GEOGRAPHIC AND ECOLOGICAL VARIATION IN CLUTCH SIZE OF TREE SWALLOWS

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ABSTRACT.—In many birds, populations breeding at higher latitudes have larger clutch sizes. It has been hypothesized that this relationship results from the greater availability of food at higher latitudes. We examined geographic variation in clutch size of Tree Swallows (*Tachycineta bicolor*) in relation to latitude, longitude, laying date, breeding density, elevation, and summer actual evapotranspiration (AE). AE is a measure of terrestrial primary productivity, and we assumed that it was correlated with resource abundance. Clutch size data were compiled from nest records throughout the breeding range in the United States and Canada ($n = 7,459$). Summer AE estimates were made from long-term climatological records, and breeding density was estimated from Breeding Bird Surveys. All variables were averaged for each 1° block of latitude and longitude ($n = 85$ latilong blocks). We found a strong positive relationship between clutch size and latitude. Absolute levels of resource abundance (summer AE) were not related to clutch size but were related inversely to latitude and longitude. After controlling for the effects of confounding variables, clutch size was related positively to latitude and relative resource abundance (summer AE after controlling for breeding density). Our results are consistent with Ashmole's hypothesis that relative, rather than absolute, levels of resource abundance determine at least some of the variation in clutch size. *Received 21 December 1998, accepted 20 July 1999.*

ONE OF THE MOST consistent patterns of variation in avian reproduction is an increase in clutch size with latitude. Numerous studies since the 1940s have documented this relationship in the Northern and Southern hemispheres (Moreau 1944; Lack 1947, 1948). Hesse (1937) and Lack (1947, 1948) suggested that in altricial birds, this pattern resulted from increased foraging time afforded by longer day length at higher latitudes. Alternatively, Ashmole (1961, 1963) suggested that clutch size depends on the relative level of resource availability during the breeding season. Thus, although temperate areas have fewer absolute resources than tropical areas, Ashmole hypothesized that populations at higher latitudes would have larger clutches because their breeding densities are much lower relative to the abundance of resources. Hence, Ashmole's hypothesis is based on the seasonality of resources. If population size is limited by periods of resource scarcity during the nonbreeding season, then highly seasonal

environments will have more resources per capita available for breeding. As a consequence, clutch sizes should be larger in environments with greater seasonal variation in resources.

Ricklefs (1980) assumed that food supply was the main limiting resource for bird populations and examined Ashmole's hypothesis using the ratio of summer to winter actual evapotranspiration (AE) as an estimate of seasonality. Actual evapotranspiration is moisture transfer from the earth's surface to the atmosphere and is a measure of terrestrial primary productivity (Rosenzweig 1968). Support for Ashmole's hypothesis has been found in analyses of passerine assemblages worldwide (Ricklefs 1980) and in woodpeckers (Koenig 1984, 1986), but not in swallows (Møller 1984) or House Wrens (*Troglodytes aedon*; Young 1994). One potential problem with testing this hypothesis for migratory species is estimating the ratio of summer to winter AE. In migratory species, one must know the location of the wintering grounds to estimate the winter AE experienced by a particular breeding population, and in many cases this information is unknown. A more direct test of Ashmole's hypothesis involves estimating relative resource
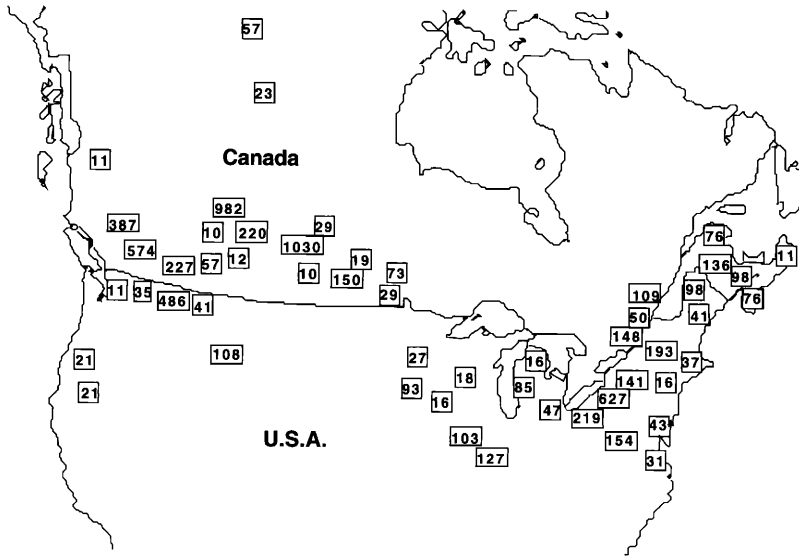
FIG. 1.   Sample sizes of Tree Swallow nests used for analysis. For clarity, we combined latilong blocks into 2° blocks. In a few cases neighboring 2° latilong blocks were combined ($n = 52$ blocks shown).

abundance using summer AE and breeding density, rather than inferring relative resource abundance from seasonality. Ricklefs (1980) and Koenig (1984, 1986) have performed the only tests of Ashmole's hypothesis using direct estimates of breeding density to calculate relative resource abundance. Thus, the generality of Ashmole's hypothesis remains unresolved.

