
100 Years Ago in The Auk



From 1885, Auk 3: 316-317:

The Popular Names of Birds.

TO THE EDITORS OF THE AUK:—

"Sirs: The 'powers that be,' I understand, are preparing a 'Check List,' and revising the scientific and popular names of our birds.

"There is no doubt that scientific names are entirely in the hands of scientists, but it seems to be overlooked that popular names are just as completely in the hands of the people. Scientists may advise, but not dictate on this point. A short analysis of the principle of common names may place the matter in a new light.

"A bird's name, to be popular, must be distinctive, and in accordance with the genius of our language. Examples of such are Thrush, Rail, Heron, Hawk, Crane, Night-Jar, and many others. These are truly popular names, evolved originally out of a description, handed down and condensed and changed until they have assumed their present terse, abrupt, and, to a foreign ear, uncouth forms, but, nevertheless, forms in accordance with the pervading spirit of the Saxon tongue; or, in other words, they are *really* popular.

"On the other hand, look at the so-called popular, but really translated, scientific or spurious English names given to our birds, taking as examples the following: Baird's Bunting, Leconte's Sparrow, Wilson's Green Black-capped Flycatching Warbler, Bartram's Sandpiper, Sprague's Lark, Wilson's Thrush, Black Ptilogonys, Semiplumated Tattler, Fasciated Tit, Florida Gallinule, etc.

"Surely, the gentlemen whose names are applied to these birds have not so slight a hold on fame as to require such aids as these to attain it, if indeed aids they be, which I question; for such nomenclature *cannot* stand the test of time.

"If you show to an 'out-wester' the two birds mentioned above as Baird's Bunting and Leconte's Sparrow, and tell him that these are their names, he will probably correct you, and say one is a 'Scrub Sparrow,' the other a 'Yellow Sparrow.' Convince him that he is wrong, and in a month he will have forgotten all but the names he formerly gave them; they are so thoroughly appropriate and natural that they cannot be forgotten. The next name in the list above given is clumsy enough to strangle itself with its own tail. A lad on the Plains once brought me a *Neo-*

corys spraguei, and asked its name. I replied that it was Sprague's Lark. Soon afterward he came again; he could not remember that name; so I told him it was a 'Skylark,' and he never forgot that. On the Big Plain that seed was sown, and not all the scientists in America can make, or ever could have made, the settlers there call that bird anything but 'Skylark.' And I consider that lad precisely represented the English-speaking race; he rejected the false name, and readily remembered the true one, and was aided by that which was apt and natural. No better illustration could be given on the fact, that phraseology may be the life or death of a cause, according as it is happy or unfortunate.

"A similar instance is the case of 'Bartram's Sandpiper.' Ever since Wilson's time this name has been continually thrust into the face of the public, only to be as continually rejected; 'Upland Plover' it continues to be in the east, and 'Quail' on the Assiniboine, in spite of Bartram and Wilson, and will continue so until some name, answering all conditions, is brought forward; for here, as elsewhere, the law of the survival of the fittest rigidly prevails. As an example of the fit ousting the false, note how, in spite of scientists, 'Veery' is supplanting 'Wilson's Thrush' throughout the length and breadth of the land.

"The spurious English names scarcely need comment, they so evidently contain in themselves the elements of their own destruction. Imagine a western farmer being told that a certain songster was a 'Ptilogonys.' In spite of the books, the other three examples cannot hold ground against 'Willet,' 'Ground Wren,' and 'Waterhen,' respectively.

"The purpose of a Check List that includes English names is, I take it, not to attempt the impossible feat of dictating to our woodmen what names they shall give their feathered friends, but rather to preserve and publish such names as are evolved in the natural way,—names which are the outcome of circumstances. Only in case of egregious error is a common name to be superseded; and in doing this it must be remembered that no name can be popular unless true to the principles of the English tongue. It must be short, distinctive, and, if possible, descriptive. Of this class are Veery, Junco, and Vireo. These are the only successful artificial names that I can at present rec-

(continued on p. 679)

SHORT COMMUNICATIONS

The Arrangement and Structure of Feather Melanin Granules as a Taxonomic Character in African Starlings (Sturnidae)

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It has long been known that the metallic colors of many birds arise from the physical structure of the feathers rather than from pigments (e.g. Strong 1902). The African starlings include many species noted for their brilliant iridescent plumage, and it has been demonstrated that these colors are due to the structure and arrangement of melanin granules in the barbules of the feathers (Durrer and Villiger 1967, 1970a).

The morphological basis of such colors must be considered a more reliable taxonomic character than the visual effects, since the physical arrangement of structures within the keratinized feather is produced under genetic control, but several different structural patterns can form the basis for the same color effects. Thus, in the African sunbirds (Nectariniidae) iridescence is produced by stacks of thin melanin platelets (Durrer and Villiger 1962), whereas in the American hummingbirds (Trochilidae) melanin platelets with a complex internal pattern of gas vacuoles are responsible for iridescent colors (Greenewalt 1960). Lattices of solid melanin rods are found in the Common Peafowl (*Pavo cristatus*) and the Congo Peafowl (*Afropavo congensis*, Durrer and Villiger 1975), and in the Emerald Cuckoo (*Chrysococcyx cupreus*, Durrer and Villiger 1970b). Air-filled melanin granules occur again in the trogons: in the genus *Pharomachrus* the melanin is organized in platelets, while in *Apaloderma*, *Galbula*, *Harpactes*, and *Trogon* the granules are round and hollow (Durrer and Villiger 1966).

Durrer and Villiger (1970a) investigated feather material from one or two species of all the extant genera of the Family Sturnidae, and commented briefly on relationships between the genera. We have examined material from all Afrotropical starlings (Table 1) except the oxpeckers (*Buphagus* spp.) by means of transmission electron microscopy.

All feathers were taken from the body plumage of museum specimens. For a few species, feathers from different body regions were investigated, but no important differences were found (except as described in the case of *Lamprolornis corruscus*). The feathers were dehydrated in a graded series of alcohols, then infiltrated and embedded in LR White resin. Thin sections were cut on a LKB ultramicrotome, and viewed unstained in a JEOL JEM-100 CX II Transmission Electron Microscope.

We have assigned species to six categories (see Table 1), distinguished on the basis of melanin granule structure and arrangement. The thickness of the outer keratin layer of the barbule (Durrer and Villiger

1970a) was less reliable because it varied in different sections. Where we examined species figured in Durrer and Villiger (1970a), we obtained identical results with the exception of *Grafnisia torquata* (see below). Our six structural types are as follows:

Type A.—Melanin granules are circular in cross section and solid. Within the barbule they are scattered, but there is a distinct outer band (Fig. 1a).

