EGG WEIGHTS AND BROOD REDUCTION IN THE EUROPEAN SWIFT (*APUS APUS*)

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Although all species of birds have characteristic egg weights (Lack 1968), there exist intraspecific differences which may reflect genotypic differences among females or phenotypic adjustment of egg size to season, food supply, laying order, clutch size or other factors (Kear 1965). This variation has received considerable attention in poultry, where egg size has long been known to influence chick quality, as judged by hatching size and survival (review in Landauer 1967), but only recently has received attention from field biologists (Parsons 1970, 1975b, Schifferli 1973, Murton et al. 1974). This paper is concerned with size variation and its adaptive significance in the eggs of the European Swift (*Apus apus*). Since swifts feed on flying insects, they may have difficulty in finding food, particularly in cold, wet or windy weather (Lack and Lack 1951, Lack 1956), and they consequently lay unusually small eggs for their body size (Lack 1968:286). A study of a species with such specialized habits seemed more likely to reveal the adaptive significance of egg size variation than is the case with poultry. I report here the results of such a study.

MATERIALS AND METHODS

Egg weights were obtained from a colony of swifts breeding in nestboxes in the University Museum Tower at Oxford (Lack 1956). Egg weights were recorded by the late David Lack in 1948–1951, 1967 and 1968. In the summers of 1969–71, I measured egg weights in relation to egg size, water loss, chick growth, and chick survival. The 1948–1951 weights were obtained to within 0.01 g using a chemical beam balance. From 1967 onwards, measurements were made with a spring balance, a quicker procedure, but accurate only to about 0.05 g. Initially, all weights were obtained on the day of laying, but once I established that the weight changes over the first two days were less than 0.5% of the initial egg weight (O'Connor, unpubl. data), I made use of all records of eggs weighed within two days of laying. In all years, but especially in 1971, weights on day 0 (weight on the day of hatching, corresponding to an average chick age of 12 h when inspected) were obtained. In 1971, the success of these chicks in relation to growth and fledging was recorded; these data were extended by occasional measurements from other years. In 1971, the lengths and breadths of a number of eggs were recorded in addition to fresh weight.

RESULTS

DATE OF LAYING

The date when the first egg was laid each year has varied between 11 May (in 1958) and 28 May (in 1955). In most years nearly all birds laid within about two weeks but in a few years one or more interruptions occurred during the laying period. In 1971, eggs were still being laid as late as 10 July. In such years the average date of laying of all the pairs is a misleading indicator of the timing of breeding. On the other hand, the date of the first egg was occasionally so far ahead of most egg-laying that it too was a poor index of the annual variation in laying. Hence I have used the date on which the fourth clutch was started, ranging from 14 May (in both 1960 and 1961) to 29 May (in 1951 and 1955), and the date by which 40% of the pairs had started, ranging from 17 May (in 1959 and 1961) to 30 May (in 1951 and 1955). Both indices are arbitrary but they correlate well with each other (r = 0.916, P < 0.01) and with more subjective assessment of the annual variation in laying. Both indices show that the start of breeding has varied by 13–15 days over the 23 years of study, a much smaller range than for passerine birds resident in the area e.g., the Great Tit (*Parus major*; Perrins 1965).

The date of laying was correlated each year with the weather for the preceding three weeks (Fig. 1). Methodological and biological problems hinder attempts to demonstrate such correlations: first, in determining the period during which weather may influence egg formation, and second, deciding how best to measure and describe the weather. The average temperature (mean of daily averages) over the first 20 days of May is used here. Other measures, such as average minimum temperature, might yield stronger correlations but, in practice, the environmental variables influencing abundance of aerial insects change throughout the season (Bryant 1975), so no a priori rule is possible. The use of average temperature here follows Bryant's (1975) practice. The date for the initiation of 40% of the clutches was delayed as the average temperature over the period 1–20 May decreased (Fig. 1). The correlation is not close, temperature accounting for about 45% of the variation in the laying date, perhaps partly because both rain and strong winds may independently reduce the numbers of airborne insects, and thus the availability of food for egg formation
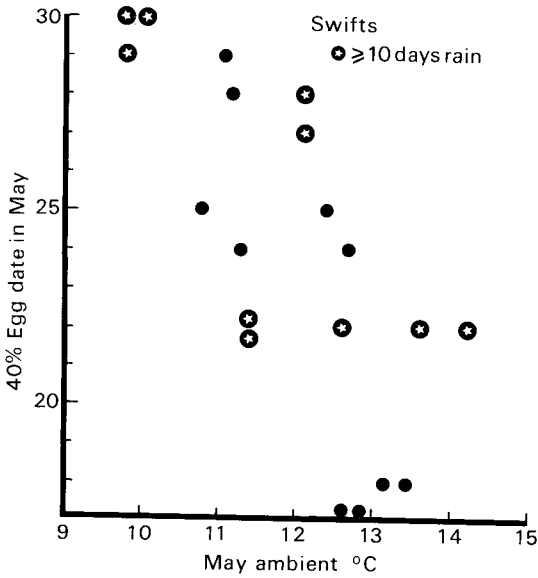
[133]

FIGURE 1. Date of egg laying each year in relation to ambient temperature in early May. Open symbols indicate wet years (at least 0.01 inches rain on 10 or more days between 1 and 20 May). Temperature obtained as average daily mean over 1–20 May.

by the female. Regressions were therefore calculated separately for wet and dry years, defining wet years as those in which at least 0.01 inches of rain fell on each of 10 or more days during 1–20 May. The results for wet years were

$$D = 45.44 - 1.71\ T \qquad r = 0.727$$

and for dry years were

$$D = 59.08 - 2.92\ T \qquad r = 0.629$$

where D is the 40% date in May and T the average ambient temperature over 1–20 May; both correlations are significant at $P < 0.05$. Thus temperature had a greater effect on laying date in dry than wet conditions (Fig. 1).

The date of laying by individual pairs of swifts tends to be constant (relative to the population as a whole) between successive years (Fig. 2). The figure shows a correlation between the dates of clutch initiation in each nestbox in 1969, 1970 and 1971. Adult mortality among the swifts in the tower is low, with only about 15% of the birds disappearing each year (Perrins 1971). Since individual pairs keep to the same boxes between years (Perrins 1971) the correlations in Figure 2 are likely to reflect individual constancy of laying date. If so, the greater turnover of population over two years should lead to a lower correlation between laying dates in 1969 and 1971 than between laying dates in successive years: for boxes used in each of the three years this is so ($r = 0.284$, not significant, vs. 0.517 for 1969 with 1970 and 0.451 for 1970 with 1971, both at $P < 0.05$). This check precludes the possibility that some boxes are environmentally more favorable for egg formation, as shown for other species breeding in the area (O'Connor 1978c).