In this study, we examined geographic variation in the clutch size of Tree Swallows (*Tachycineta bicolor*). The Tree Swallow is a socially monogamous aerial insectivore that uses secondary cavities as nest sites, although it readily accepts nest boxes (Robertson et al. 1992). Tree Swallows typically raise a single brood per season and breed throughout most of the United States and Canada north to tree line. Clutch size typically varies from three to eight eggs (Paynter 1954, Dunn and Hannon 1992) and is positively correlated with food abundance during laying (Hussell and Quinney 1985, Dunn and Hannon 1992, Winkler and Allen 1995). Large variation in clutch size, wide geographic range, single-broodedness, and willingness to use nest boxes makes Tree Swallows an excellent choice for studying large-scale patterns of variation in clutch size.

METHODS

We examined 40 years of data (1952 to 1992) from more than 21,000 nest record cards supplied pri-

marily by the North American Nest Record Program (Cornell University, 1970 to 1992), the British Columbia Nest Records Scheme (BC Wildlife Branch, 1952 to 1991), the Ellis Bird Farm (Lacombe, Alberta, 1981 to 1986), the Maritimes Nest Records Scheme (Canadian Wildlife Service, 1962 to 1990), the Prairie Nest Records Scheme (Manitoba Museum of Man and Nature, 1958 to 1986), and the Quebec Nest Records Scheme (National Museum of Canada, 1959 to 1988). These records span most of the known breeding range of Tree Swallows across the United States and Canada (Fig. 1). All records used in this study came from nest boxes, which have larger mean clutch sizes than natural cavities (Robertson and Rendell 1990). We used only records with at least two visits to the nest box during May or June (the normal laying period) in which eggs or nestlings were recorded on both visits. We did not use any records where it appeared that our estimates may have been biased by egg dumping or brood reduction after hatching. We assumed that any potential biases such as observer error (see McNair 1987), type of nest box, and maternal age effects (DeSteven 1978) were similar with regard to our predictor variables (e.g. latitude, elevation, and evapotranspiration). We also included date of clutch initiation (laying date) in the analysis because it has been suggested that geographic variation in clutch size is caused by variation in the timing of laying (Hendricks 1997), and clutch size is affected strongly by laying date in Tree Swallows (Stutchbury and Roberston 1988, Winkler and Allen 1996). Laying date was estimated only at nests in which the number of eggs differed between the two (or more) visits. Laying date was estimated by back-

TABLE 1.   Pearson correlation coefficients among clutch size of Tree Swallows and geographic and ecological variables (n = 67 latilong blocks with data for all variables). Significant correlations after adjusting critical values with sequential Bonferroni correction (Rice 1989) are indicated in boldface.

	Latitude	Longitude	Laying date	Breeding density[a]	Summer AE	Elevation	Mean May temperature
Clutch size	**0.42**	**0.40**	0.04	0.17	−0.08	**0.36**	−0.07
Latitude		**0.60**	**0.36**	0.18	**−0.72**	0.29	**−0.52**
Longitude			0.09	0.28	**−0.63**	**0.60**	−0.12
Laying date				0.27	−0.37	**0.50**	**−0.73**
Breeding density[a]					−0.12	**0.39**	**−0.36**
Summer AE						**−0.41**	**0.44**
Elevation							**−0.47**

[a] Breeding density of all swallow species.

dating one egg per day from the date of the first record of eggs in the nest. Clutches with fewer than three eggs (n = 43) were dismissed because these numbers likely were due to abandonment. Clutches with more than eight eggs (n = 26) also were not used owing to the likelihood of egg dumping or of two females nesting in the same box (Robertson et al. 1992). Varying numbers of samples were collected from the same general location (Fig. 1). To reduce the problem of pseudoreplication, we estimated the mean of each variable from all nests within 1° blocks of latitude and longitude (latilong). Analyses were restricted to latilong blocks with at least 10 nest records. Our final sample size was based on 7,459 Tree Swallow clutches in 85 latilong blocks ($\bar{x}$ = 88 clutches per block; Fig. 1).