Type B.—Melanin granules appear as thin, solid platelets, with either a stratified surface layer (Fig. 1b) or a distinct single outer layer (Fig. 1c).

Type C.—Melanin granules are circular, hollow, and scattered within the barbule (Fig. 1d).

Type D.—Melanin granules are circular, hollow, and arranged in layers near the surface (Fig. 2a).

Type E.—Melanin granules are oblong, hollow, with a single outer row placed end-to-end around the perimeter of the barbule, and others scattered in the interior (Fig. 2b). The granules may be short and thick, or slender and elongated. The dull ventral plumage of *Lamprolornis corruscus* shows the typical arrangement, but the granules are apparently solid, not hollow (Fig. 2c).

Type F.—The melanin granules are oblong, hollow, and arranged in several rows on the dorsal surface of the feather, with only a single row on the ventral surface (Fig. 2d).

Durrer and Villiger (1970a) found that all non-African starlings had solid, circular melanin granules, corresponding to their types A and C (type A in our study). This may represent the primitive condition. A cladogram of our structural types (Fig. 3) closely resembles Fig. 2 of Durrer and Villiger (1970a), except that they did not record a category equivalent to our type C. If shared derived characters are taken to be the best indicators of relationship between different species, this scheme implies that if species share type A, this character by itself provides no information concerning their relationships to each other.

All modern treatments of the starling family have followed Amadon's (1962) arrangement of the genera and species. The only major modifications of this system have been proposed by Wolters (1976). Their different views will be considered briefly in the light of the evidence from the melanin granules.

The largest genus of African starlings is *Lamprolornis*, which may include *Coccycolius* (Amadon 1943,

TABLE 1. The Afrotropical Sturnidae.

Species ^a	Melanin granule type
<i>Cinnyricinclus femoralis</i>	A
<i>C. leucogaster</i>	D
<i>C. sharpii</i>	A
<i>Coccycolius iris</i>	F
<i>Cosmopsarus regius</i>	E
<i>C. unicolor</i>	C
<i>Grafisia torquata</i>	C
<i>Lamprotornis acuticaudus</i>	E
<i>L. australis</i>	E
<i>L. caudatus</i>	E
<i>L. chalcurus</i>	E
<i>L. chalybaeus</i>	E
<i>L. chloropterus</i>	E
<i>L. corruscus</i>	E
<i>L. cupreocauda</i>	B
<i>L. mevesii</i>	E
<i>L. nitens</i>	E
<i>L. ornatus</i>	E
<i>L. purpureiceps</i>	B
<i>L. purpureus</i>	E
<i>L. purpuropterus</i>	E
<i>L. splendidus</i>	E
<i>Neocichla gutturalis</i>	A
<i>Onychognathus albirostris</i>	A
<i>O. blythii</i>	A
<i>O. frater</i>	A
<i>O. fulgidus</i>	A
<i>O. morio</i>	A
<i>O. nabouroup</i>	A
<i>O. salvadorii</i>	A
<i>O. tenuirostris</i>	A
<i>O. tristramii^b</i>	A
<i>O. walleri</i>	A
<i>Poeoptera kenricki</i>	B
<i>P. lugubris</i>	B
<i>P. stuhlmanni</i>	B
<i>Speculipastor bicolor</i>	A
<i>Spreo albicapillus</i>	C
<i>S. bicolor</i>	C
<i>S. fischeri</i>	C
<i>S. hildebrandti</i>	E
<i>S. pulcher</i>	E
<i>S. shelleyi</i>	E
<i>S. superbus</i>	E

^a The nomenclature follows Hall and Moreau (1970).

^b *Onychognathus tristramii* is not found in Africa, being restricted to the Arabian peninsula and Israel, but is included as it certainly belongs to the Afrotropical starlings.

1962). Amadon (1956) recognized *Coccycolius* as a separate genus, as did Hall and Moreau (1970) and Wolters (1976). Although feather type F can certainly be derived from type E, the two are strikingly different, and this would favor the retention of two genera. The other species of *Lamprotornis* share type E, with the exception of *L. cupreocauda* and *L. purpureiceps*. These two species constitute Wolters's (1976) subge-

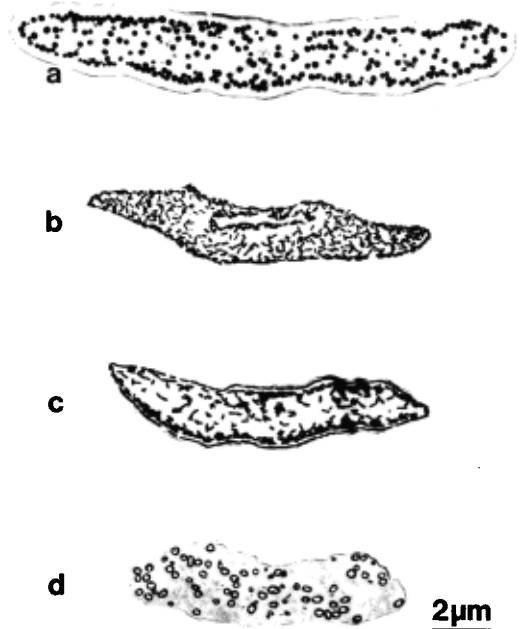


Fig. 1. Electron micrographs of transverse sections of starling feathers, showing different structural types: (a) type A, *Creatophora cinerea*; (b) type B, *Poeoptera kenricki*; (c) type B, *Lamprotornis purpureiceps*; (d) type C, *Spreo fischeri*.

us *Hylopsar*, and are grouped as a superspecies by Hall and Moreau (1970). Here similar colors apparently are produced by a very different underlying structure. While these species share type B with the genus *Poeoptera*, there are differences in the details of the melanin granule arrangement, as well as other morphological differences.

The differences in structure in the granules from the dull ventral plumage of *Lamprotornis corruscus* evidently are related to changes in the development of the melanin granules. In *L. chloropterus* (Durrer and Villiger 1967) the melanin granules in developing feathers are initially solid but later become filled with proteinaceous material, which finally disappears and leaves an airspace inside the granule. It appears that this injection of protein has failed to occur in melanin granules from the ventral feather tracts of *L. corruscus*, but in other respects the normal arrangement has been preserved.