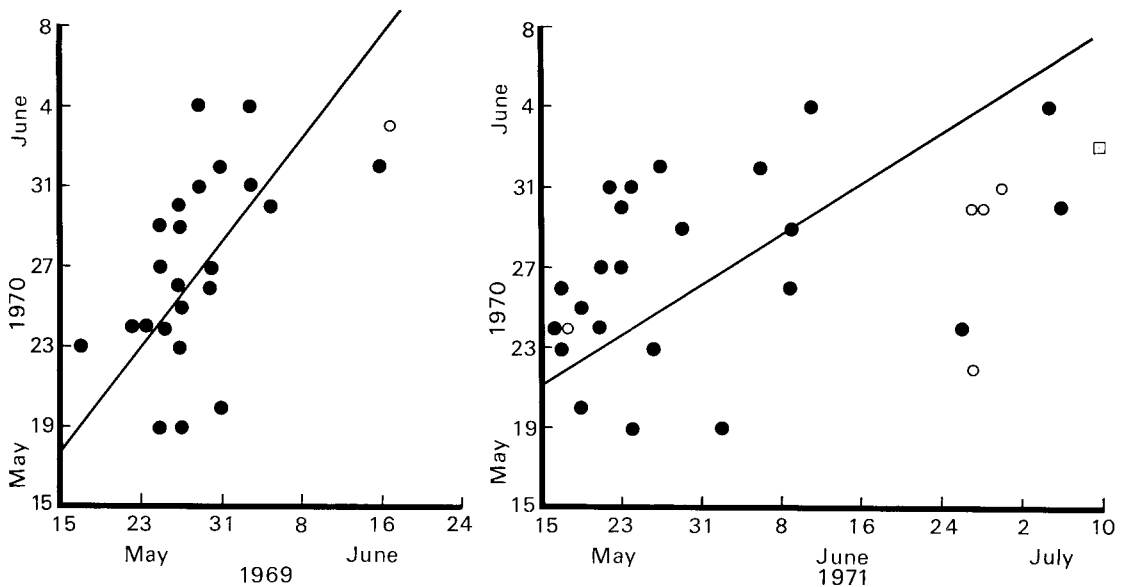In many years there were periods during the main laying season when no new clutches were

FIGURE 2. Timing of egg laying by the same female in successive years (open symbols) or over three successive years (closed symbols). See text for details of assumptions. Lines fitted by eye. Open square, 1971 laying date = July 1.

TABLE 1. Gaps in the start of new clutches in relation to weather.[a]

Year	Inclusive dates between which no new clutches were started[b]	Preceding weather[c]
1948	28 May–11 June (one egg 3 June)	rain each day 22 May–6 June, cold, mod. breeze 2–7 June
1949	29 May–4 June (one clutch 1 June)	mod. breeze 24–31 May, rain
1950	27 May–1 June (one clutch 28 May)	cold, little sunshine, northeast winds, 24–27 May
1958	26–29 May	fresh breeze on 16, 18, 21–24 May
1959	19–26 May (one new clutch on both 22 and 23 May)	northeast winds 11–27 May, mod. breeze on 17–25 May except 20 May, sunless 19–21 May
1960	22–28 May	northeast winds 15–21 May, mod. breeze 18–21 May, cold 18–21 May, rain 19–20 May
1967	23–29 May	fresh breeze 19–23 May, rain each day 13–31 May
1970	21 and 28 May	cold, mod. breeze 17 May, 21–22 May, rain on 21 May
1971	28–29 May	cold, heavy rain 22–30 May
	11–16 June	heavy rain 8–19 June except 12 and 17, cold except 13 and 19, mod. breeze on 10 June

[a] Further details in Lack (1956).
[b] In main laying period only (see text).
[c] Note the four to five day lag in some years.

started and which were preceded by low temperature, rain or strong winds (Table 1). Lack (1956) showed that bad weather inhibits the start of new clutches and that the return of good weather is followed by new clutches after a five-day lapse. He concluded that a swift required five days between the initiation and the laying of an egg during good weather, though the five-day periods for individual eggs of each clutch are themselves overlapped (for model see King 1973).

INTERVALS BETWEEN THE EGGS OF A CLUTCH

Considering all years, not merely those in which the eggs were weighed, the second egg was laid two days after the first in about three-

quarters of the clutches, irrespective of whether a third egg was laid. In the remaining clutches the second egg was normally laid after three days. As previously shown by Lack (1956), three-day intervals were commoner in cold than in warm weather. In clutches of three, the third egg was laid two days after the second in about a third of the cases and after three days in practically all other cases.

CLUTCH SIZE

The normal clutch of the swift is two or three, and is adapted to the number of young that the parent can feed (Lack and Lack 1951, Perrins 1964). The proportion of three-egg clutches decreases regularly from about 75% in mid-May to about 5% in the first days of June and none thereafter, a variation presumably evolved in relation to the average number of young the parents can raise at different dates. In addition, the proportion of clutches of three at the same date has differed markedly between years, being higher when preceded by good weather than by bad (Lack and Lack 1951, Lack 1956).

SIZE OF THE EGG

The mean weight of 459 eggs weighed fresh was 3.54 g, about 8.5% of the weight of the bird. The distribution of weights is skewed: omitting one freak egg which had an exceptionally large air space, the lightest was 2.48 g and the heaviest 4.25 g, respectively 30% below and 20% above the mean; 95% of the eggs weighed between 3.1 and 4.1 g. The mean weight of the first two eggs laid was the same whether the clutch consisted of two or three eggs (for clutches laid in the same period and therefore under the same weather conditions).

First and second eggs were similar in both length and breadth (Table 2) but third eggs were substantially longer and slightly narrower than the second or first eggs, even when compared with the other eggs in the same clutch. In Table 3 all three egg dimensions are seen to be inter-correlated but weight and breadth are more closely correlated than either of the other pairs of variables. Partial correlations show that egg weight is related independently and strongly to both length and breadth, but with considerable variability in shape.

DIFFERENCES IN WEIGHT WITHIN CLUTCHES

In 178 clutches examined, the second egg was lighter than the first in about 30%, equal in 7%, and heavier in 63%. Second eggs were

TABLE 2. Swift egg dimensions in 1971.

