LATITUDINAL VARIATION IN BREEDING PRODUCTIVITY OF THE ROUGH-WINGED SWALLOW

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PRODUCTIVITY and turnover in bird populations has been the subject of lively discussion and debate for more than 20 years, since Lack (1947, 1948) formally introduced the problem of clutch size variation into the literature. It has frequently been pointed out that one cannot measure relative turnover rates in populations simply by the number of eggs laid in a clutch. Other factors, such as the survival of the young and the number of broods raised per season, are also crucial components of the population equation. Because requisite data for survival and productivity are difficult to obtain for most species, a more direct approach to measuring recruitment seemed desirable. If one could assess the ratio of immature to adult birds in a population at the proper time of the year, i.e. after the survival rates of young of the year had reached adult levels, it would be possible to estimate the annual recruitment rate of the population by the proportion of first-year birds among the breeding population (Snow, 1956).

This report summarizes an effort to measure recruitment rates in a single widespread species, the Rough-winged Swallow (*Stelgidopteryx ruficollis*). Because birds of the year cannot be distinguished from adults after their first fall, accurate estimates of annual recruitment are not possible. The method has nonetheless revealed latitudinal gradients in fledgling productivity and suggests that, for suitable species, annual population turnover may be estimated directly from museum collections.

A large geographical and seasonal series of museum specimens was examined to determine ratios of immature to adult individuals in a population. The relationship of these estimates to actual recruitment rates depends on certain assumptions about the ecology of the species and about the behavior of collectors in the field. First one must be sure that age, i.e. first year vs. adult, can be determined for museum specimens. One must also ascertain that collectors do not prefer one age class to another. To be conservative, the impartiality of the collector cannot be relied upon, but rather one must choose species that the collector cannot age until the birds are in the hand. Collectors pose additional problems with the seasonality of their activities. As recruitment estimates are based on ratios that may be obtained at any suitable point in time, seasonal bias in samples does not limit the accuracy of the estimate so much as it may cause frustration by the unavailability of data for the entire year. Assuming that one can find a suitably wide-ranging species to provide interesting intraspecific comparisons, a species in which age can be determined in the hand but not in the field, one must further assume that the behavior of the birds themselves does not differ appreciably between the adults and immatures. To the extent that age classes differ in their wariness to the approach of man, in the timing and extent of their seasonal movements, and in their ability to obtain nest sites and mates during the following breeding season, estimated values of recruitment rates will deviate from real values. In the final analysis, many of these assumptions cannot be verified, and we may have to wait for detailed banding studies to assess population turnover rates accurately.

Materials

I considered several species for this study, although I did not exhaust, or even explore, all possibilities. I was interested in finding a bird that ranges widely throughout both temperate and tropical regions, that has been collected in abundance, and in which age is readily determined from museum specimens. Also, to compare age-ratio data with breeding parameters (clutch size, nesting success, and number of broods), the species must also have been the subject of one or more life history studies. The Rough-winged Swallow satisfies these requirements well. Its breeding range extends from southern Canada (about 45° N in some localities) to Argentina (about 40° S). Mayr and Greenway (1960) recognize 10 subspecies. Most individuals north of Mexico belong to *S. r. serripennis*, those of subtropical Mexico, to *psammochroa*. Central America and the Yucatan Peninsula contain *ridgwayi*, *fulvipennis*, *stuarti*, and *decolor*. The races *uropygialis*, *aequalis* and *cacabata* are essentially tropical South America (including Panama), and *ruficollis* extends from the Amazon basin south into temperate areas of South America. The northern *serripennis* is migratory or partially migratory. Winter distribution extends from the southern part of the breeding range through central America to the northern part of South America. I do not know whether southern populations of *ruficollis* are migratory, although it is probable (Olrog, 1963).

Breeding biology.—Although this species is not so well-known as some other swallows, two important studies have been made: Lunk (1962) includes all aspects of breeding in Michigan, and Skutch (1960) provides some data from Costa Rica, though his study is based on few nests and lacks information on nesting success. Miscellaneous records of breeding biology are scattered through the literature.

