

LAYING DATES, CLUTCH SIZE AND EGG WEIGHT OF CAPTIVE MALLARDS

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Factors affecting clutch or litter size have interested ecologists because they relate directly to reproductive rates and help to explain reproductive habits. Clutch size can be measured directly with little error, and the possible functional relationships with environmental or social variables can be examined. This has led to several major reviews on the possible determinants of clutch size in birds (Cody 1971, Klomp 1970, von Haartman 1971). Waterfowl have posed particular problems because the chicks are precocial and do not require parental feeding, a factor that correlates with clutch size in many altricial species (Lack 1968a). Most hypotheses concerning the evolution of clutch size in waterfowl have implied that food supply for the female prior to laying and/or for the young is both a proximate and an ultimate determinant (Bengston 1971, Johnsgard 1973, Lack 1967, 1968a, 1968b, Ryder 1970).

We report the results of an experiment in which single pairs of Mallards (*Anas platyrhynchos*) were held in identical breeding compartments and were thereby subjected to the same environmental cues for breeding. We determined laying dates, clutch sizes and egg weights for the same pairs of birds in 1973, 1974 and 1975. The responses of the birds in terms of the three parameters of nesting were considered to closely reflect interactions between genotype and environment. They should provide bases for evaluating proximate environmental effects in wild populations.

METHODS

Standard procedures for maintenance of captive birds were used throughout (Ward and Batt 1973). During the first week of April 1973, 1974 and 1975, up to 80 randomly assigned pairs of Mallards were randomly placed in individual breeding pens at the Delta Waterfowl Research Station in Manitoba, Canada. The same members of a pair were kept together for the three years. The pens were 7 m²; one-half swimming water and one-half dry concrete floor. Each contained a nest box and a feed dish. The birds were kept flightless by clipping or pinioning. Compartments were separated by 0.7-m walls that prevented physical and visual contact between pairs but allowed them to hear each other. Food was supplied freely.

Birds used in the study were all reared from eggs taken from wild nests prior to 1973. In 1973, one-

half were yearlings while the remainder were a mixture of two- to four-year-olds. An earlier analysis failed to detect significant age-related effects on the three nesting parameters under discussion here (Batt and Prince 1978), so all the birds are treated as "equals" for our analyses.

During daily visits to each compartment, we recorded the occurrence of new eggs and egg weight. New eggs were numbered, returned to the nest and left until the the female had completed the clutch and incubated it for five days. Nests completed and incubated in a normal manner are designated as "good" nests. Deserted nests were also left until laying had not occurred for five consecutive days. In each case the eggs were then collected, all the nesting material was replaced and the females allowed to renest. This routine continued until all females ceased nesting and began their pre-basic molt.

Data analyses followed Nie et al. (1975), Sokal and Rohlf (1969), and Becker (1967). For statistical significance, a 0.05 probability level was used unless otherwise stated.

We estimated repeatability for the three reproductive parameters to evaluate the role of the individual genotypic breeding response. Repeatability is the ratio of variance among individuals to the total phenotypic variance (among and within individuals) and can take values from 0 to 1. Thus, it is not a measure of product-moment correlation but is analogous to the coefficient of determination (Kempthorne 1969:230).

RESULTS AND DISCUSSION

LAYING DATES

The earliest and latest dates of starting first nests were separated by 58, 50 and 43 days in 1973, 1974 and 1975, respectively (Fig. 1). The birds were held in the same breeding pen for the three years, diet was not changed, and the same birds were mated together each year. Therefore, annual variation was assumed to be primarily the result of climatic differences between years and the experience of the birds themselves. A one-way analysis of variance indicated significant differences between females for the three years. The repeatability of an individual's nesting date was determined to be 0.57 (SE = 0.07, N of females = 60). This suggests that individual females are consistent and that within the population there is a wide range of individual phenotypic responses. In the wild, one would expect to find some pairs with a full commitment to nesting while others would be paired but show no breeding behavior. This may explain why some investigators have had dif-