Laying order	Weight g Mean ± SD (N)	Length mm Mean ± SD (N)	Breadth mm Mean ± SD (N)
1	3.45 ± 0.28 (16)	24.36 ± 0.97 (14)	16.33 ± 0.58 (14)
2	3.37 ± 0.36 (26)	24.31 ± 1.23 (15)	16.36 ± 0.64 (15)
3	3.32 ± 0.18 (7)	29.95 ± 0.42 (9)	15.99 ± 0.72 (9)
Pooled	3.38 ± 0.18 (49)	24.24 ± 0.97 (38)	16.26 ± 0.63 (38)
Coefficient of variation %	9.82	4.01	3.88

Lewontin's (1966) test for differences in coefficients of variation gives: F (weight, length) = 6.00, $P < 0.001$; F (weight, breadth) = 6.41, $P < 0.001$; F (length, breadth) = 1.07, not significant.

thus significantly heavier than first eggs ($\chi^2 = 21.1$, $P < 0.001$). The weight difference ranged from 0.40 g lighter to 0.55 (once 0.85) g heavier and averaged 0.10 g heavier both in clutches of two and of three.

During bad weather when no new clutches were started (Table 1), pairs which had already laid one egg laid a second, but only rarely a third. Under such conditions a second egg laid two days after the first weighed an average of 0.11 g less, instead of 0.10 g more, than the first egg (Table 4). However, eggs laid three, four or more days after the first had weights similar to normal second eggs. The proportion of clutches with lighter second eggs was greater in bad than in good weather for clutches laid at two-day intervals ($\chi^2 = 16.8$, $P < 0.001$) but not for those laid over a longer period ($\chi^2 = 0.10$, N.S.). The proportion of clutches laid at a two-day interval was significantly lower in bad weather (47.4%, Table 4) than in good weather (78.2%) ($\chi^2 = 8.38$, $P < 0.01$).

On the average, the third egg weighed 0.19 g less than the first and second eggs in the same clutch (49 clutches measured over nine years), but the difference was much greater in some years than in others. The variation in the weight of the third egg was correlated with the difference in weight between first and second eggs in all clutches laid in the same period ($r = 0.754$, one-tailed $P = 0.045$; Fig. 3). This is to be expected if second eggs were par-

ticularly heavy relative to the first egg in conditions favorable for egg formation, as birds laying a third egg might then be expected to lay a heavy one.

EJECTED EGGS

The swifts ejected from the nest any cracked or chipped eggs. Many apparently normal eggs were also ejected, usually in bad weather, and if one egg was ejected the next of the clutch usually followed within a day or two. Whenever I returned an ejected egg to the nest it was usually discarded again. Such behavior is not understood but since ejected eggs (omitting the few chipped ones) hatch if placed in an incubator, it is presumably the adults' behavior, not the egg, which is abnormal under the circumstances. The average weight of the ejected eggs did not differ significantly from that of other eggs laid in the same period.

WEIGHT OF CLUTCHES LAID
BY THE SAME FEMALE

Swifts at Oxford raise only one brood per year, but if they eject or lose a clutch they sometimes lay a replacement, enabling comparison of successive clutches of the same individual.

TABLE 3. Correlations between egg dimensions in 1971.

Variables in correlation	Correlation coefficient[a]	
	Simple	Partial[b]
Weight: length	0.798	0.893
Weight: breadth	0.912	0.952
Length: breadth	0.535	−0.777

[a] All correlations were significant at $P < 0.01$ or better.
[b] Each partial correlation controls for the remaining variable of the trio length, breadth and weight.

TABLE 4. Difference in weight between the first two eggs of the clutch.

Interval between eggs (days)	Percentage of clutches with second egg lighter than the first egg[e]		Mean weight difference between second and first eggs[a] (grams)	
	Poor[b] weather	Good[c] weather	Poor[b] weather	Good[c] weather
2	88.9 (9)	24.3 (111)	−0.11	+0.10
3	28.6 (7)	34.6 (26)	+0.05	+0.06
4 or more[d]	33.3 (3)	40.0 (5)	+0.11	+0.10

[a] Positive when the second egg was the heavier.
[b] Data for dates in the main laying period when no new clutches were initiated.
[c] Data for all clutches not covered by [b] above.
[d] Some intervals of four or more days between eggs may have been recorded as a result of the female laying a second egg after two days but losing it from the nest before the next inspection.
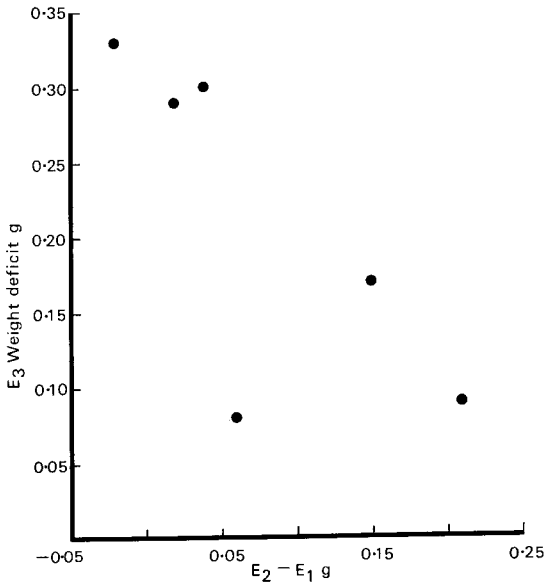[e] Figures in parentheses show the total numbers of clutches in each category.

FIGURE 3. Weight of third eggs in relation to that of the second egg of the clutch. Weight of third eggs shown as a deficit from the average of the first two eggs of the clutch, and weight of second eggs as a difference from the first egg of the clutch, in both cases to correct for phenotypic variation. See text for details.