All species of *Onychognathus* share the primitive type A, but all also have rufous-colored primary remiges in both sexes. Amadon (1943) suggested a relationship to the genus *Poeoptera*, in which the females have rufous primaries but not the males. Wolters (1976) included *Poeoptera* in *Onychognathus*, although he placed the 13 species in 7 subgenera. However, the 3 species of *Poeoptera* show the dis-

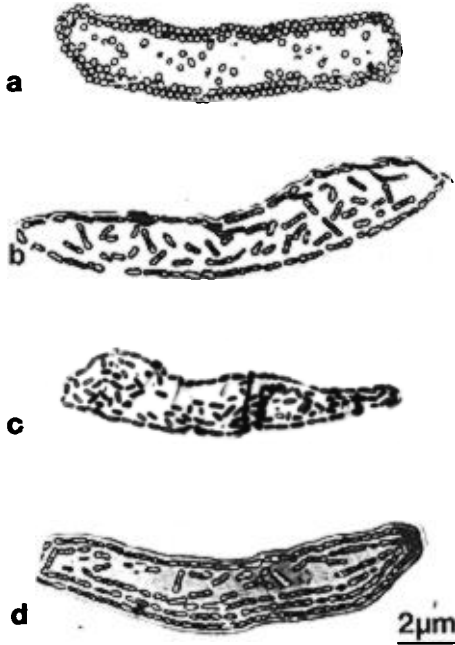


Fig. 2. Electron micrographs of transverse sections of starling feathers, showing different structural types: (a) type D, *Cinnyricinclus leucogaster*; (b) type E, *Lamprotornis chalybaeus*; (c) type E, *Lamprotornis corruscus*; (d) type F, *Coccoyolius iris*.

tinctive type B melanin granule arrangement, and because the female of *Cinnyricinclus leucogaster* also has rufous primary feathers, this character should not be overemphasized as indicative of close relationship.

The three species of *Cinnyricinclus* are associated primarily on the basis of their similar immature plumages. Hall and Moreau (1970) commented that *C. femoralis* and *C. sharpii* are certainly closely related, but they may be rather distant from *C. leucogaster*. Wolters (1976) placed them in three monotypic genera. The melanin granule arrangement clearly separates *C. leucogaster* (type D) from the other two species, which share the type A arrangement. Thus, the present study provides no further information on the closest relatives of *C. femoralis* or *C. sharpii*.

Durrer and Villiger (1970a) examined feathers only from *Spreo superbus* and found the melanin granule structure to be typical of the genus *Lamprotornis*. We confirmed this, and found the same pattern in *S. hildebrandtii*, *S. pulcher*, and *S. shelleyi*. Amadon (1956) admitted that the genus *Spreo* was a somewhat artificial group but urged its retention for convenience. Wolters (1976) used monotypic genera for *S. bicolor* and *S. albicapillus*, placing the other species in Roberts's (1922) genus *Lamprospreo*. Clancey (1958) and

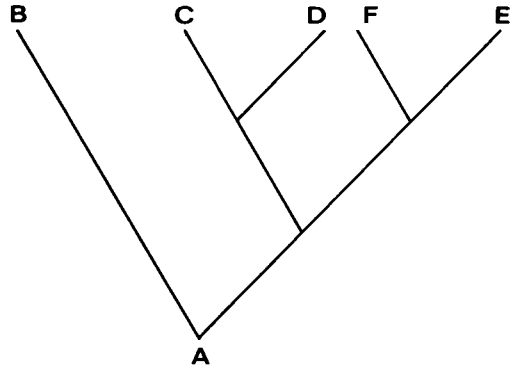


Fig. 3. A hypothetical sequence for the derivation of the different structural types. Round, solid, scattered melanin granules are taken to represent the primitive condition. Hollow granules, oblong or flattened granules, and stratified arrangements are all derived states.

Brooke (1971) have independently proposed that *Spreo* should be restricted to the species *S. bicolor*, *S. fischeri*, and *S. albicapillus*, while the other species should be included in *Lamprotornis*. Our data support such an arrangement.

Recently, Sibley and Ahlquist (1984) presented a diagram of relationships among the Sturnidae, based on DNA-DNA hybridization measurements. They examined material from *Spreo bicolor* and *Lamprotornis nitens* and concluded that these two genera are closely related. Their results also indicate a clear separation between the African starling genera *Lamprotornis*, *Spreo*, *Onychognathus*, *Cinnyricinclus* and the Oriental and Palearctic genera. However, *Creatophora* is closely associated with *Sturnus* and *Acridotheres*, which is in full agreement with earlier views (Amadon 1943, 1956; Hall and Moreau 1970; Wolters 1976) and is also supported by studies of the jaw musculature (Beecher 1978).

Cosmopsarus regius falls into type E, while *C. unicolor* shares type C with some members of *Spreo* and *Grafsia torquata*. This is surprising as the close relationship of the two species of *Cosmopsarus* has never been questioned. Amadon (1943) included both species of *Cosmopsarus* in an enlarged genus *Spreo*, together with *Grafsia* and *Speculipastor*, but later changed his views.

The monotypic genera *Creatophora*, *Neocichla*, and *Speculipastor* all show the primitive type A arrangement. However, for *Grafsia torquata* our specimens showed hollow granules of type C, not solid type A structures as figured in Durrer and Villiger (1970a). This does not appear to be an artifact due to different methods, and according to the acknowledgments in their paper they obtained feathers of this species from the same source as we did (BMNH). We can only conclude that in one case feather material has been misidentified. Reichenow (1909) originally described

this species as *Spreo torquata*, but for the present its relationships remain obscure.

A systematic revision of the African starlings is long overdue. Our results suggest that the composition of the genera *Cinnyricinclus*, *Cosmopsarus*, *Lamprotornis*, and *Spreo* should be reexamined.

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Clutch Size, Daylength, and Seasonality of Resources: Comments on Ashmole's Hypothesis

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Clutch size tends to increase with latitude both within and among bird species. For nidicolous birds, Lack (1947) suggested this might be due to the longer daylength at higher latitudes that allowed parents to collect more food and feed larger broods. Ashmole (1961) proposed an alternative hypothesis: that clutch size depends on the relationship between resource level and population density during the breeding season. If populations are limited by nonbreeding season resources, clutch size will increase as the seasonality of resources increases, regardless of average resource level. Ricklefs (1980) called this Ashmole's hypothesis. I am prompted by the recent renewal of interest in this topic (Ricklefs 1980; Koenig 1984a, b; Møller 1984) to offer some comments on the mathe-

matical representation and predictions of Ashmole's hypothesis.