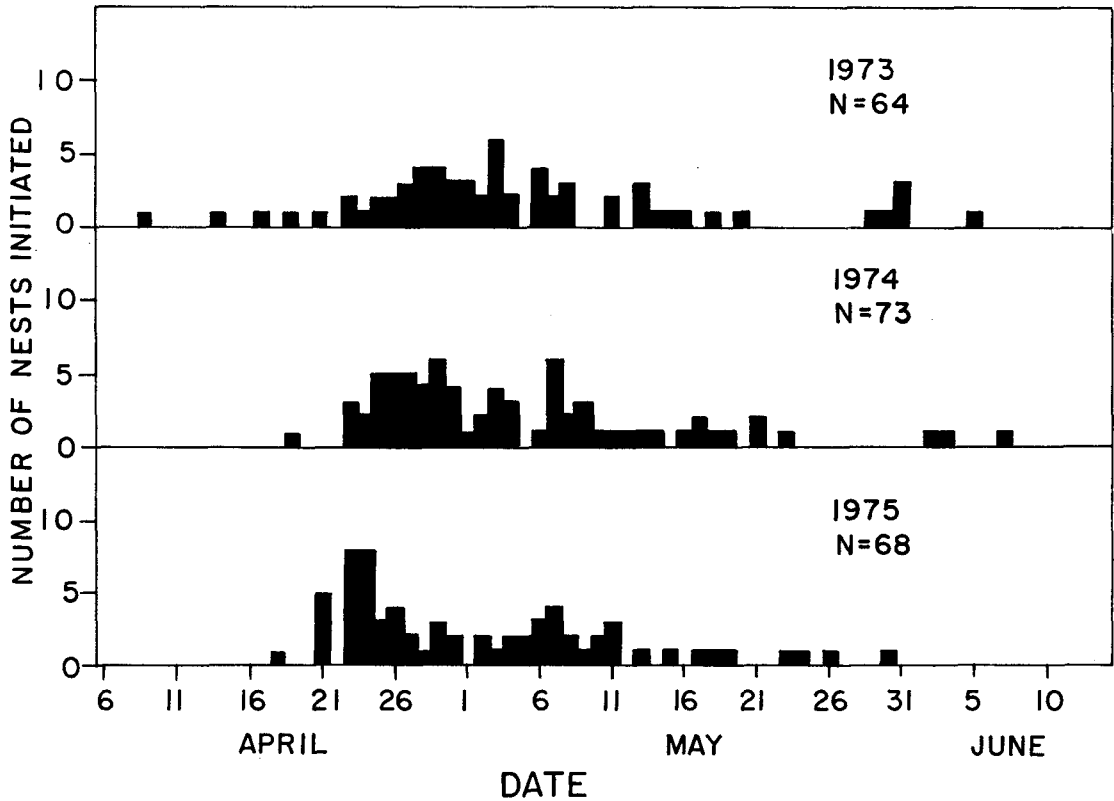


FIGURE 1. Distribution of the initiation of first nests by captive Mallards in separate breeding pens.

difficulty in separating the breeding pairs from pairs that were: (1) transient and on their way to other breeding areas; (2) resident pairs nesting for the first time on different schedules; or (3) resident pairs reneesting after losing a first nest (Dzubin 1969).

Immelmann (1971:373) discussed intraspecific variation in laying dates and accounted for most of it as being adjustments to local ecological conditions or age-related factors. Our results better define intraspecific variation and are consistent with the idea that variability in temperate environments causes disruptive selection and results in a wide range of genotypes in the population. The wide range of responses might also arise from population pressures that accrue some benefit to those birds who delay breeding until the density of nesting pairs is diminished.