Age determination.—Adult male Rough-winged Swallows are characterized by serrations on the leading edge of the outer primary. It has been stated that, at least for the male sex, this characteristic, which is readily determined, may be used reliably to distinguish birds in their first breeding season. Bent (1942) states that "At the time of leaving the nest the young birds are similar to their parents in size, feathering, and length of the wing and tail, but the first primary lacks the roughness of the adult feather; indeed, it is probable that nearly a year passes before the young birds acquire this saw edge that gives them their name. Also, the plumage is tinged with rufous or cinnamon, especially on the throat and upper breast; the wing coverts and tertials are margined with the same ruddy tint." Lunk (1962) felt that "It was of interest, whenever possible, to distinguish adults in their first breeding season. There seems to be considerable correlation with age in the degree of development of the serration of the first primary. I do not believe, however, that this is entirely dependable. I have seen birds I would otherwise judge to be only a year old which had relatively well-developed serrations; others, which appeared fully adult, had them rather weak." Migratory populations of swallows, including *Stelgidopteryx*, often undergo a complete postjuvenal molt after the migration. Dwight (1900) says that "First winter plumage is acquired by a postjuvenal molt after the birds have migrated southward in September, or very likely while they move leisurely along in flocks." In this case feather characteristics would be useful only for a limited period after the end of breeding season. This agrees with the material gathered in this study.

If the roughness of the first primary is a reliable criterion of age for only a brief part of the year in migratory subspecies, what is the schedule of the postjuvenal molt in tropical subspecies? If the molt were to occur soon after fledging, before all young of the season could be expected to have fledged, some young would be taking on this particular adult characteristic before all of the nestlings had fledged. This would tend to reduce the ratio of immatures to adults in the population, and hence reduce the estimate of productivity. Snow and Snow (1964) found that adult molt of most passerines generally occurs well after the breeding season in Trinidad. Moreover, the Rough-winged Swallow has a relatively short breeding season probably limited to one brood even in the tropics (Skutch, 1960), and thus the timing of the postjuvenal molt of the flight feathers is probably not a major problem.

Specimens.—A total of 1,197 male Rough-winged Swallows from 15 museums and representing 10 subspecies were examined (Table 1). Data were lumped according to subspecies. Because the only subspecies sufficiently represented to make finer geographical distinctions, *serripennis*, is migratory, wintering individuals are not assignable to particular breeding localities. Within the broad geographical scope of the study, subspecific groups are probably adequate for assessing variation in population parameters. Although some of the tropical subspecies could have been further lumped to increase sample size, this was not done.

Table 1 presents the age and collection data of Rough-winged Swallow specimens for the 10 subspecies. Several of the races are too poorly represented for further analysis. Others, particularly *serripennis*, show marked seasonal collecting biases. To analyze the ratios between immatures and adults, data for several months were lumped in many cases to obtain sufficent samples to make the ratios meaningful. In lumping data I began with months that were represented by enough individuals to be analyzed separately, combining months in either direction until a sufficient number of specimens had been accumulated. Immature/adult ratios (I/A) are presented in Table 2 for the five most abundantly collected subspecies.

DISCUSSION

Validity of the method.—The data in Table 2 point to several problems for estimating annual recruitment rates in the Rough-winged Swallow. First, the age criterion used here, the roughness of the leading edge of the first primary, does not hold up until the following breeding season. Banding studies, have shown that the annual adult mortality of small Temperate Zone passerine birds is on the order of 50 percent per year (Farner, 1955), give or take 10 or 20 percent. Therefore we would expect at least 30 percent of the males present on the breeding grounds

TABLE 1

SUMMARY OF MALE ROUGH-WINGED SWALLOW SPECIMENS EXAMINED[1]

Subspecies	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
serripennis	1/9	2/6	1/47	10/84	10/156	12/81	42/24	28/4	3/2	6/1	2/4	0/2	537
fulvipennis	0/3	1/5	1/13	0/10	0/8	14/5	8/7	4/0	0/2	2/4	1/4	0/1	93
psammochroa	0/2	1/2	0/9	1/9	1/13	9/9	3/2	1/1	2/0	1/2	0/0	0/0	68
ridgwayi	0/0	0/3	0/3	0/0	0/0	1/1	3/0	1/0	1/0	0/0	0/1	0/0	14
stuarti	0/0	0/4	0/0	0/3	0/1	1/1	1/0	5/4	0/1	0/1	0/0	0/0	22
decolor	0/0	0/1	0/0	0/0	0/0	0/0	0/1	0/0	0/0	0/1	0/1	0/1	5
uropygialis	0/8	1/7	0/12	3/12	1/10	3/8	3/5	5/2	2/6	2/10	3/9	1/9	122
aequalis	2/5	1/13	0/11	0/8	5/15	3/5	3/6	0/8	2/5	4/8	1/3	0/11	119
cacabatus	0/0	0/0	0/1	0/1	1/1	0/0	0/0	0/0	0/0	0/0	0/1	0/0	5
ruficollis	6/5	11/10	2/10	6/9	2/8	4/12	1/22	3/14	1/23	2/21	10/19	4/7	212

[1] Data are grouped by subspecies, month, and the condition of the leading edge of the first primary: rough (A) or smooth (I). Data are presented as number of individuals in category I/number of individuals in category A.