Though there is no simple correlation between the weights of original and replacement clutches ($r = 0.277$, N.S.), when the egg weights of these clutches are expressed as deviations from the averages of all eggs laid about their times of laying, as in Figure 4, the correlation coefficient approaches significance
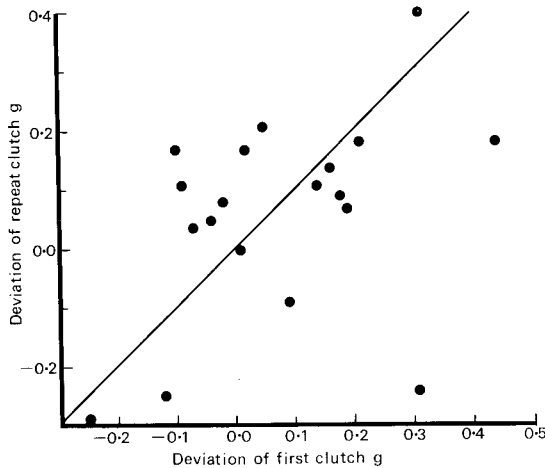

FIGURE 4. Weights of repeat clutches in relation to weights of initial clutches, each relative to the average of all clutches laid in the colony at that time. Only the weights of the first two eggs of a clutch are considered. The line indicates the position of repeat clutches equal in weight to the original after correction for phenotypic variation.
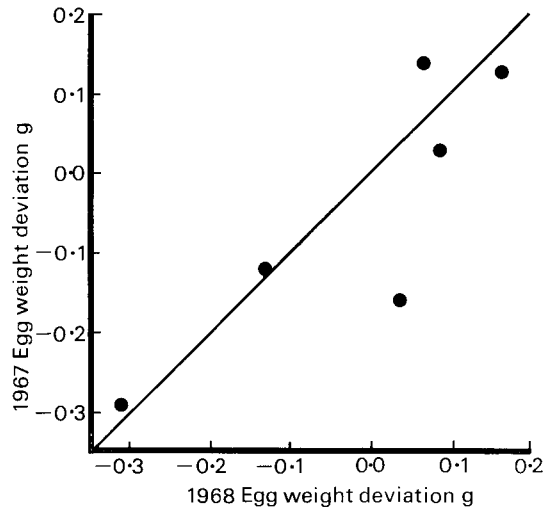

FIGURE 5. Weights of the first two eggs of six banded pairs laying in 1967 and 1968. The line indicates the positions of clutches unchanged in weight between years (see text). Egg weights were expressed as deviations from the average of all eggs laid concurrently, to correct for the (phenotypic) effects of the weather prevailing at the time.

($r = 0.388$, $P < 0.07$). The differences in absolute weight between original and replacement clutches are irrelevant here, being essentially determined by the weather conditions prevailing at laying (cf. Fig. 1).

Evidence for individual constancy of egg weight between years is presented in Figure 5. Perrins (1971) retrapped the same pairs in certain nestboxes in both 1967 and 1968, so the clutches in these boxes probably were laid by the same females. (Trapping was confined to the immediate post-fledging period to avoid desertions, so this assumption must be made.) The weights of these clutches, after correction for phenotypic variation, were highly correlated between years ($r = 0.856$, $P < 0.05$). In addition, data are available for a banded female that laid clutches in 1948, 1949 and 1950, and show relatively constant clutch weight between

TABLE 5. Weight of eggs from the same banded female in different years.

	1948	1949	1950
Date of first egg	25 May	5 June	2 June
Weight of first egg (g)	3.63	4.00	3.88
Weight of second egg (g)	3.57	4.05	4.12
Mean weight of eggs in that period (g)	3.48	3.65	3.62
Difference from mean (g)	0.12	0.38	0.38

The means were based on 16 eggs 21–27 May 1948, 12 eggs 5–7 June 1949 and 10 eggs 2–4 June 1950. The bird changed its box in 1948, probably as a result of banding but used the same box in 1949 as in 1950. Its sex was inferred from that of a former partner.
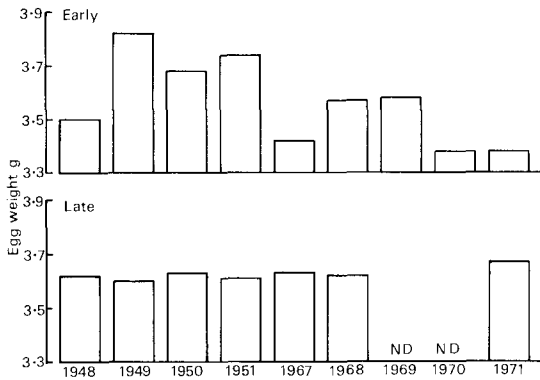
FIGURE 6. Annual variation in mean egg weight for eggs laid in May (above) and in June (below). N.D. indicates no data available, the laying season not extending significantly into June in that year.

years (Table 5); the birds' rather low relative egg weights in 1948 were associated with general reduction in the weights of all eggs laid at that time (cf. also Fig. 6 below).

Individual females laid eggs of very different weights (Figs. 4 and 5). Typical variation in egg weight in the population was about 5–6% among eggs laid at about the same time. The extreme recorded was between two clutches started within 24 h of each other, which averaged 2.98 g and 4.08 g for the first two eggs.

ANNUAL DIFFERENCES IN MEAN EGG WEIGHT

In presenting annual variations in mean egg weight (Fig. 6), the laying period has been divided for convenience into a main part essentially confined to May, and a later part in early June; these two were often separated by poor weather (Table 1). A few late clutches clearly outside the main laying season have been omitted from this analysis. In May, but not in June, the average weight differed substantially from year to year; the difference be-

tween the two periods is highly significant [$F = 53.7$, $P < 0.001$ on Lewontin's (1966) test between the two coefficients of variation]. This pattern may simply reflect annual variation in insect numbers in May and the relative stability of insect abundance in June (cf. Bryant 1975), but if so the effect is not consistently apparent when adult and egg weights are compared from year to year. Both adults and eggs were unusually heavy in 1949 (Lack and Lack 1951), and unusually light in May 1968 (Table 6; when May weather was particularly cold), but the birds were heavier in 1967 than in 1968 even though the eggs were lighter in the former year. However, I have no guarantee that the adults trapped were, in fact, British breeding birds.

Although the average clutch size decreased steadily from mid-May to early June, there was no consistent variation in the mean weight of eggs laid through this period. Nor was there significant difference in the mean weight of the first two eggs in clutches of two and three respectively. Few eggs were laid in late June and July, except in 1971 when poor weather and heavy rain in late May and June postponed laying. These late eggs varied as much as those of May. Such eggs were largely repeats after earlier losses, though some were first clutches, possibly laid by first-time breeders.

CONTENT OF EGGS

In 1967 and 1968 the ejected eggs were collected under license from the Nature Conservancy. Most of them were hard-boiled and the shell, white and yolk were separated and weighed (Table 7). The proportion of the egg contents (i.e. omitting the shell) formed by the yolk was 25%, considerably higher than the 15–20% reported for various nidicolous species by Heinroth (1922).

In the unusually bad weather of May 1967

TABLE 6. Body weights of adult European Swifts.