We tested Ashmole's hypothesis using estimates of relative resource abundance based on AE. Long-term estimates of AE (Thornthwaite Associates 1964) were gathered from the weather station nearest the mean latitude and longitude of the nest locations within a particular latilong block. Mean AE for the breeding season (summer AE) was calculated from the average of the May, June, and July AE values, because swallows have finished breeding by the end of July at almost all of our study locations. Above 60°N, however, swallows do not begin breeding until June, so for these locations (n = 3 latilong blocks) we used the mean of AE values for June, July, and August. Mean elevation for each latilong block was estimated from the elevation of these weather stations, as elevation was not recorded on most nest record cards. We also obtained long-term averages of monthly mean temperature in May (when most birds begin laying) from all weather stations in each latilong block ($\bar{x}$ = 2.8 stations per block; Peterson and Vose 1997) as an additional indicator of climate.

Following Koenig (1986), we examined Ashmole's hypothesis using summer AE and breeding density to estimate the relative level of resources available for breeding. We estimated relative resource abundance using the residuals from the regression of summer AE on swallow density. Breeding density of Tree

Swallows (as well as all species of swallows) was estimated using abundance indices from the Breeding Bird Survey program of the United States Fish and Wildlife Service (Price et al. 1995). Mean abundance values were calculated for each latilong block using means of multiple surveys and years where available ($\bar{x}$ = 4.3 routes per block; 76.7 total survey years). Breeding density of Tree Swallows was weakly but positively correlated with density of all species of swallows (R^2 = 0.07, n = 78, P = 0.02). Because food abundance for Tree Swallows may be influenced by other species of aerial insectivores, we present the results of analyses using the density of all species of swallows; however, our results were similar using just the density of Tree Swallows. Data for all six predictor variables were not available for 18 latilong blocks, so sample sizes were reduced to 67 blocks in multivariate analyses.

RESULTS

Mean clutch size and laying date increased significantly with latitude (Table 1). Latitude and longitude were correlated positively (r^2 = 0.36, P < 0.01; Table 1) because our data from the west were generally from farther north (Canada rather than the United States; Fig. 1). Because summer AE was correlated negatively with latitude and longitude (Table 1), summer AE was lower at higher latitudes and farther west. Tree Swallows initiated their clutches earlier where summer AE was higher, elevation was lower, and average temperatures in May were warmer (Table 1). There was no correlation between clutch size and summer AE (r^2 = 0.01, P > 0.50), an indicator of absolute resource abundance, nor was there a correlation between clutch size and breeding density of all swallow species (r^2 = 0.03, P > 0.20; Table 1).

Ashmole's hypothesis predicts that clutch

TABLE 2.   Multivariate analyses of Tree Swallow clutch size in relation to geographic and ecological variables
($n = 67$ latilong blocks with data for all variables). Shown are regression coefficients (β), their standard
errors (SE) and probability values (P), and standardized partial regression coefficients (β') from a multiple
regression analysis (dependent variable = mean clutch size; $R^2 = 0.52$), and partial correlation coefficients
for each variable with clutch size.

	Multiple regression analysis				Partial correlation coefficients
	β	SE	P	β'	
Intercept	1.86	1.52			
Latitude	0.096	0.016	<0.0001	1.016	0.61
Longitude	−0.003	0.003	0.35	−0.181	−0.12
Laying date	−0.009	0.008	0.27	−0.159	−0.14
Elevation	0.0006	0.001	0.0002	0.659	0.45
Relative resource abundance	0.012	0.003	<0.0001	0.584	0.48
Mean May temperature	0.054	0.022	0.018	0.394	0.30

size will be correlated positively with relative resource abundance, which we estimated with the residuals from the regression of summer AE on total swallow density. In a simple regression analysis, we found no relationship between clutch size and relative resource abundance ($r^2 < 0.01$, $n = 78$, $P = 0.98$). However, this analysis was confounded by several other variables. For example, relative resource abundance was correlated positively with mean temperature in May ($r^2 = 0.15$, $n = 70$, $P = 0.001$) and correlated negatively with latitude ($r^2 = 0.46$, $n = 78$, $P = 0.0001$), longitude ($r^2 = 0.35$, $n = 78$, $P < 0.0001$), mean elevation ($r^2 = 0.12$, $n = 71$, $P = 0.003$), and mean laying date ($r^2 = 0.08$, $n = 75$, $P = 0.016$). Thus, we used multiple regression to examine the effects of relative resource abundance on clutch size while holding all other variables constant.