TABLE 2

RATIOS OF IMMATURE TO ADULT SPECIMENS BY MONTH, OR GROUPS OF MONTHS, FOR FIVE SUBSPECIES OF THE ROUGH-WINGED SWALLOW

Subspecies	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
serripennis	0.176		0.021	0.119	0.064	0.148	1.75	7.0		1.57		
fulvipennis				0.032			2.17				0.211	
aequalis			0.031			0.042			0.286			0.158
uropygialis	0.083				0.167			0.769		0.214		
ruficollis	1.13			0.370			0.147		0.103			0.538

TABLE 3
MAXIMUM RATIOS OF IMMATURES TO ADULTS FOLLOWING BREEDING FOR DIFFERENT SUBSPECIES OF THE ROUGH-WINGED SWALLOW

Subspecies	Latitude range	Month(s) of sample	Size of sample	I/A ratio	95% confidence limits[1]
serripennis	30–50° N	July	66	1.75	1.00–3.35
psammochroa	20–30° N	June–July	23	1.09	0.43–2.95
ridgwayi	20° N				
stuarti	15–20° N	July–Sept.	11	1.20	0.22–4.88
fulvipennis	10–20° N	June–July	34	1.83	0.91–4.00
uropygialis	10° S–10° N	July–Sept.	23	0.76	0.31–1.72
aequalis	0–10° N	May–July	37	0.42	0.19–0.83
cacabata	0–10° N				
ruficollis	0–40° S	Jan.–Feb.	32	1.13	0.55–2.41

[1] Calculated on the basis of table W in Rohlf and Sokal (1969).

to be in their first year. Yet for *S. r. serripennis*, I/A ratios for the spring (March–June) are less than 0.05 when they should be on the order of at least 0.43 (0.30/0.70. The winter sample (December through February) has a ratio of about 0.2, which is substantial but not as high as would be expected. This suggests that the acquisition of the rough edge of the first primary does not occur uniformly throughout the entire population of first-year birds, and that a small fraction of individuals may retain the smooth primary through the first breeding season, as stated by Lunk (1962).

Second, the high ratio of immatures to adults in the August sample (mostly from the United States) of the *serripennis* subspecies (I/A = 7.0) suggests that adults and birds of the year migrate at different times, the adults leaving the breeding grounds first. This has been demonstrated for the Least Flycatcher (*Empidonax minimus*) by Hussell et al. (1967). Differential migration of the Least Flycatcher is apparently linked to the period of molt; the postjuvenal molt occurs before, and the postnuptial molt after, migration.

The reduction of I/A ratios following breeding does not appear to reflect differential mortality of the age groups except, perhaps, for summer to fall comparisons. Thus only ratios calculated for the period immediately following breeding are useful for determining recruitment.

I/A ratios.—Maximum ratios of adults to immatures among different races immediately following breeding are presented in Table 3. Where egg dates are available, these maxima can be shown to occur at the end of the period when young are fledged from the nest. Table 4 gives egg dates for various races and localities. From data on laying, incubation, and nestling periods (Table 5), the length of time from the egg to departure from the nest is on the order of 40 days, or 1.3 months.

TABLE 4
EGG DATES FOR THE ROUGH-WINGED SWALLOW

Subspecies and locality	Source	No. of clutches	Range of egg dates
serripennis			
Washington	Bent, 1942	6	11 June–4 July
Montana	Weydemeyer, 1933	7	14 June–6 July
Illinois	Bent, 1942	9	17 May–6 June
Pennsylvania	Bent, 1942	14	3 May–15 June
California	Bent, 1942	23	15 April–9 July
Florida	Howell, 1932	3	2 May–1 June
Kansas	Johnston, 1964	14	11 May–30 June
Connecticut	Sage et al., 1913	?	22 May–24 June
Kentucky	Mengel, 1965	13	1 May–10 June
Michigan	Lunk, 1962	Many	10 May–25 June
fulvipennis			
Costa Rica	Skutch, 1960	8	16 April–18 May
aequalis			
Trinidad	Belcher and Smooker, 1937	?	April–June

Most eggs of *Serripennis* are laid by early June, and one could expect most of the young to have left the nest by mid- to late July. Similarly, in Costa Rica (race *fulvipennis*) most eggs are laid by early May and maximum I/A ratios occur during the June–July–August period. As one would expect, the Southern Hemisphere race, *ruficollis*, has maximum I/A ratio during our winter (January–February).