Individual consistency of laying dates has been found in Great Tits (*Parus major*, Kluijver 1951), Manx Shearwaters (*Puffinus puffinus*, Harris 1966), Short-tailed Shearwaters (*P. tenuirostris*, Serventy 1963), Adélie Penguins (*Pygoscelis adeliae*, Spurr 1975), Yellow-eyed Penguins (*Megadyptes antipodes*, Richdale 1957), Velvet Scoters (*Melanitta fusca*, Koskimies 1957a), and Common Eiders (*Somateria mollissima*, Spurr and Milne

1976). The last authors hypothesized that individual eider females had genetically-determined minimum laying dates. These birds are affected either directly or indirectly through a mediating factor such as feeding ability. This idea is consistent with that of Perrins (1970) who suggested that the differential ability to find food results in the observed individual consistency. Our results suggest that food, in a proximate sense, may not be the only explanation and that this breeding response may simply be a reflection of individual genotype-environment interactions. In the environment where this experiment took place, the genetic control appears to be more "direct." In the wild, other factors must certainly interact with a bird to modify the basic nature of the response. Food availability, as an ultimate factor, may have caused (at least in part) the type of breeding season response demonstrated by our data.

CLUTCH SIZE

Clutch size data from all good first nests and all good reneests for the three years were submitted to analysis of variance. We found significant decline in clutch size between first nests and subsequent reneests. Clutch size was

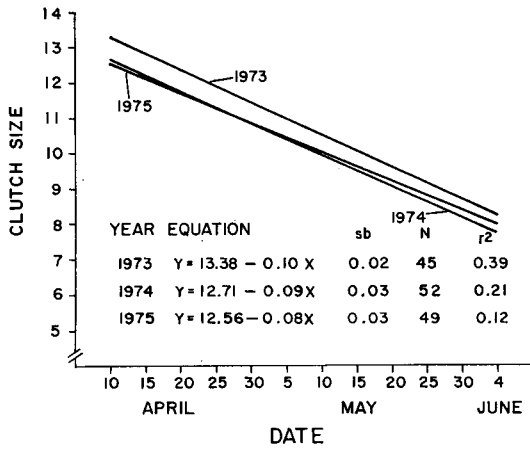


FIGURE 2. Relationship of clutch size to laying date for first nests by year. All slopes are significantly different from zero ($P < 0.01$; Day 1 = 1 April).

10.4 ± SE of 0.2 (N = 151), 9.5 ± 0.2 (N = 116), 8.4 ± 0.3 (N = 59), and 8.2 ± 0.8 (N = 13) from the first through the fourth nest, respectively.

We performed regression analyses on first, second and third nests for each year to determine if clutch size declined within an individual sequence. Data for first nests in all

three years showed a significant mean decline of approximately 0.1 egg per day as the season progressed (Fig. 2). Covariance analysis indicated no significant differences between the means or slopes of the lines. For second nests, the 1974 data showed a corresponding significant downward linear trend, the regression equation being $Y = 15.84 - 0.10X$ (N = 54, $r^2 = 0.20$, $P < 0.01$, Day 1 = 1 April). Covariance analyses showed no differences among the heights for the three years nor among the slopes. The 1973 and 1975 data, however, did not yield significant slopes ($F = 2.76$, N = 32; and $F = 0.05$, N = 37, respectively).

For third nests, the 1973 data showed a significant decline ($Y = 14.42 - 0.07X$, N = 13, $r^2 = 0.36$). Covariance analyses also showed no difference among the means or slopes for the three years but the 1974 and 1975 slopes were not significant ($F = 1.30$, N = 31; and $F = 0.04$, N = 20, respectively).