Ricklefs (1980) introduced the notion that fluctuation in food resources available to bird populations can be represented by the seasonal pattern of actual evapotranspiration (AE). He expressed Ashmole's hypothesis in terms of summer and winter AE as

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

where a is an arbitrary constant, S is summer (breeding season) AE, and W is winter (nonbreeding season) AE. In this formulation, clutch size is directly proportional to seasonality of resources (i.e. the ratio of summer to winter AE) and does not depend on the absolute level of resources.

TABLE 1. Spearman rank correlation coefficients (r_s) for relationships among clutch size and several other variables.^a

	Clutch size	Latitude	Breeding season	W	S	S - W
Clutch size	—	0.69**	-0.68**	-0.68**	-0.37	0.53*
Latitude	13	—	-0.68**	-0.93**	-0.67**	0.62*
Breeding season	11	11	—	0.85**	0.70*	-0.52
W	12	12	10	—	0.73**	-0.58*
S	12	12	10	12	—	0.08
S - W	12	12	10	12	12	—

^a Data from Ricklefs (1980: Table 1). r_s is given above the diagonal (* = $P < 0.05$, ** = $P < 0.01$) and sample size below the diagonal. Calculations performed by SPSS program NONPAR CORR (Nie et al. 1975). The r_s value of -0.45 ($P > 0.05$) given by Ricklefs (1980: 44) for the correlation between clutch size and W is incorrect (Ricklefs pers. comm.).

As Ricklefs (1980) correctly depicted in his Fig. 1, however, and noted in the caption thereto, under Ashmole's hypothesis "clutch size is proportional to the ratio of the breeding season surplus to the adult population" (italics added). Or, more precisely stated, clutch size is proportional to the ratio of surplus breeding season resources (i.e. surplus to those needed to maintain the adult population) to winter resources. Because winter resources are postulated to limit population size, the winter resource level equals the portion of summer resources required to maintain the adult population in summer. The remaining summer surplus is available to the population for reproduction. Thus, instead of Eq. (1), Ashmole's hypothesis should be expressed as

$$C = a(S - W)/W, \quad (2)$$

where a is a new constant and S and W are as previously defined. Equation (2) provides for use of a portion of summer resources to maintain the adult breeding population, whereas Eq. (1) devotes summer resources entirely to reproduction.

In a completely seasonless environment, $S = W$ and Eq. (2) gives $C = 0$. This is correct under a strict interpretation of Ashmole's hypothesis since breeding would not occur if there were no surplus resources. As Ashmole (1961) suggested, however, under such extreme conditions in the real world we would expect breeding to occur at all times of the year and clutch size to be low. Surplus resources would be scarce and would be created by temporary reductions of the population below the level that could be maintained by the resource base. Obviously, such refinements are not represented by Eq. (2), which models only the major features of Ashmole's hypothesis. Moreover, the relationship between clutch size and AE operates through the food supply and is likely to be more complex than the direct proportionality of the equation.

Ricklefs (1980) determined that there was a significant correlation between C and S/W (Spearman rank correlation, $r_s = 0.65$, $P < 0.05$, for 12 localities). He

also performed a multiple regression-partial correlation analysis of the same data, using the generalized transformed form of Eq. (1):

$$\log C = \log a + b \log S - c \log W, \quad (3)$$

which showed that clutch size was inversely correlated with winter resources but was not correlated with summer resources. Koenig (1984b) used the same procedure for the Northern Flicker (*Colaptes auratus*), with similar results. The equivalent generalized transformation of Eq. (2) is

$$\log C = \log a + b \log(S - W) - c \log W, \quad (4)$$

and the corresponding analysis distinguishes between the effects of summer surplus ($S - W$) and winter resources (W) instead of between summer and winter resources.

Application of this analysis to Ricklefs's (1980) data shows that $\log W$ remains significantly inversely correlated with $\log C$ but that $\log(S - W)$ is not correlated with $\log C$ after controlling for $\log W$ (Ricklefs pers. comm.). However, the ability to distinguish between the effects of $\log(S - W)$ and $\log W$ in this analysis is relatively poor since these two variables are significantly correlated with each other ($r = -0.65$, $P < 0.05$) whereas $\log S$ and $\log W$ are not significantly related ($r = 0.32$, $P > 0.05$).

Following Ricklefs (1980), Møller (1984) suggested several predictions from Ashmole's hypothesis: (1) clutch size and level of winter resources should be negatively correlated, (2) clutch size and level of summer resources per breeding pair should be positively correlated, (3) clutch size and the relation between summer and winter resources should be positively correlated, and (4) clutch size and summer resource level should vary independently. Møller's predictions (1) and (4) do not follow directly from Ashmole's hypothesis, however, but derive from the subsidiary hypothesis that winter resource levels (or breeding densities of adults) are primarily responsible for the correlation, if any, between C and S/W , as found by Ricklefs (1980). Møller's prediction (3)

follows from Eq. (1) if we read "ratio of summer to winter resources" for "relation between summer and winter resources," and it remains correct under Eq. (2).

If Ashmole's hypothesis is true, we would expect clutch size and resource data to be consistent with its predictions. We must not be seduced by an attractive hypothesis, however, into believing that correlation of climatic or other environmental variables with clutch size provides more than meager support for any hypothesis. Many, perhaps most, environmental and biological variables are correlated with latitude and also will be correlated with clutch size in those avian species and groups within which clutch size varies with latitude. It is not surprising, therefore, to find that clutch size is often positively correlated with daylength (e.g. Hussell 1972) and is negatively correlated with winter AE (Ricklefs 1980; Koenig 1984a, b). The data in Ricklefs (1980: Table 1) show that clutch size is correlated with winter AE, latitude (and therefore maximum daylength), length of breeding season, and summer AE minus winter AE (Table 1). Moreover, most pairs among these variables are significantly related (Table 1). Koenig (1984b) shows that neither winter AE nor breeding density accounts completely for the latitudinal trend in his clutch size data. Clearly, the possibility remains that the latitudinal trend in clutch size may be explicable in terms of any of these variables or a complex relationship among several of them or others not considered here (e.g. see Royama 1969). Demonstration of a correlation between clutch size and an environmental variable provides little insight into the causative agents of clutch size determination and merely allows that variable to remain as a viable candidate for consideration as an element of an explanatory hypothesis. We need to find other ways to test such hypotheses.