Site :	Rye Meads, Hertfordshire[1]		Wintersett Reservoir, Yorkshire[2]
Month :	May	June	May
Year	Mean ± SD (N)[3]	Mean ± SD (N)	Mean ± SD (N)
1962	39.88 ± 2.54 (293)	44.8 ± 2.37 (71)	—
1963	43.27 ± 1.35 (888)	43.3 (6)	—
1964	45.3 (7)	39.5 (10)	46.40 (5)
1965	36.26 ± 1.81 (413)	39.6 (6)	41.22 ± 2.32 (229)
1966	42.02 ± 0.57 (34)	—	43.56 ± 0.80 (35)
1967	41.25 ± 0.96 (751)	39.7 (48)	40.20 ± 1.09 (40)
1968	40.08 ± 1.37 (161)	37.5 (5)	42.12 ± 1.47 (168)

[1] Data from Rye Meads Ringing Group, per A. J. Prater.
[2] Data from A. Archer and C. Bower.
[3] Standard deviations calculated from daily means but means and sample sizes reflect the total number of individuals measured. Standard deviations omitted to indicate only a single day's data available for that year.

TABLE 7. Composition of swift eggs.

Year	Number	Mean weight of			Percentage of egg due to	
		Egg	Shell	Yolk	Shell	Yolk
1967	10	3.52	0.306	0.761	8.7	21.6
1968	15	3.48	0.351	0.784	10.1	22.5
Pooled	25	3.50	0.333	0.775	9.5	22.2

In each of the two years, the fresh weights of the eggs concerned ranged between 3.1 and 3.7 g and were typical of their year and time of laying.

the eggs appeared to have abnormally soft shells and several were broken, both by the birds and by our handling. Seven of these eggs analyzed by the Nature Conservancy did not have obvious traces of toxic chemicals (N. Moore, pers. comm.), such as have been associated with egg shell thinning in certain other species (Ratcliffe 1970). The soft shells may have been the result of undernourishment; the shells were slightly lighter in 1967 than in 1968 (Table 7).

THE SURVIVAL VALUE OF EGG WEIGHT

The data presented above (Table 4) suggest that there is some selective value in maintaining egg size even in time of food scarcity. Clutches of two or three in which all eggs hatched successfully averaged slightly heavier than clutches in which one or more eggs failed to hatch (Fig. 7). However, the 14 eggs which failed other than as a result of ejection were not themselves much lighter than a sample of 14 eggs matched to them for date, clutch size and laying order but which hatched successfully (hatching mean ± SD, 3.58 ± 0.30 g; failing: 3.45 ± 0.26 g; Student's t = 1.22, N.S.). Hence egg weight only weakly affects hatchability.

Figure 8 shows the relationship between egg weights and the weights of the chicks on the day they hatched, i.e. at an average age of 12 h, and therefore including the weight of early feeding in some cases. Clearly, heavier eggs produced heavier chicks (r = 0.368, P < 0.001), thus indicating a further possible advantage in not allowing the egg weight to fall in poor weather (cf. Table 4). Separate analyses for first, second and third eggs gave correlations between egg and chick weight of 0.445 (P < 0.01), 0.217 (N.S.) and 0.468 (P < 0.05), respectively, showing that it was the lighter first and third eggs which most influenced the chick weight.

The higher weights of chicks hatched from large eggs could be due to (a) their large yolk reserves at hatching, or (b) their large body size. To distinguish between these hypotheses I measured chick wing length as a measure of body size. Chick wing lengths were well correlated with body weights (r = 0.793, P < 0.001) and with egg weights (r = 0.353, P < 0.001). If we control for the effects of chick size by partial correlation of chick weight with egg weight (with wing length controlled) the correlation shown in Figure 8 drops to 0.108
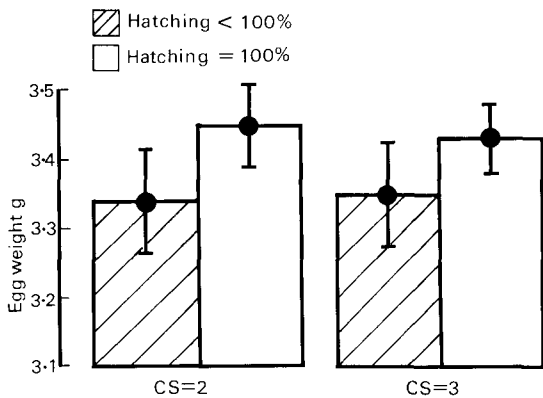

FIGURE 7. Egg weight and hatching success in clutches of different size. Vertical lines indicate ± 1 standard error. No corrections have been made for phenotypic variations.
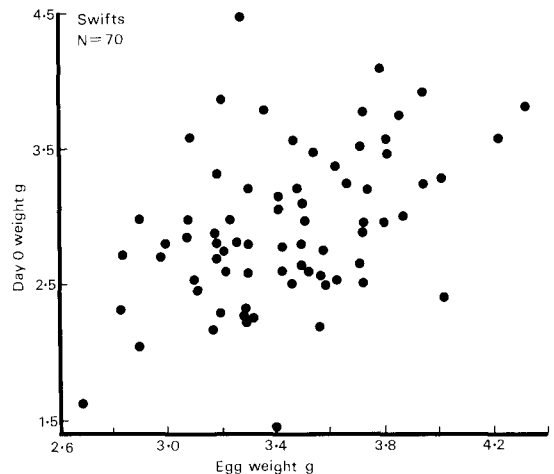

FIGURE 8. Hatching-day weight in relation to egg weight in European Swifts.

TABLE 8. Chick survival in relation to egg weight and hatching size.

	Chicks fledging Mean ± SD (N)	Chicks failing* Mean ± SD (N)	t	Significance
Egg weight (g)	3.49 ± 0.33 (41)	3.36 ± 0.42 (10)	1.11	0.30
Hatching-day weight (g)	2.94 ± 0.49 (40)	2.34 ± 0.70 (10)	3.15	0.01
Hatching-day wing (mm)	8.71 ± 0.44 (40)	8.22 ± 0.54 (9)	2.88	0.01

* Including those which disappeared prematurely from the nest.

(N.S.). Conversely, controlling body weight reduces the correlation between wing length and egg weight from 0.353 to 0.155 (N.S.). Hence the results shown in Figure 8 must be attributed to large eggs yielding large chicks rather than to chicks with large yolk reserves.