To summarize the relationship of clutch size and laying date, we pooled data from all good nests for the three years for regression analysis. The best fit of regression lines is a curvilinear relationship between the date of first laying and clutch size (Fig. 3). The rate of

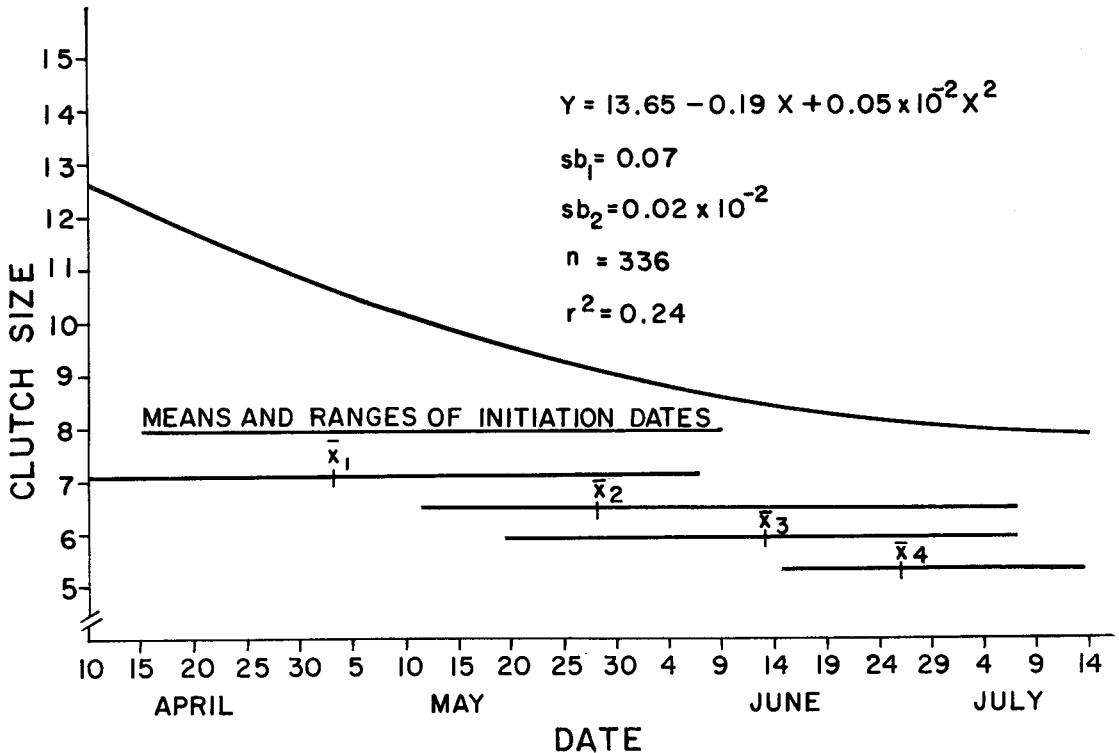


FIGURE 3. Relationship of clutch size and initiation dates for all good nests for the three years data combined. Means and ranges for each clutch initiation are shown. (\bar{x}_1 = mean date for all first clutches, etc.; Day 1 = 1 April.)

decline in the number of eggs per clutch decreases in the latter part of the nesting season. This decrease may indicate that clutches have a minimum size below which it is not advantageous for Mallards to undertake the risks and expense of nesting. The number of young produced from late, minimum-sized clutches may only balance the advantage accrued by a female if she does not re-nest but instead waits until the next year.

The seasonal decline of waterfowl clutch sizes is well documented (see reviews by Dzubin and Gollop 1972:125, Klomp 1970, Johnsgard 1973). Numerous cause and effect relationships have been inferred, but, apparently, little consideration has been given to the genetic aspects of the decline, or to clutch size variation within an individual nest sequence.

One-way analysis of variance for the three years indicated a significant difference between individual females in clutch size. Repeatability for this trait (using only good first nests) was calculated to be 0.54 ± 0.07 , (N of females = 30). Thus, laying date and clutch size are relatively consistent within individual females. Koskimies (1957a) showed that in Velvet Scoters, which do not re-nest, clutch sizes were smaller in later nesting females than in those nesting earlier. He suggested that clutch size was probably genetically linked to laying date. His data did not support the hypothesis that only laying date was genetically determined while clutch size was phenotypically dependent on laying date. We tested this with our data by comparing clutch size from the earliest and latest nesting dates of individual females. A paired t -test indicated significant differences with later clutches being smaller than earlier clutches ($t = 2.30$, $N = 52$). Therefore, we cannot fully accept Koskimies' hypothesis as applying to the Mallard. There does seem to be a phenotypic response of producing larger clutches when laying occurs earlier. This suggests genetic control of both traits, each of which responds phenotypically to year to year variations in the nesting environment.