Finally, in his discussion of Ashmole's hypothesis, Lack (1968: 167) noted that "while the summer day is about one-and-a-half times as long in mid-Europe as in the tropics, the average passerine clutch is twice as large, so some factor in addition to daylength must be concerned." Although Lack attributed this insight to Ashmole, apparently it was not his (Ashmole 1961 and pers. comm.). It is not necessary to invoke factors other than daylength available for feeding young to explain the observed differences in clutch size between the tropics and mid-Europe (Hussell 1972). As with food resources, it is the surplus available for reproduction that is important in the postulated relationship between daylength and clutch size. Consider a hypothetical example: If daylength is 12 h in the tropics and 18 h in mid-Europe (i.e. 1.5 times greater), and if adults spend 6 h feeding and maintaining themselves at each locality and devote the remainder of the day (6 h in the tropics and 12 h in

Europe) to raising their broods, then the observed clutch size ratio of 2 between Europe and the tropics is exactly as expected from the daylength hypothesis alone. Although it is unlikely that adult birds use exactly the same amount of time to maintain themselves in the Temperate Zone as in the tropics, this example shows that time budgets of the adults influence the extent to which the discrepancy between the clutch size and daylength ratios is unexplained by the daylength hypothesis. Very little is known about variation in time budgets of birds breeding at different latitudes, and more detailed examination of this aspect of the problem may prove to be fruitful. Nevertheless, more than correlational evidence will be necessary to determine whether daylength, seasonality of resources, other variables, or several variables acting together are primarily responsible for the evolution of geographic variation in clutch size.

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A Test of Water Depth Niche Partitioning by Western Grebe Color Morphs

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Dark- and light-phase Western Grebes (*Aechmophorus occidentalis*) have been described by Storer (1965) and Ratti (1981). Ratti (1979) and Nuechterlein (1981) reported on reproductive separation and isolating mechanisms between the color morphs. Data from Ratti (1979) indicate that "dark- and light-phase birds represent reproductively independent populations" and that the morphs are separate species. Ratti (1979) stated that "morphologically and ecologically, dark- and light-phase Western Grebes are practically indistinguishable" and may represent "one of the best avian examples of an exception to the competitive exclusion principle" (Grinnell 1904). However, Nuechterlein (1981) reported that light-phase birds tend to feed farther from shore than dark-phase birds. He also noted a preponderance of "level dives" by dark-phase birds and a preponderance of "springing dives" by light-phase birds. The light-phase diving posture is more perpendicular to the water surface and may facilitate diving to greater depths. These findings led to Nuechterlein's (1981) hypothesis that "the two color phases may be segregating behaviorally into two subtly different ecological forms specialized for feeding at different depths." The objective of this research was to test Nuechterlein's (1981) hypotheses.

Data were gathered at Goose Lake, Lower Klamath National Wildlife Refuge (NWR), and Tule Lake NWR, California; Upper Klamath Lake, Oregon; and Bear River NWR, Utah. Goose and Upper Klamath lakes are natural water basins; Lower Klamath, Tule Lake, and Bear River NWRs are artificial water impoundments. All surveys were initiated at sunrise,

when most birds were actively feeding, and usually terminated by midmorning. Survey routes were determined from previous field work (Ratti 1979). One survey was conducted at each study area and, thus, all data are statistically independent. Birds were classified as dark-phase or light-phase (Ratti 1981); rare intermediates were not recorded. Each bird observed was recorded into 1 of 3 categories, based on an ocular estimation of distance from shore; A = <25 m, B = 25-75 m, and C = >75 m. The location, number of birds, and color phase also were recorded on a map of the survey route. After completion of bird surveys, I returned to bird observation sites and conducted a minimum of 3 water-depth transects. Transect lines were 100 m apart, parallel, and generally perpendicular to the shoreline of the observation site. I traversed the transect lines from a canoe, and recorded water depth from ocular estimated distances of 15, 50, and 100 m from shore to correspond with the distance categories of bird observations. Throughout the study, distances were measured periodically from shore to verify my ocular estimations. Data from bird observations were tested using Chi-square analysis and mean depths were compared by *t*-test.

Between 15 June and 20 July 1981, I observed 1,132 dark-phase and 596 light-phase Western Grebes and measured water depth from 106 transects. Variation in the number of water-depth transects measured at each location was a function of the distribution of birds along the survey route.

Distance from shore.—Observations of the color morphs in categories of distance from shore were not random (Table 1). There was a clear tendency for

TABLE 1. Observations of dark- and light-phase Western Grebes in categories of distance from shore (A = <25 m, B = 25-75 m, C = >75 m) in 1981, and Chi-square test of pooled data.

Location	Color morph	A	B	C	χ^2_{a}
		n (%)	n (%)	n (%)	
Goose Lake	Dark	4 (8.7)	4 (8.7)	38 (82.6)	16.5**
	Light	1 (0.4)	41 (16.1)	213 (83.5)	
Bear River NWR	Dark	97 (38.0)	37 (14.5)	121 (47.5)	6.6*
	Light	22 (25.9)	9 (10.6)	54 (63.5)	
Tule Lake NWR	Dark	56 (14.0)	65 (16.3)	278 (69.7)	3.79
	Light	5 (8.2)	6 (9.8)	50 (82.0)	
Lower Klamath NWR	Dark	54 (34.0)	75 (47.2)	30 (18.9)	17.46**
	Light	11 (39.3)	3 (10.7)	14 (50.0)	
Upper Klamath Lake	Dark	67 (24.5)	146 (53.5)	60 (22.0)	13.25**
	Light	17 (10.2)	101 (60.5)	49 (29.3)	
All areas	Dark	23.8%	28.0%	48.1%	
	Light	16.8%	21.5%	61.7%	

* $P < 0.05$, ** $P < 0.01$.

TABLE 2. Mean water depth (cm) for categories of distance from shore (A = <25 m, B = 25–75 m, C = >75 m) measured at Western Grebe observation sites, 1981. Data from distance categories joined by a solid line were not different ($P > 0.05$); all other categories were significantly different ($P < 0.05$).

Location	Distance category			No. water-depth transects measured
	A	B	C	
Goose Lake ^a	13 (3.6)	32 (11.4)	82 (6.4)	11
Bear River NWR ^b	120 (110)	66 (31.2)	54 (38.8)	28
Tule Lake NWR ^b	102 (44.1)	111 (36.8)	117 (28.3)	20
Lower Klamath NWR ^b	113 (51.7)	65 (11.4)	69 (13.6)	38
Upper Klamath Lake ^a	205 (58.9)	364 (65.4)	290 (83.4)	9

^a Natural water basin.

^b Artificial water impoundment.

light-phase birds to occur farther from shore, with 62% of light-phase observations in category C vs. 48% for dark-phase. These data are consistent with, and provide a new aspect to previous reports of, "spatial segregation" between the color morphs (Ratti 1979). However, the data were not consistent among all study areas. At 3 of the 5 areas (Bear River, Lower Klamath, and Upper Klamath) the data revealed significantly greater use of category C by light morphs. At Tule Lake, use of each distance category showed no difference between color morphs. At Goose Lake, sample sizes were inadequate in categories A and B, and use of category C was nearly equal.