Postbreeding I/A ratios show a very clear latitudinal gradient, decreasing as one approaches the equator (Figure 1). The values vary from a maximum of 1.75 for the northern race *serripennis* to a minimum of 0.42 for the tropical *aequalis*. The high value for *fulvipennis* may be due to inclusion of two broods of advanced nestlings (collected on the same date and locality) totaling five individuals. If these are excluded, the June–July ratio becomes 17/12 or 1.42. For July the ratio in 8/7, or 1.14, which is very close to the regression line for the other subspecies.

TABLE 5
LENGTH OF THE NEST CYCLE OF THE ROUGH-WINGED SWALLOW IN MICHIGAN AND IN COSTA RICA

Locality	Laying period (days)	Incubation period	Nestling period (days)	Total (days)	Source
Michigan	5	15–16	18–21	38–42	Lunk, 1962
Costa Rica	4	16–18	20–21	40–43	Skutch, 1960

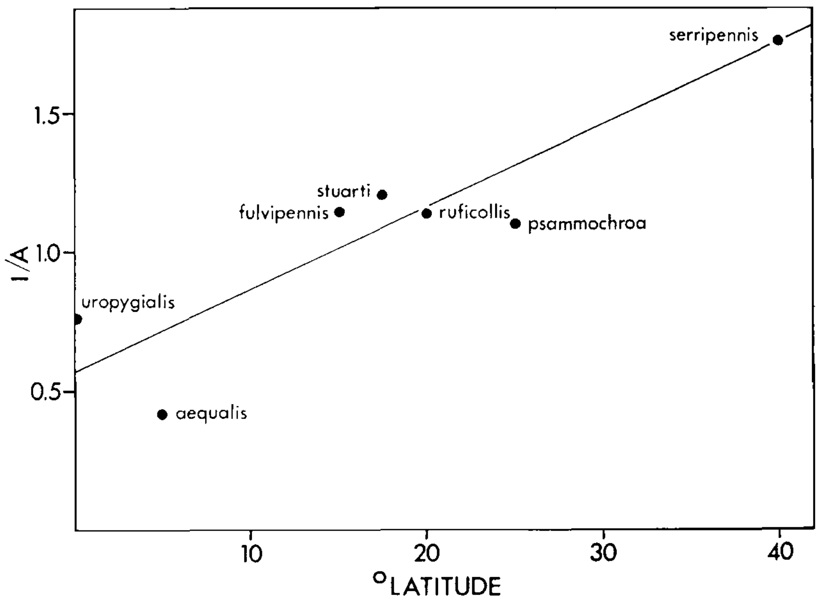

Figure 1. The ratio of immatures to adults in museum collections of breeding populations in relation to latitude. Data are from Table 3.

These data, though crude, suggest a fourfold increase in the productivity of young from equatorial to temperate regions.

Components of productivity.—From knowledge of the breeding biology of the Rough-winged Swallow, it is possible to assess the relative roles of clutch size, number of broods, and nesting success in the total production of young. Clutch size of the Rough-winged Swallow, unlike other species, does not decrease substantially with decreased latitude (Table 6). Average clutch size for the northern *serripennis* varies within the range of the subspecies but is generally between five and six eggs. Data for tropical subspecies suggest that the average clutch size at the equator might be about an egg (15–20 percent) less. Thus clutch size alone can explain only a small part of the decrease in productivity with latitude.

Although replacement clutches are known for the Rough-winged Swallow in the United States, Lunk (1962) states that only one brood is raised if the first is successful. Skutch (1960) is of the same opinion for the species in Central America. Belcher and Smooker (1937) indicate that eggs are laid in Trinidad only over a 3-month period, which is short considering the long nesting periods of most passerines on that island (Snow and Snow, 1964; Ricklefs, 1966). Probably only one brood is raised there as well. It is known, however, that some swallows, e.g. the

TABLE 6
CLUTCH SIZE OF THE ROUGH-WINGED SWALLOW

Subspecies and locality	Number of clutches	Clutch size		Source
		Average	Range	
serripennis				
Michigan	61	6.25	5–8	Lunk, 1962
Florida	3	5.3	5–6	Howell, 1932
Kansas	4	5.0	4–6	Johnston, 1964
Connecticut	?		5–7	Sage and Bishop, 1913
fulvipennis				
Costa Rica	6	4.7	4–5	Skutch, 1960
aequalis				
Trinidad	?		4–6	Belcher and Smooker, 1937

Mangrove Swallow *Tachycineta albilinea* (Ricklefs, MS), may raise more than one brood in a season. Any tendency towards multiple broods in the tropics would tend to work against the pattern observed in Figure 1, and we can reasonably assume that the species is one-brooded, for the most part, over its entire range.