The results of the analyses of clutch size are consistent with the bulk of data obtained in the field by other investigators (see review by Klomp 1970). However, because of the equal exposure to environmental variables by all pairs in this experiment and the unlimited food supply, most cause and effect relationships reviewed by Johnsgard (1973) are not acceptable explanations, that is: (1) later smaller clutches are produced by younger birds; (2) food supply is limiting later in the

season; or (3) population density affects clutch size. Wagner's (1960) suggestion that the decline may result from exhaustion of the female's body stores does not explain the decline within first nests. We are left with a conclusion that there is some ultimate reason (perhaps average availability of food for the young and the female) why Mallard clutch size declines seasonally. Prior analyses have considered ultimate factors primarily as they caused differences among species (e.g., Lack 1967, 1968b, Johnsgard 1973).

Dane (1966) suggested a mechanism by which a bird may respond to changes in photoperiod and temperature. He found a relatively constant clutch size during the first half of the breeding season for 155 Blue-winged Teal (*Anas discors*) nests, and Low (1945:48) recorded the same for 122 Red-head (*Aythya americana*) nests. These examples indicate different adaptive habits among the three species.

EGG WEIGHT

In an earlier paper (Batt and Prince 1978), we showed that mean egg weight appears to be under effective genetic control and independent of hen weight or age. The repeatability calculated for this trait is 0.62 (SE = 0.08, N of hens = 60).

Mean egg weight data by clutch number for individual birds were analyzed using a t -test for paired comparisons. The results indicate that egg weight increased significantly in second and third nests but that the fourth nest was not different from the first. Data for the three years were next pooled and analyzed for variance. Mean egg weights from second nests (51.5 ± 0.3 , $N = 118$) were significantly heavier than those from first nests (51.0 ± 0.3 , $N = 147$). Eggs from third nests (52.9 ± 0.4 , $N = 61$) were significantly heavier than all others. Those from fourth nests were significantly lighter (50.1 ± 1.0 , $N = 13$) than those from second and third nests, but not different from the first nest.

We compared mean egg weight by clutch size for individual sequences to test the hypothesis that within a given sequence, later (thus smaller) clutches would have larger eggs (Fig. 4). The analysis did not support the hypothesis. Significant regressions were calculated, but with positive slopes, indicating that larger clutches also have larger eggs within each clutch sequence. In agreement with the earlier finding, covariance analysis verified the relative differences in egg weight between clutches but there were no significant differences in the slopes of the lines. Thus,

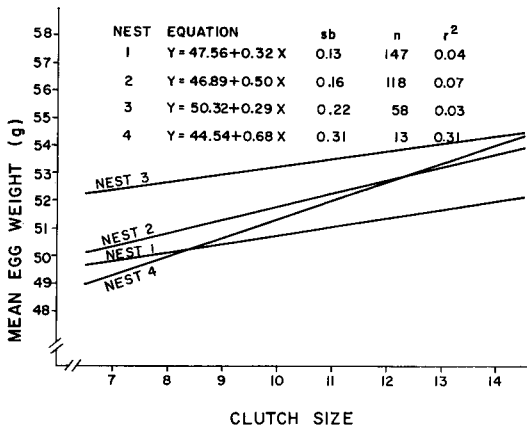


FIGURE 4. The relationship of mean egg weight and clutch size for first nests and all renesting attempts. Data for the three years are combined. All slopes are significant ($P < 0.02$).

equal-sized clutches have larger eggs when compared between nesting attempts. The biological meaning of this relationship is not clear but Kendeigh et al. (1956) also recorded heavier eggs in larger clutches of the House Wren (*Troglodytes aedon*). Koskimies (1957b) found no significant relationship between clutch size and egg size in the Velvet Scoter but the trends in his data were negative rather than positive.

