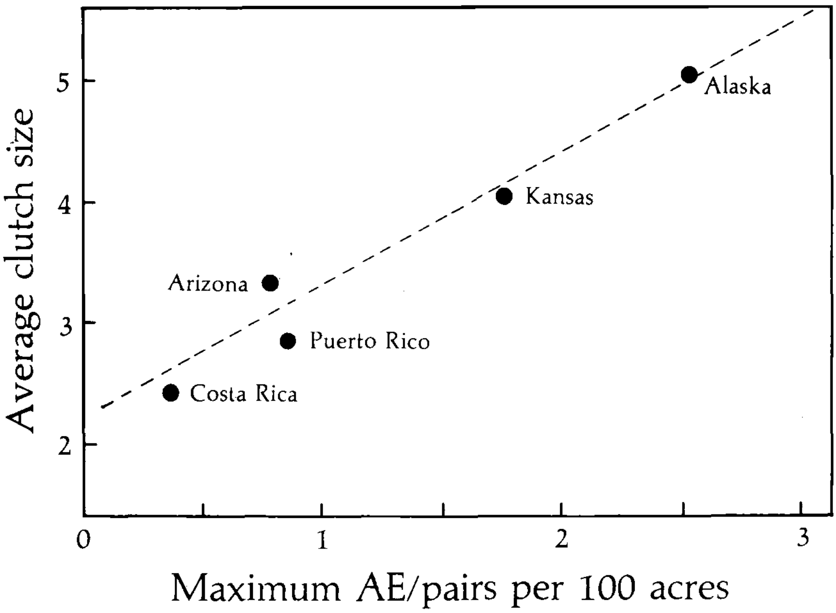

Fig. 4. Relationship between clutch size and the ratio of maximum actual evapotranspiration to density of breeding birds in five localities. Data from Table 3. Line drawn by eye to suggest the trend.

POPULATION DENSITY AND CLUTCH SIZE

Actual evapotranspiration in winter provides an indirect index to population density. Censuses of breeding birds, available for some areas, estimate population density directly. According to Ashmole's hypothesis, clutch size should vary in direct proportion to the ratio of summer AE to population density. To test this prediction, I compiled data on densities of breeding passerines, summer AE, and clutch size for localities in Costa Rica, Puerto Rico, Arizona, Kansas, and Alaska (Table 3 and Fig. 4). In this sample, clutch size is highly correlated with the ratio of breeding season production to population density ($r_s = 0.90$, $P \leq 0.05$). It is also inversely related to population density ($r_s = -0.90$, $P \leq 0.05$), but it is not related to breeding season production ($r_s = -0.50$, $P \geq 0.05$).

DISCUSSION

Patterns in clutch size and seasonality of actual evapotranspiration are consistent with Ashmole's hypothesis. The data used here to test the hypothesis are, however, indirect, and conclusions have been based largely on circumstantial evidence. One could argue that actual evapotranspiration does not accurately predict primary production in humid habitats, where light or nutrients may limit photosynthesis, that AE does not adequately estimate resources directly available to birds, or that in extratropical latitudes, winter AE does not reflect resources available to species that migrate elsewhere during the nonbreeding season.

These factors may be important, but geographical trends in clutch size are so general that their explanation can, indeed must, be expressed in the most general terms possible. Whether AE is directly related to the food available to each species of bird or not, it nonetheless agrees with intuition about production and certainly ranks localities appropriately according to their production (Whittaker and Likens 1973). AE also provides a quantitative handle by which to evaluate Ashmole's hypothesis. By any acceptable criterion, we must conclude that geographical variation in mean clutch size is more strongly correlated with winter production than with summer production, regardless of causation. If one believes that predation and optimization of reproductive effort exert only minor diversifying influences on clutch size (Ricklefs 1977a, 1977b), and if one regards seasonal variation in food supply as the primary cause of geographical trends in clutch size, one must accept two conclusions: (1) population density is regulated primarily by winter mortality and not by territorial behavior during the breeding season, and (2) population density influences the access of breeding individuals to resources. It follows from (1) and (2) that populations of birds are capable of reducing the supplies of their food resources during both winter and summer sufficiently to affect adversely survival and reproduction.

Winter AE undoubtedly estimates population density in general, although some species migrate elsewhere, even to the tropics, outside the breeding season. For the localities considered here, however, migration is relatively unimportant. Of the 5 common breeding passerines at Cape Thompson, Alaska, 3 (Common Redpoll, *Carduelis flammea*; Lapland Longspur, *Calcarius lapponicus*; and Snow Bunting, *Plectrophenax nivalis*) migrate no farther south than the middle latitudes of the United States, and 2 (Savannah Sparrow, *Passerculus sandwichensis,* and White-crowned Sparrow, *Zonotrichia leucophrys*) winter exclusively in temperate zones. Of the passerines of Finland, about half winter within their temperate-zone breeding distributions (Haartman 1969). Few species of the American prairies (Kansas) and deserts (Arizona) are neotropical migrants (MacArthur 1959). Thus winter AE appears to be a reasonable relative index to resources on the wintering grounds for birds that breed at the localities in Table 1, and the relationship of clutch size to winter AE (Fig. 3) therefore supports Ashmole's hypothesis in broad terms. A more direct test of the influence of population density on clutch size, based upon the ratio of summer AE to density of breeding adults (Fig. 4), confirms this result.

Ashmole's hypotheis emphasizes the direct influence of variation in food supply relative to population density on clutch size. Ashmole's hypothesis and those based on optimization of reproductive effort with respect to life expectancy or nest predation are not mutually exclusive, because the fruits of reproductive effort, at whatever level it may be adjusted by selection, depend on the availability of resources. Empirical evidence and theoretical arguments lead me to believe, however, that variation in the seasonality of resources experienced by a population is the single most important cause of geographical patterns in clutch size.

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