Water depth.—Water depths were not always directly related to distance from shore, especially at artificial water impoundment areas such as Bear River NWR (Table 2). Construction of dike roads often

created a "borrow ditch" parallel to roads, from dredging of fill material. The deepest water zone at several areas was immediately parallel to dike roads. Thus, distance categories were assigned to low-, medium-, and high-water categories according to mean depth (Table 3). Examination of Tables 1 and 3 allows comparison of some water-depth categories with distance categories (e.g. Goose Lake "C" = high-depth zone; Upper Klamath "C" = medium-depth zone). Some depth categories were not significantly different (Table 2) and were pooled for analysis (Table 3).

Chi-square tests were used to test for random use of water-depth categories by Western Grebe color morphs (Table 3). Only data from Upper Klamath Lake revealed greater use of high-water zones by light-morph Western Grebes. Although Goose Lake data were significant, most of the χ^2 value was gen-

TABLE 3. Chi-square analysis of water depth use by dark- and light-phase Western Grebes. Low, medium, and high water-depth categories were tested where mean depths were significantly different ($P < 0.05$).

Location	Color morph	Number observed (%) by water depth			χ^2
		Low	Medium	High	
Goose Lake ^b	Dark	4 (8.7)	4 (8.7)	38 (82.6)	16.7*
	Light	1 (0.4)	41 (16.1)	213 (83.5)	
Upper Klamath Lake ^b	Dark	67 (24.5)	60 (22.0)	146 (53.5)	14.4*
	Light	17 (10.2)	49 (29.3)	101 (60.5)	
	Dark	16.6%	15.4%	68.0%	
	Light	5.3%	22.7%	72.0%	
Lower Klamath NWR ^{c,d}	Dark	105 (66.0)		54 (34.0)	0.38
	light	17 (60.7)		11 (39.3)	
Bear River NWR ^{c,d}	Dark	158 (62.0)		97 (38.0)	4.2
	Light	63 (74.1)		22 (25.9)	
	Dark	64.0%		36.0%	
	Light	67.4%		32.6%	

* $P < 0.01$.

^b Natural water basin.

^c Artificial water impoundment.

^d No difference between low and medium depth zones; low and medium were pooled for χ^2 test.

erated from cells with inadequate sample sizes. No test was conducted on the Tule Lake NWR data because *t*-tests indicated the mean water-depth categories were not different. Bear River NWR and Lower Klamath NWR data sets revealed no difference in water-depth use by Western Grebe color morphs.

I also tested for differences in the proportion of each color morph at each water-depth zone (Miller 1981: 219). Of 15 cases tested, only 3 were significantly different: medium and high zones at Lower Klamath NWR and the low zone at Upper Klamath Lake.

The data support the hypothesis that light-phase Western Grebes feed farther from shore than dark-phase birds. However, the data are not totally consistent and, thus, this question warrants further study.

The data do not support the hypothesis that light-phase Western Grebes feed at greater water depth than dark-phase birds. However, the data must be viewed with caution due to several confounding factors: (1) water-depth categories were not directly related to distance categories; (2) 3 of 5 study areas were artificial water impoundments with relatively little change in water depth throughout the water basin (with the exception of "borrow ditches" adjacent to dike roads); and (3) the depth categories were only relative to other measurements on the same lake. Future research should concentrate on natural water basins to minimize these factors. Unfortunately, however, nearly all of the sympatric breeding populations in the U.S. are on artificial impoundments. One notable exception is Upper Klamath Lake.

A general hypothesis can be developed from these data. Most natural water basins have the shallowest water zones adjacent to shore, and water depth increases with approach to the approximate center of the basin. Light-phase birds may have evolved behavioral patterns closely associated with water depth. Use of a particular water-depth zone commonly may occur at a fairly consistent distance from shore. Thus, distance from shore may be an environmental "cue" regarding water depth and niche partitioning between the color morphs. Reduced niche overlap may

limit competition for food resources, i.e. a "coexistence mechanism" (Cody 1974: 7). An alternative hypothesis is that niche partitioning is accomplished by spatial separation of near shore vs. farther from shore, and water depth and the evolution of "springing dives" are secondary to spatial factors. In either case, at artificial water impoundment areas where mean water depth is relatively similar (compared to natural water impoundments), distance from shore may influence spatial behavior of birds more than water depth.

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The Importance of Open Habitat to the Occurrence of Kleptoparasitism

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Direct competition among predatory birds for potential prey often is observed because of the large size of predator and prey, the often lengthy pursuit, and the open terrain in which many of these birds live. Such competition was brought to my attention vividly when I watched the interaction among four species of raptors over an open grassy prairie near Clewiston, Hendry County, Florida on 26 November

1961. A Merlin (*Falco columbarius*) flew rapidly over the prairie about 0.5 m above the ground and flushed two male Red-winged Blackbirds (*Agelaius phoeniceus*). It followed one blackbird closely until a male Northern Harrier (*Circus cyaneus*) rose from the prairie in front of them and struck at but missed the passing blackbird. The blackbird dropped to the ground and flew up again, and the Merlin forced it

down a few meters farther on. The harrier caught up with them and captured the blackbird on the ground, where it rested with its prey as the Merlin flew away.

The harrier then flew up without the blackbird and landed a short distance away, and an adult Red-tailed Hawk (*Buteo jamaicensis*) landed on the blackbird a few seconds later. The harrier presumably saw the other hawk approaching and relinquished its prey. The Red-tailed Hawk rested on the ground for a few minutes, but then it also flew up with the blackbird as two Crested Caracaras (*Polyborus plancus*) arrived from a distant palm clump and began to dive at it. The Red-tailed Hawk was joined by another Red-tailed Hawk, possibly its mate, and they flew away with the blackbird, the caracaras in pursuit. The two hawks and the pair of caracaras repeatedly dived at one another in flight until the Red-tailed Hawk with the blackbird landed about 1 km from the capture site and the caracaras flew away. I had lost sight of the second Red-tailed Hawk, the harrier, and the Merlin by that time.

This interaction involved six raptors of four species for about 10 min. The first three species were vying for possession of the prey, but the caracaras may have been displaying interspecific territoriality (Newton 1979: 45) or aggression toward potential predators. Caracaras may nest during November in Florida (Kale 1978), and the catholic food habits of Red-tailed Hawks (Craighead and Craighead 1956) make them possible predators of nestlings. All of these raptors have been reported as kleptoparasites (Brockmann and Barnard 1979). Most reports of kleptoparasitism involve two species, but Bent (1938: 133) cited a report of a crow (*Corvus* sp.) taking a mouse from a Northern Harrier and losing it to a Crested Caracara.