The multiple regression model examined the effects of latitude, longitude, mean laying date, relative resource abundance, mean elevation, and mean temperature in May on clutch size (Table 2). In this model, clutch size still was related positively to latitude after controlling for all other variables ($n = 67$, $P < 0.0001$; Fig. 2). In contrast to the bivariate analysis noted above, clutch size was related positively to relative resource abundance ($n = 67$, $P < 0.001$; Fig. 2), as predicted by Ashmole's hypothesis. The increases in clutch size with both latitude and relative resource abundance were linear, because neither quadratic regression (Fig. 2) nor LOWESS plots (locally weighted scatterplot smoothing; SYSTAT 1992) revealed any evidence of curvilinearity. Overall, 52% of the variance in clutch size was explained by latitude (standardized partial regression coefficient [β]

$= 1.02$, $P < 0.0001$), longitude ($\beta = -0.18$, $P = 0.35$), mean laying date ($\beta = -0.16$, $P = 0.27$), relative resource abundance ($\beta = 0.58$, $P < 0.0001$), mean elevation ($\beta = 0.66$, $P = 0.0002$), and mean temperature in May ($\beta = 0.39$, $P = 0.018$).

We also examined how the relationship between clutch size and ecological variables changed with latitude by performing an analysis of covariance using three regions of latitude (40 to 44°N, 45 to 49°N, 50 to 54°N; Fig. 3). The relationship between clutch size and relative resource abundance did not differ in slope among the three regions (interaction of relative resource abundance and region, $P = 0.16$), but the intercepts differed (effect of relative resource abundance after removal of interaction term, $P < 0.001$; Fig. 3). This ANCOVA also included the following covariates: longitude ($P = 0.34$), mean elevation ($P = 0.03$), mean laying date ($P = 0.25$), and mean temperature in May ($P = 0.49$). The results were not affected qualitatively by excluding mean laying date, mean temperature in May, or longitude. The results were also similar when we divided our latilong blocks into eight geographic regions of both latitude and longitude (i.e. slopes were similar among regions, but intercepts differed). Thus, it appeared that clutch size increased with relative resource abundance at similar rates throughout the breeding range; however, clutch size was larger at 50 to 54°N, even after controlling for levels of relative resource abundance (Fig. 3).

DISCUSSION

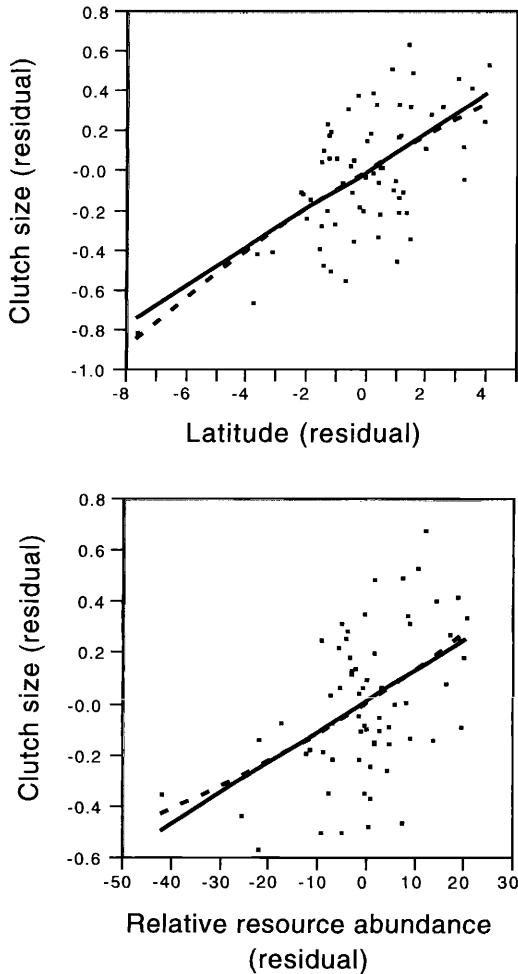Mean clutch size of Tree Swallows increased with latitude (Table 1, Fig. 2), as has been found
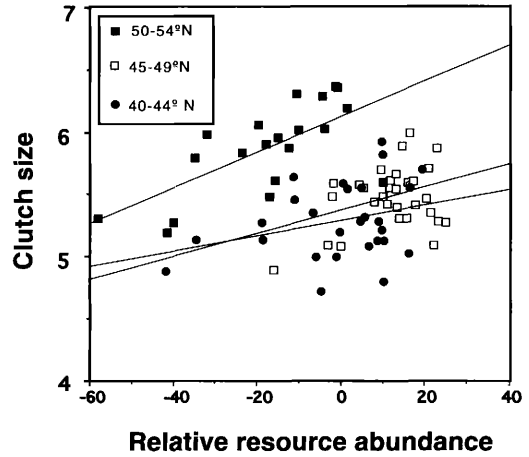
FIG. 3. Clutch size in relation to relative resource abundance for three regions of latitude (40 to 44°N, 45 to 49°N, 50 to 54°N). The relationship between clutch size and relative resource abundance did not differ in slope among the three regions ($P = 0.16$), but the intercepts differed ($P < 0.001$; see text). Breeding bird survey data were not available for the northernmost of our latilong blocks ($>60°$N), so we could not estimate relative resource abundance for those areas.