Some chicks whose egg and day 0 weights were known died in the nest. They hatched from eggs slightly lighter than eggs which hatched survivors (Table 8), though this was not statistically significant. More striking, however, was the difference in day 0 weights, for chicks which died later hatched at significantly lighter weights than survivors ($t = 3.15$, $P < 0.01$). This difference was probably the outcome of sibling competition during the nestling phase, for except in one instance the chicks who died were the last of their broods to hatch, and such chicks suffer in competition for limited food. Reflecting the general correlation between egg weights and chick size, the body size of newly hatched chicks paralleled the variation in egg weight with laying order (and hence with hatching order) (Fig. 9). Hence even if the third egg hatched synchronously with the first two, its chick wo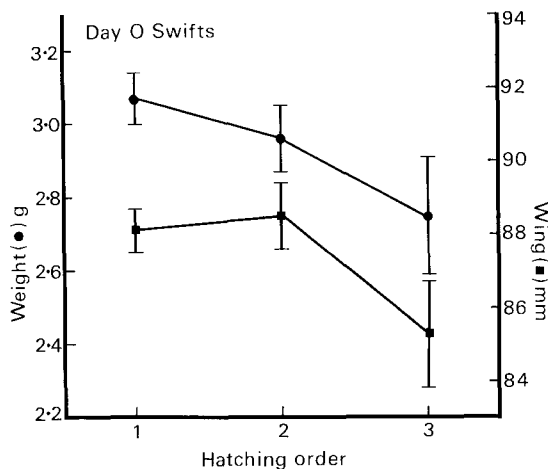uld be at a size disadvantage with respect to the others. In practice this size difference is enhanced (as a competitive disadvantage) by the delay of one to three days already noted of this egg.

If this poor survival of late-hatched chicks from light eggs is indeed due to food competition between nestlings, egg weight should correlate with growth rate. In swifts and other aerial insectivores, daily growth rates vary erratically, the nestling period is prolonged under conditions of poor feeding, and the growth curve (weight versus age) is poorly defined (Lack and Lack 1951, O'Connor 1978a). Hence only the length of the nestling period can serve as a measure of growth rate in these species, despite the availability of rate measures for specified growth forms (Ricklefs 1968). Nestling period proved unrelated to egg weight for the swift (Fig. 10a), despite

FIGURE 9. Hatching-day wing length and weight in relation to hatching order. Vertical lines indicate ± 1 standard error.
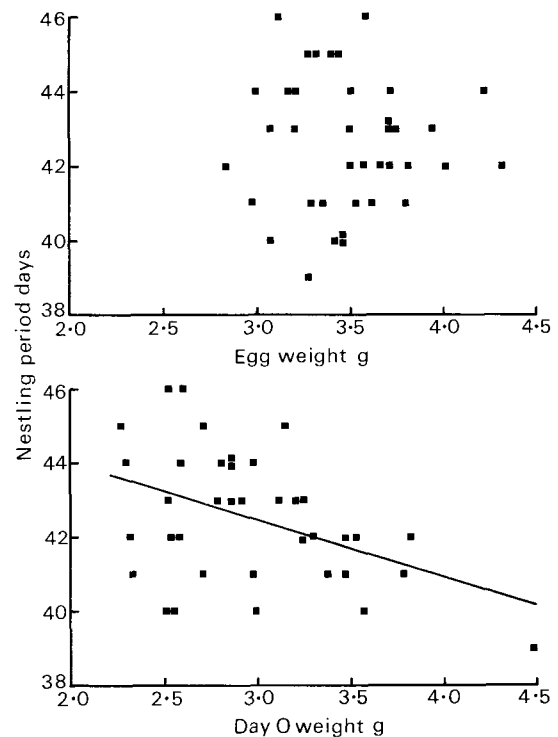
FIGURE 10. Nestling period in relation to egg weight (above) and hatching-day weight (below).

the hypothesis above, but was more strongly dependent on the hatching-day weight (Fig. 10b): heavy chicks had significantly shorter nestling periods than had initially light chicks ($r = -0.428$, $P < 0.01$). This result was independent of egg order. Partial correlation showed that this effect was also independent of egg size ($r_p = -0.460$, $P < 0.01$). Conversely, controlling for the effect of hatching-day weight had no effect on the relationship between nestling period and egg size ($r_p = 0.187$, N.S.). These results thus show that egg weight influenced chick growth and development time only through its influence on hatching-day weights and not through any independent effect of its own.

DISCUSSION

THE SIGNIFICANCE OF EGG SIZE

Variations among eggs in the swift appeared to have two effects, one relating to the development of the egg itself, the other affecting the development of the chick during the post-hatching phase. The analysis of the size of hatching versus non-hatching eggs (Fig. 7) indicated that light eggs were less likely to be successful during incubation. Similar effects have been found in the Little Bunting (*Emberiza pusilla*; Koivunen et al. 1975), Wood Pigeon (*Columba palumbus*; Murton et al. 1974), and House Sparrow (*Passer domesticus*; Dawson 1972), and probably also in Ring-billed Gulls (*Larus delawarensis*; Ryder 1975). Reduced hatching success may be due to such eggs being formed at times of poor food availability and thus being of poor "quality." Herring Gull (*Larus argentatus*; Parsons 1975a) and House Martin (*Delichon urbica*; Bryant 1975) eggs laid during unfavorable weather had lower hatching success than normal, and as already indicated, eggs of swifts laid during such weather were somewhat lighter unless egg formation was prolonged (Table 4). Alternatively, small eggs might cool more rapidly during parental absences, with adverse effects on the embryo. Such absences are necessary due to the fluctuations in aerial insect abundance and eggs have evolved a remarkable resistance to chilling death (Lack 1956), so the small difference in cooling rate between large and small eggs is not likely to affect hatchability.

The principal influence of egg size on swift development is in its effect on hatching size: heavy eggs produce more fledglings, largely because heavy eggs give rise to heavy hatchlings which survive better (Table 8). Greater survival is due to chicks being structurally larger and not merely possessing larger yolk reserves. Furthermore, nearly all chicks that died were third-hatched chicks competing with siblings who were larger than they were. Since nestling periods were shorter for larger eggs at all three laying orders these factors are to some extent independent. That is, growth is faster when hatching from larger eggs, irrespective of effects of competition. Parsons (1975b) has shown that both egg weight and hatching sequence affect the survival of Herring Gull chicks, and egg weight and hatching-day size have also proved important in the development and survival of passerine nestlings (Schifferli 1973, O'Connor 1975).