The succession of interspecific interactions probably was determined by size, with the Red-tailed Hawk (1,220 g) dominant to the Northern Harrier (530 g), which was dominant to the Merlin (215 g; mean female weights from Newton 1979). Birds are not the primary prey of either Red-tailed Hawks or harriers (Craighead and Craighead 1956); therefore, pursuit by the Merlin and capture by the harrier made the blackbird more accessible to the larger species. The rapid reaction of the larger raptors indicates that avian predators are often aware of the activities of other predators.

Brockmann and Barnard (1979) enumerated six ecological conditions facilitating the evolution of kleptoparasitism: (1) large concentrations of hosts; (2) large quantities of food; (3) large, high-quality food items; (4) predictable food supply; (5) food visible; and (6) shortage of food. I believe their "food visible" condition is a consequence of another important condition, the openness of the habitat in which both the host and the parasite live. The openness condition has four effects: (1) potential and actual hosts can be watched, even continuously, at a longer distance; (2) capture and carrying of prey is visible for

a longer distance; (3) hiding from kleptoparasites is difficult or impossible; and (4) prey items can be found easily after they are relinquished by the host. The following observations support each of these conclusions.

(1) Kleptoparasites can observe and follow hosts more easily in open habitats. African Fish Eagles (*Haliaeetus vocifer*) were important kleptoparasites on Goliath Herons (*Ardea goliath*, Mock and Mock 1980), and it may have been the eagles' ability to observe several hunting herons simultaneously that made food stealing a successful strategy (S. Carroll pers. comm.). In Washington I have observed most migrant Parasitic Jaegers (*Stercorarius parasiticus*) near flocks of their host species, Bonaparte's Gulls (*Larus philadelphia*) and Common Terns (*Sterna hirundo*). Laughing Gulls (*Larus atricilla*) and Heermann's Gulls (*Larus heermanni*) follow Brown Pelicans (*Pelecanus occidentalis*) as the pelicans forage and attempt to take prey from each successful pelican (Anthony 1906, Schnell et al. 1983). Similarly, I watched six Laughing Gulls follow two Great Egrets (*Casmerodius albus*) that were foraging on a sand flat in Florida. Although I did not observe the egrets capture prey, it seemed clear that the gulls were attending the egrets for possible kleptoparasitism.

(2) Kleptoparasites can observe prey capture and carrying more easily in open habitats. The Red-tailed Hawk that took the blackbird from the harrier (discussed above) was not visible to me when the interaction began and seemingly flew from a distance, perhaps beginning its approach as the Merlin chased the blackbird. Similarly, I have seen Parasitic Jaegers that were in cruising flight suddenly accelerate to harass a gull or tern with prey as far as 0.5 km away. Clearly, the visibility of prey is directly related to the openness of a specific habitat, an important variable to birds with long-distance vision.

(3) Hosts are less able to hide from kleptoparasites in open habitats. Furness (1978) found that Parasitic Jaegers were more successful in taking prey from a species of gull and a species of tern (33–44% of chases successful) than from three species of alcids that could dive to escape (11–21% successful). The ability of the host to "hide" was important in determining the success of these kleptoparasitic attempts. Similarly, Atlantic Puffins (*Fratercula arctica*) gave up their prey in 51% of kleptoparasitic attempts by Parasitic Jaegers when flying over land and only 22% of similar attempts when above the sea, where they could dive or descend to the surface (Andersson 1976). I rarely saw an intended host escape with its prey during many observations of Parasitic and Pomarine (*Stercorarius pomarinus*) jaegers kleptoparasitizing gulls and terns at sea. These birds can neither dive below the surface nor escape to the relative safety of a breeding colony. For the majority of these observations, only those birds that swallowed prey during the chase were able to retain it.

(4) Relinquished prey items can be found by kleptoparasites more easily in open habitats. Andersson (1976) observed that Parasitic Jaegers secured 15 of 18 items dropped by Atlantic Puffins. Although I have few recorded data, my impression after many years of watching jaegers with their many host species is that prey items dropped by hosts are rarely lost by jaegers. Most fish probably are disabled during the time it takes the parasite to force the host to drop them and are unlikely to escape the parasite. This is certainly true for a fish carried by a bird to feed its young.

Brockmann and Barnard (1979: 494) stated that "habitat as well as the behavior of the host may affect its chances of being parasitized," but they did not specify openness of habitat and overwater foraging as important considerations. Further, they suggested that "mixed colonies of fishing birds provide the ideal environment for kleptoparasitism with a plentiful supply of food items which are easily stolen" (Brockmann and Barnard 1979: 498) but did not mention that the major groups of marine kleptoparasites (frigatebirds, jaegers, and gulls) often display this behavior while away from these colonies. This is a reasonable oversight, because the best-known kleptoparasite, the Parasitic Jaeger, has been studied at seabird colonies in the north Atlantic rather than in the north Pacific, where it is a predator on its breeding grounds (Maher 1974) and a kleptoparasite at sea.

Although most seabirds use open habitats, raptors also can be used to test the hypothesis that openness of habitat is an important factor leading to kleptoparasitic behavior. The prediction is that raptors of open country are likely to be kleptoparasites while those of woodland are not. I used the list of kleptoparasitic raptors presented by Brockmann and Barnard (1979), with the addition of *Falco sparverius* as a kleptoparasite (S. Carroll pers. comm.), to test the hypothesis. The categorization is my own, based on extensive experience with all species on the list and information summarized by Brown and Amadon (1968). Of 22 North American falconiforms that forage primarily in open country, 10 (marked with asterisks) are known to be kleptoparasites: *Coragyps atratus*, *Cathartes aura**, *Gymnogyps californianus*, *Pandion haliaetus*, *Elanus caeruleus*, *Rostrhamus sociabilis*, *Ictinia mississippiensis*, *Haliaeetus leucocephalus**, *Circus cyaneus**, *Parabuteo unicinctus*, *Buteo swainsoni*, *B. albicaudatus*, *B. jamaicensis**, *B. regalis*, *B. lagopus**, *Aquila chrysaetos*, *Polyborus plancus**, *Falco sparverius**, *F. columbarius**, *F. peregrinus**, *F. rusticolus*, and *F. mexicanus**. However, none of the following 10 species, which forage primarily within forest and woodland in the same region, displays this behavior: *Elanoides forficatus*, *Accipiter striatus*, *A. cooperii*, *A. gentilis*, *Bu-*

teogallus anthracinus, *Buteo nitidus*, *B. lineatus*, *B. platypterus*, *B. brachyurus*, and *B. albonotatus*. The difference between these two groups is significant (Fisher's exact test, $P = 0.01$).