This suggests that the third component of productivity, the fledging success of the nest, is responsible for most of the observed decrease in productivity in tropical populations. This is consistent with the observed decrease in nesting success from temperate to tropical localities, summarized by Ricklefs (1969). If one assumes that clutch size at the equator is 0.8 of the clutch size at 40° N, nest survival in the tropics must be about 0.5 that of temperate regions to obtain a fledgling productivity of 0.4 that of temperate regions. Any tendency towards multiple or replacement broods would increase the inferred discrepancy in survival rates. Comparisons between the nesting success of hole-nesting species in the Temperate Zone (Nice, 1957: 66 percent) and in the tropics (Skutch, 1966: 44 per cent) indicate only a one-third reduction in nesting success in the tropics. Assuming the data to be straightforward, this discrepancy may be resolved by postulating that a smaller proportion of the adults in tropical populations breed in any one year. It is also possible that the survival of young immediately out of the nest is lower in the tropics than in temperate regions, though there is no evidence on this point other than incidental observations. For example, of five fledgling Mangrove Swallows one pair of birds produced on Barro Colorado Island in the Canal Zone during 1968, all survived until independence, more than a month after fledging (Ricklefs, MS).

TABLE 7
MAXIMUM TURNOVER RATES OF POPULATIONS FOR GIVEN RATIOS OF IMMATURE TO ADULTS IN THE POSTBREEDING POPULATION

I/A ratio	Minimum percent of adults in following breeding population	Maximum percent of annual adult survival rate
1.75	36	64
1.50	40	60
1.00	50	50
0.50	67	33
0.25	80	20

Breeding data gathered by Lunk (1962) in Michigan are consistent with the observed I/A ratio for the subspecies *serripennis*. The average clutch size in Lunk's study was 6.25 eggs and the egg success of 66 nests was 61 percent, yielding an average of 3.8 young per nest, or 1.9 young per breeding adult. The observed I/A ratio for the race immediately following fledging is 1.75, which is in close agreement with predicted values.

While productivity estimates cannot be used to calculate the absolute rate of turnover of the population each year, they can provide maximum estimates, assuming mortality of first-year birds to be at least as great as that of adults. Thus in *serripennis* the composition of the breeding male population can be at most 1.75 first-year birds to 1 adult, or at least 36 percent adults. This indicates a maximum adult annual mortality of 64 percent, which would be near the top of the range Farner (1955) indicated for temperate passerines. Maximum turnover values for other I/A ratios are presented in Table 7. In some tropical populations adult survival is almost surely greater than 67 percent per year. The annual survival of adults from temperate populations cannot be lower than about 33 percent and still maintain the population.

Snow's (1956) study of the annual mortality of the Blue Tit (*Parus caeruleus*) provides an interesting comparison. The study was based on the proportions of first-year and adult specimens collected during the breeding season. Young birds can be distinguished by the color of the primary coverts. Snow found that I/A ratios (calculated by me from Snow's data on percent adult specimens) varied from a high in Britain of 2.33 (ca. 55° N) to a low of 0.82 in the Canary Islands (ca. 35° N) and the Iberian Peninsula. Moreover, the I/A ratios almost precisely parallel variation in clutch size, from 11.6 eggs in Britain to 4.3 eggs in the Canary Islands. This finding contrasts with the results of this study and suggests that geographical variation in productivity and annual recruitment may reflect different factors, or combinations of factors, affecting the productivity equation, depending on the species.

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Summary

Museum specimens were examined to determine the ratio of immature (first-year) to adult birds, and hence the recruitment or annual turnover rate of the population. The Rough-winged Swallow was chosen for the study because it is widely distributed geographically (southern Canada to Argentina), it is collected in abundance but cannot be aged in the field, first-year birds can be distinguished in the males by the absence of serrations on the leading edge of the first primary, and its breeding biology is reasonably well-known.

It was found that the aging criterion is reliable only for those months immediately following the breeding season. Ratios of immatures to adults at that time, hence the productivity of young per adult, was found to vary from a high of 1.75 in the Temperate Zone race *serripennis* to a low of 0.42 in the tropical race *aequalis*. The ratio was highly correlated with latitude, exhibiting a roughly fourfold increase from the equator to 40° N.

Analysis of clutch size and the number of broods raised per season suggest that most of the variation in productivity is due to variation in nesting success, which has been shown to decrease with latitude towards the equator. Estimates of the minimum adult survival rate necessary to maintain the population are 33 percent per year at 40° N and 67 percent per year at the equator.

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