The data collected here do not explain why large eggs yield large hatchlings. The effect could be due to embryos in large eggs growing faster, so that at hatching they are further along the growth curve common to both small-egg and large-egg chicks. Growth rates in domestic fowl (*Gallus gallus*) may be retarded by lack of space within the egg (Wiley 1950). On the other hand, analysis of newly hatched gull and Japanese Quail (*Coturnix coturnix*) chicks has shown that large-egg chicks are not simply larger versions of small-egg chicks; they differ selectively in the size of certain organs or constituents (Parsons 1970, 1976, Ricklefs et al. 1978, O'Connor and Owen, unpubl. data).

Swift hatchlings can survive unusually long periods without food; cases of survival for over 48 h are known (Lack 1956). Swift eggs have atypically high levels of egg yolk (Table 7; Heinroth 1922, Collins and LeCroy 1972) and newly-hatched swifts have more total lipid than comparable nestlings of other species (O'Connor, unpubl. data). As similar trends are present in the ecologically similar House Martin (O'Connor 1978a), the high yolk content of the egg may be an adaptation that enables a chick to survive if it hatches during a spell of bad weather. In several species yolk content and/or lipid content increases to some extent with egg size (Parsons 1970, Ricklefs 1977, Ricklefs et al. 1978) but I did not investigate this in swifts. However, it is possible that the increase in hatchling size with egg size may be adaptive for extended survival beyond any correlation with lipid content because, among adult passerines, the ability to survive starvation on internal reserves is a power function of body size (Calder 1974). When applied to neonates, Calder's equation predicts an increase in survival time of about 54% for a 33% increase in egg weight from 3.0 g to 4.0 g. The validity of this extension of the equation is not known, but Ricklefs et al.

(1978) have made a similar suggestion in relation to the size dependence of water reserves in newly-hatched Laughing Gulls (*Larus atricilla*).

EGG FORMATION

That female swifts have difficulty in collecting food for egg formation is indicated by seven points: 1) the ratio of egg weight to adult weight is unusually low for a bird of this size, 2) eggs are laid at two-day intervals, whereas most birds of comparable size lay daily, 3) dates of laying are later in years of cool or wet weather (Fig. 1), 4) initiation of clutches is suspended during unfavorable weather (Table 1), 5) second eggs laid at two-day intervals are lighter in such conditions, 6) clutches of three eggs are more frequent in favorable weather, and 7) the third eggs in clutches with heavy second eggs are heavier. In addition, there is greater annual variation in mean May weights compared to June weights, since food supplies are more stable in June (Bryant 1975). I assume that weather conditions influence the abundance of insects (Williams 1951, Bryant 1975), and that birds responding directly to this—an assumption which has only rarely been satisfactorily demonstrated (e.g. by Bryant 1975 for the House Martin). Since Bryant's study took place less than 50 mi from Oxford and overlapped my work in time, it seems reasonable to assume that temperature and egg-laying in swifts are correlated with changes in abundance of flying insects. The cessation of clutch initiation in spells of adverse weather also supports this interpretation.

Although no new clutches were begun during unfavorable weather, second eggs were nevertheless added to first eggs already laid. This suggests that it is energetically feasible to complete an egg already partly formed, extending the process over an extra day if necessary (Table 4). A similar phenomenon occurs in titmice, where some birds lay daily while others are postponing clutch initiation (C. M. Perrins, pers. comm.); in domestic hens egg formation is much more costly (at 7–24% of food intake) than the laying of eggs already begun (2–10% of intake; Bordas and Merat 1976). Since third eggs were underweight if the second egg was light (Fig. 3), difficulty in obtaining food for egg initiation also accounts for the reduction in frequency of three-egg clutches in May in years of poor weather.

These data suggest that female swifts have difficulty in gathering enough nourishment for egg formation. However the difficulty may be in acquiring a specific nutrient rather than energy because the species composition of the diet of swifts changes significantly in bad weather (Lack and Owen 1955). Unusually thin shells of eggs laid during poor weather suggest a lack of calcium (cf. Jones 1974). In domestic hens, the balance of amino acids rather than their absolute levels determines egg size response of birds fed with different amounts of dietary proteins or with diets supplemented in amino acid content (March and Biely 1963). Hence diet quality, not quantity, may underlie the observations reported here for the swift.

DIFFERENCES AMONG FEMALES

Individual pairs differed in their rates of feeding young under given weather conditions (Lack and Lack 1951). This would explain the constancy of laying date (Fig. 2) and egg size (Fig. 3 and 4, Table 5). Similar constancies have been described for other species (Kluijver 1951, Jones 1973, Bryant 1975), and, following Perrins (1970), can be interpreted in terms of individual variation in energy requirements for egg formation. Owing to individual differences in cost of maintenance or egg formation, some individuals can breed sooner than others if the food supply increases seasonally. Data from intraspecific (Jones 1973) and interspecific (Dunn 1976) studies support this model, as do analyses of thermal variations between nestboxes in two passerine species (O'Connor 1978c). This would also account for variation in laying dates as weather conditions, low temperatures and wet weather would effectively delay the date when the seasonal increase in flying insects exceeds the threshold formed by maintenance plus egg costs. These factors act by both raising female thermoregulatory costs and depressing the rate of increase in insect abundance.

Bryant (1975) suggested an alternative model for the timing of breeding by birds which feed on aerial insects. He argued that such species are unable to breed during the earliest periods of energy surplus because of a risk of food failure during clutch formation, and must therefore postpone breeding until food levels have stabilized. Recently he has found a pattern of individual date constancy (relative to the population mean) overlying this (Bryant, pers. comm.). The data on annual variation in egg weight presented above (Fig. 6) may reflect these same ideas, for the mean weight of eggs laid in May was particularly light in, for instance, 1967 and 1971, years with poor feeding conditions in

May, whereas the June weights were average in these years.

THE LAYING PATTERN OF THE SWIFT

When a female swift has limited food for egg formation, she lays fewer eggs of some standard size rather than a normal clutch of small size. This is shown in four ways. In poor weather, second eggs laid after two days were lighter than average but most eggs laid in such conditions were laid after three, not two, days and were then up to normal weight (Table 4). Second, third eggs were heavy only if the second egg was close to normal weight, otherwise the third egg was light (Fig. 3). Third, the mean weight of the first two eggs was independent of clutch size. Finally, although clutch size declined seasonally there was no coincident variation in egg weight.