FIG. 2. Mean clutch size (for each latilong block) in relation to latitude (upper panel). Shown are residuals of clutch size and latitude from the regressions of clutch size or latitude on longitude, relative resource abundance, laying date, elevation, and mean temperature in May. Mean clutch size (for each latilong block) in relation to relative resource abundance (lower panel). Shown are residuals of clutch size and relative resource abundance from the regressions of clutch size or relative resource abundance on latitude, longitude, laying date, elevation and mean temperature in May. Relative resource abundance is estimated by the residuals of the regression of summer AE on breeding density. Lines through the data points indicate simple (solid) and quadratic (dashed) regressions.

in many other groups of birds (Moreau 1944, Lack 1947, Cody 1966, Klomp 1970, Kulesza 1990) in the Northern and Southern hemispheres (Yom-Tov et al. 1994, Young 1994). It is

likely that environmental or life-history factors related to latitude are the proximate causes of this relationship. In this study, relative resource abundance (summer AE controlling for breeding density) was a better correlate of clutch size than the absolute level of resource abundance (summer AE alone) once we controlled for confounding variables. These results are consistent with Ashmole's hypothesis that relative rather than absolute levels of resources determine clutch size. However, our results are correlative and do not identify the mechanism that produces the pattern. In particular, we do not know if the pattern is produced by density-dependent mortality during the nonbreeding season, as suggested by Ashmole (1961), or by density-dependent competition for resources during the breeding season. Regardless of the precise mechanism, it is likely that the proximate cause is related to competition for food, because detailed studies indicate that much of the variation in clutch size is related to food abundance (Hussell and Quinney 1985, Dunn and Hannon 1992).

Studies of geographic variation in clutch size have found mixed support for Ashmole's hypothesis. Surprisingly, the only other study to

examine Ashmole's hypothesis in swallows (*Hirundo rustica* and *Delichon urbica* in Europe) found no significant increase in clutch size with latitude, nor a positive relationship with seasonality (ratio of summer to winter AE; Møller 1984). Møller (1984) suggested that he did not detect an increase in clutch size with latitude because most sites were within a range of 15° of latitude. In our study, most clutches of Tree Swallows also were within a range of 15° of latitude, so there may be more important ecological differences between these species of swallow; for example, the effects of latitude in Europe may be ameliorated by the Gulf Stream. In swallows (Møller 1984) and House Wrens (Young 1994), no relationship was found between clutch size and seasonality; however, in these studies the authors had to determine the wintering grounds of particular breeding populations in order to estimate winter AE. The failure to find a correlation may have been due to inaccurate identification of the wintering grounds and, thus, winter AE and seasonality. All three studies that found support for Ashmole's hypothesis (Ricklefs 1980, Koenig 1984, this study) used density estimates of breeding birds to estimate relative resource abundance. Future studies that examine this hypothesis should also try to obtain direct estimates of breeding density.

We found that clutch size of Tree Swallows was related positively to relative resource abundance. This is consistent with detailed studies of clutch size and food abundance in Tree Swallows (Hussell and Quinney 1985) and other species (Martin 1987, Korpimäki and Hakkarainen 1991). However, the relationship between clutch size and relative resource abundance differed geographically (Fig. 3). For a given level of relative resource abundance, swallows laid larger clutches at northern (50 to 54°N) than southern latitudes, although the rate of increase in clutch size did not vary significantly (Fig. 3). This suggests that swallows responded similarly to changes in resource abundance, but some unknown factors allowed swallows to lay larger clutches in the north. As a consequence, relative resource abundance provided only a partial explanation for the latitudinal increase in clutch size. Hussell (1985) suggested that time budgets of birds vary with latitude, in which case birds farther north might have more time to feed and raise a larger

brood. Another possibility is that fewer non-swallow competitors (other aerial insectivores, including bats) occur at more northern latitudes.

In conclusion, we found support for Ashmole's hypothesis that relative, rather than absolute, levels of resource abundance influence geographic variation in clutch size. However, other factors that we did not measure also must have a significant influence on geographic patterns of clutch size.

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Associate Editor: T. W. Arnold