The increase in egg weight for renest clutches when combined with the evidence of clutch size decline from the preceding section, suggests an interesting adaptation. Hypothetically, the decrease in potential numbers of young produced may be offset by a female's laying larger eggs that presumably produce larger ducklings. These may have a greater potential for survival. Duckling weight (taken 12 to 16 h after hatch) and egg weight in 1975, were significantly correlated (Fig. 5).

This analysis was not carried beyond the hatching of ducklings but a necessary assumption in the above hypothesis is that larger body size accrues some positive benefit to the ducklings. Parsons (1970) found that chicks from larger eggs of the Herring Gull (*Larus argentatus*) survived better during the first week than those from smaller eggs. In Great Tits, Schifferli (1973) found young hatched from larger eggs to be significantly heavier up to the fourteenth day. Thus, some evidence from other species supports this hypothesis.

As Schifferli (1973) pointed out, larger weight may confer two advantages on the young: (1) the chick may actually have a larger body which may reflect a relatively ad-

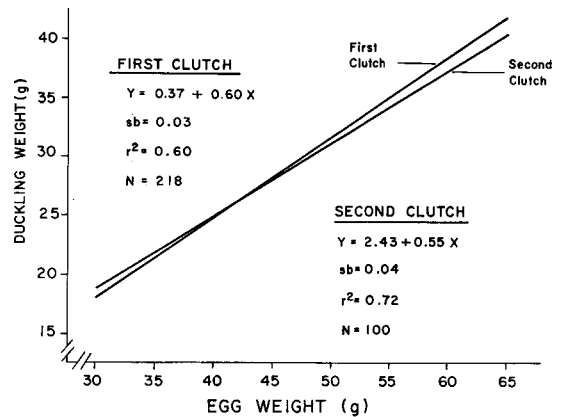


FIGURE 5. Regressions of initial egg weight on duckling weight for first and second clutches.

vanced stage of development, thereby shortening the fledging period; or (2) the chick may have more food reserves in the form of a larger yolk sac. In respect to thermal homeostasis, ducklings from renest clutches are hatched later in the year when weather is usually warmer. The net gain in energy available for the maintenance of homeothermy is probably far greater than just that reflected in body weight. Further, if ducklings from renest clutches are produced after the peak of food supply, additional body reserves may allow a longer period before they must maintain themselves solely on food from the environment.

The increase in egg size later in the season is not unique but various situations have been found among species of birds and no single trend is apparent. Koskimies (1957b) found that eggs tend to become larger in the Velvet Scoter as the season advanced. He found records of similar increase in Red-winged Blackbirds (*Agelaius phoeniceus*), Rock Doves (*Columba livia*), Cuckoos (*Cuculus canorus*), Bobwhites (*Colinus virginianus*), and Song Sparrows (*Melospiza melodia*). Perrins (1970) found the same trend in Great Tits. On the contrary, in Black-legged Kittiwakes (*Rissa tridactyla*; Coulson 1966), Shags (*Phalacrocorax aristotelis*; Coulson et al. 1969), Gannets (*Morus bassanus*; Nelson 1966) and Herring Gulls (Parsons 1972, 1976), eggs become smaller as the breeding season progresses. The relationship of egg size, laying date and duckling vigor should provide a fruitful area for further research.

SUMMARY

The relationships of clutch size, laying dates and egg weight were studied with pairs of

captive Mallards for three consecutive years. High repeatability estimates were calculated for all three traits. This indicates relatively low variability for individual performance from year to year even though there was a high degree of variation in the entire sample studied. Laying dates of individual females probably reflect phenotypic responses to the breeding environment. In the wild this may be modified by other factors such as the ability of the individual to find food (Perrins 1970).