Clutch size appears to increase at the expense of egg weight in a few species, e.g., the Great Tit (*Parus major*; Jones 1973) and Song Sparrow (*Melospiza melodia*; Nice 1937), but most other altricial species studied are similar to the swift (Kendeigh et al. 1956, Snow 1960, Hussell 1972). Parsons (1975a), Coulson and Horobin (1976), and Jones and Ward (1976) all found that clutch size rather than egg size is reduced at times of food shortage. In the Storm Petrel (*Hydrobates pelagicus*; Scott 1970), Wood Pigeon (Murton et al. 1974), and Herring Gull (Parsons 1970), small egg size is selectively disadvantageous because nearly all eggs below a critical size fail to yield fledged young. These results match the reduced hatching success of small eggs (Fig. 10) and the poorer fledging rate of small-egg chicks (Table 8) documented here for the swift.

Although egg weight was independent of clutch size, the third egg in a clutch of three generally weighed less than the first or second egg. The final egg also is lighter than preceding eggs in all gulls and terns examined (Vermeer 1969, Nisbet and Cohen 1975, Ricklefs et al. 1978) and in the House Sparrow (Dawson 1972) but is equal or heavier than preceding eggs in geese (Kear 1965), Shag (*Phalacrocorax aristotelis*; Coulson et al. 1969), House Wren (*Troglodytes aedon*; Kendeigh et al. 1956), Song Thrush (*Turdus philomelos*; Pikula 1971), Wood Pigeon (Murton et al. 1974) and Common Grackle (*Quiscalus quiscula*; Howe 1976). A lighter final egg is thus correlated with the use of a method for "brood reduction" (Lack 1954, O'Connor 1978a). Reducing the size of the final egg

can be seen as predisposing the resulting chick to an early death should food be scarce at hatching, thus concentrating the available food on young more likely to survive. Evidence for this correlation is provided by Lack and Lack (1951), Parsons (1975b) and Nisbet and Cohen (1975) and Dawson (1972). The converse argument, that a large final egg is a positive adaptation to block "accidental" brood reduction, has been advanced by Murton et al. (1974) for the Wood Pigeon, by Nolan (1978, pers. comm.) for the Prairie Warbler (*Dendroica discolor*) and the Indigo Bunting (*Passerina cyanea*), and by Howe (1976) for the Common Grackle. I suggest, therefore, that in swifts both the early incubation of the a- and b-eggs and the small size of the c-egg represent adaptive components within the scheme of brood reduction originally described by Lack (1954) and subsequently given a theoretical basis by O'Connor (1978a, 1978b).

In summary, the breeding habits of the European Swift are geared to the exploitation of a nestling food supply that is quantitatively unpredictable. To exploit that food supply efficiently, a female must distribute the resources available for egg formation optimally. A two-egg clutch is nearly always more productive than a one-egg clutch (Lack 1956) so it pays to lay a second egg even if three or more days are needed to form it. A third egg will enhance reproductive output only if conditions for nestlings are rather good (Lack 1956), hence it can be laid only as a gamble and should be laid only if the stake is reasonable in relation to the probability of success. The data here suggest that success requires a minimum egg size, with additional commitment of resources being made only if the other eggs are up to normal weight. The breeding patterns of the swift thus depend on conditions not only during the nestling period but also during egg laying.

SUMMARY

In southeast England, the timing of egg laying in the European Swift is related to ambient temperature, rain and strong winds. Individual females lay at dates constant with respect to the population mean for the year and tend to lay eggs of constant size for the weather conditions prevailing at the time. Eggs are normally laid at two-day intervals but in adverse weather egg formation is prolonged to three or even four days and clutch size is reduced; in such conditions, clutch initiation is postponed by females who are otherwise about to lay.

Egg weights are small relative to the size of the bird but contain more yolk than in comparable nidicolous passerines. Egg weights vary annually except for eggs laid late in the season. Clutches in which at least one egg fails to hatch tend to be lighter than those in which all eggs hatch but successful and unsuccessful eggs differ little in weight. Heavy eggs are large in linear dimensions and produce large chicks which more frequently survive to fledging. The egg-chick size correlations hold for eggs laid at each position in the clutch but the greater mortality of small eggs is due mainly to third-hatched chicks who fail in food competition with older, larger siblings. Chicks from large eggs fledge quicker than those from small eggs but this effect is due almost entirely to the larger hatching size of these chicks and not to egg size itself.

These results suggest that female swifts normally have difficulty in accumulating enough energy reserve to form eggs, thus sensitizing egg formation to weather-influenced fluctuations in insect abundance. Within these constraints the relative sizes of the eggs within the clutch are adjusted to optimize sibling competition and brood reduction as an adaptation to unpredictable food supplies for the nestlings.

ACKNOWLEDGMENTS

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RECENT PUBLICATIONS

Analysis of Ecological Systems.—Edited by David J. Horn, Rodger D. Mitchell, and Gordon R. Stairs. 1979. Ohio State University Press, Columbus. 312 p. $27.50. This is not a textbook, as its title suggests, but a collection of nine papers that grew out of a 1977 symposium. None of the papers is explicitly about birds, yet most of them will interest theoretical avian ecologists. Their diversity of approaches, theories, and methods reflects the flowering of ecology in recent decades. The symposium was intended to stimulate interaction among the speakers but none of this—if it happened—is conveyed here. Each of the papers stands on its own, for the editors have provided no commentary or overview to tie them together.

Proceedings of the workshop [on] management of southern forests for nongame birds, January 24–26, 1978; Atlanta, Georgia.—Edited by Richard M. DeGraaf. 1978. Forest Service General Technical Report SE-14, U.S. Dept. of Agriculture, Southeastern Forest Experiment Station, Asheville, North Carolina. 176 p. Paper cover. This workshop is significant because it addressed forest management from a new viewpoint, that of nongame wildlife. The 14 papers given at the meeting deal with avian communities in forests of the southern and southeastern U.S.: their structure, effects of forestry practices on the birds, and management of certain kinds of habitat for birds. Discussions that presumably followed the papers are not reported. The collection will be of interest to avian community ecologists, wildlife biologists, and forest managers.

Management and Biology of Pacific Flyway Geese.—Edited by Robert L. Jarvis and James C. Bartonek. 1979. OSU Book Stores, Inc., Corvallis, Oregon 97330. 346 p. Paper cover. $5.50. The five species (and how many subspecies?) of geese which occur near the coast of western North America were the subject of a symposium sponsored by the Northwest Section of The Wildlife Society. This book contains the 24 papers that were presented on the taxonomy, breeding biology, migration, wintering habits, status, and management of the birds. It will be valuable to goose biologists for its wealth of current data.