Clutch size declined between the first nest and each subsequent reneest, as has been frequently recorded in the wild. The decline was also evident within a given nest sequence with earlier clutches being larger. A single regression equation describes clutch size decline within first nests and all reneesting attempts. Even though laying date and clutch size appear to be under significant genetic control, earlier nesting by an individual results in a larger clutch being laid. This suggests that the main factor controlling clutch size is laying date. The analysis strongly points to an underlying genetic control, probably mediated through photoperiod.

Eggs were heavier in larger clutches in first nests and all reneesting attempts. Eggs were larger in successive reneests suggesting that some of the loss in production of young from smaller clutches may be compensated for by production of larger ducklings later in the season. Duckling weight and egg weight were highly correlated. Further work is needed on the relationship of duckling weight and egg weight and on the possible physiological advantage inherent in duckling body size.

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RECENT PUBLICATIONS

Species Index to Florida Bird Records in *Audubon Field Notes* and *American Birds*, Volumes 1-30, 1947-1976.—Margaret Coon Bowman. 1978. Special Publication No. 1, Florida Ornithological Society, Gainesville, Florida. 42 p. Paper cover. \$3.75. Available: Treasurer, F.O.S., 1701 NW 24th St., Gainesville, FL 32605. For many years, most of the published records of birds in Florida appeared in the regional reports in *AFN* and its successor, *AB*. This carefully-prepared index now makes them accessible. It will be invaluable, not only for studying changes in the distribution and abundances of Florida birds, but also for uncovering observations on their habits.

The Birds of South Dakota/An Annotated Check List.—Nathaniel R. Whitney, Jr. et al. 1978. The South Dakota Ornithologists' Union, Vermillion, South Dakota. 311 p. Paper cover. Available: W. H. Over Museum, Vermillion, SD 57069. Thanks to South Dakota's variety of habitats (though grassland predominates) and its location in the transition zone between eastern and western avifaunas, some 377 species of birds are recognized from the State. This book by members of the S.D.O.U. Check List Committee is the first comprehensive list of these birds to have been published since 1946. For each species, the status, habitat, and seasonal occurrence are summarized and a range map is given. A long list of citations documents the records. Indexes. A useful reference for birders in South Dakota and adjoining states.

Birds of the Southwest Pacific.—Ernst Mayr. 1978. Charles E. Tuttle Co., Rutland, Vermont. 316 p. Paper cover. \$5.75. This is a reprint edition of a

work first published in 1945 and long out of print. Nothing has yet appeared to replace it as an authoritative field guide to the birds in the broad area between Samoa, Fiji, New Caledonia, and Micronesia. It is organized differently than guides which cover smaller, more homogeneous avifaunas. The first part treats the seabirds and shorebirds and—in a general manner—the land and freshwater birds of the region. The second part then treats the land and freshwater birds of each island group in a specific manner. Illustrated with color plates by Frances Lee Jacques and line drawings by Alexander Seidel. Glossary and index. Peripatetic birders will welcome the return of this practical handbook, particularly in its pocket-size format.

Upland Birds of Northeastern New Guinea.—Bruce McP. Beehler. 1978. Wau Ecology Institute Handbook No. 4. 156 p. Paper cover. Available: Wau Ecology Institute, Box 77, Wau, Papua New Guinea. This is a field guide to the hill and mountain birds of the Morobe Province, a mountainous region in Papua New Guinea (PNG). The avifauna is diverse: over 50 families of birds—almost as many as in the entire U.S.—in an area about as large as Vermont and New Hampshire together! To aid birders who are new to the region, Beehler characterizes each of the families and lists the species to be found in each of several habitats. The species accounts briefly describe field marks, similar species, habitat, altitudinal range, abundance, and voice. They are illustrated with monochrome and color plates by William J. Adams. Since the guide includes about two-thirds of the known breeding birds in PNG, it will be useful throughout the country.