I believe the observations presented here support what is an intuitively reasonable hypothesis, even though a bias is introduced by humans being able to detect kleptoparasitic interactions more easily in open terrain.

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Adaptations of Black Tern (*Chlidonias niger*) Eggs for Water Loss in a Moist Nest

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Eggs of Black Terns (*Chlidonias niger*) are laid in damp, spongy nests 3–5 cm above water line. The daily mass loss of 31 tern eggs in their nests was 70.9 ± 20.3 mg/day (mean \pm SD), resulting in a 14.7% loss of mass during the 22-day incubation period. Eggshell water vapor conductance was 28.13 ± 7.52 mg·day⁻¹·kilopascal (kpa)⁻¹, a value 1.5 times greater than predicted for bird eggs with similar mass and incubation period and 1.4 times greater than predicted for other tern eggs in particular.

The increased eggshell conductance, relative to other eggs laid in drier circumstances, is the result of an increased number of pores in the shell. The water vapor conductance per pore of the Black Tern egg is not significantly different from the pore conductance of eggs of 7 other tern species and of eggs of other bird species. This observation is consistent with the argument that all bird eggs may have a similar water vapor conductance per pore (Ar and Rahn 1979). The adaptation of shell conductance to a humid nest microclimate is accomplished by increasing the number of pores in the shell rather than by altering the ratio of pore surface area to pore length.

Favorable conditions for the development of avian embryos are achieved through species-specific combinations of nest-site selection, nest construction, parental behavior, and eggshell structure. Eggs must be maintained at a high, relatively constant temperature throughout incubation (Drent 1970, 1975; White and Kinney 1974). In addition, the rate at which the eggs lose water is regulated so that total mass loss during incubation amounts to between 10 and 20% of initial egg mass (Ar and Rahn 1980). Egg temperature and water loss are intimately related. If a typical bird egg is to lose an appropriate fraction of its mass, its average temperature must exceed 35°C (Ackerman and Seagrave 1984) and, on the average, the vapor pressure difference between the inside and the outside of the eggshell must be about 3.33 kpa (Rahn and Ar 1974). Because the vapor pressure inside the egg is fixed by the egg temperature, systematic variation in the nest vapor pressure so as to alter the vapor pressure difference away from 3.33 kpa must be compensated for by changes either in egg temperature or in the eggshell water vapor conductance. Pied-billed Grebe (*Podilymbus podiceps*) eggs incubated in wet, floating nests lost 16% of their initial mass. Egg water loss in a humid microenvironment occurs because the eggshell water vapor conductance of the grebe egg is 2.7 times higher than eggs of similar mass and incubation period in dry nests (Davis et al. 1984).

Black Terns belong to a family of birds (Laridae) that may be characterized as nesting on dry substrate

(Harrison 1975, Rahn et al. 1976). However, Black Terns build crude, spongy nests of algae and bits of damp plant material on floating mats of vegetation (Provost 1947, Cuthbert 1954, Weller and Spatcher 1965, Bergman et al. 1970). The location and construction of the nests may produce a microclimate around the eggs that is more humid than that found in dry nests (Rahn et al. 1976). Vleck et al. (1983) reported that some species of terns and herons nesting on the ground appear to have a higher nest humidity than other similar species nesting in trees. However, the floating, moist nest of Black Terns should have a nest microclimate that is even more humid than the exposed scrapes of sand or gravel used as nests by most other species of ground-nesting terns. This should decrease the water vapor concentration difference between the inside and the outside of the egg and, therefore, either an increased egg temperature or an increased eggshell conductance is expected if Black Tern eggs are to lose about 15% of their initial mass during incubation. On the other hand, Black Tern eggs may lose less water during incubation than other tern and other bird eggs.

Black Tern eggs and nests were studied in marshes near West Lake Okoboji, Dickinson County, Iowa. The nests were found by searching likely areas in May and June. The brown-spotted eggs were marked with white waterproof ink and weighed every 3–4 days to obtain daily mass loss (\dot{M}_{H_2O} : mg/day). Nests were revisited until hatching occurred. Egg mass was measured with either a 30-g Pesola spring balance (to 0.1 g) or a Torbal torsion balance (to 0.02 g). The calibration of the balances was checked against a set of standard weights. Eggs found in nests floating over deep water were weighed with a torsion balance in a boat using the apparatus described in Fig. 1.

Eggs of various ages were collected from tern nests during the first half of the incubation period. The water vapor conductances (G_{H_2O} : mg·day⁻¹·kpa⁻¹) of these eggs were measured in desiccators over silica gel at 25°C (Ar et al. 1974). Subsequently, the initial mass of the eggs was estimated by injecting the air cell with distilled water and weighing the eggs in air (Grant et al. 1982). Dimensions of the eggshells were measured thereafter. Pores in the eggshells of Black Terns were counted according to methods described by Rahn and Hammel (1982) and Davis et al. (1984). The area of the eggshell was estimated using the equation for surface area as a function of initial mass presented by Paganelli et al. (1974).

The mean \dot{M}_{H_2O} of Black Tern eggs in the nest was 70.9 ± 20.3 mg/day ($n = 33$, Table 1), which resulted in a $14.7 \pm 1.85\%$ loss of initial mass during incuba-

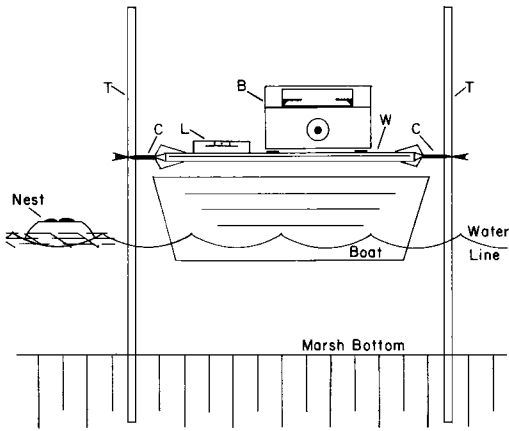


Fig. 1. Apparatus for weighing eggs found in nests floating over deep water. Two 3-m long, 2-cm diameter sections of galvanized conduit tubing (T) are pushed into the marsh bottom, with one on each side of the boat. A three-fingered thermometer clamp and a screw clamp (C) attach the wood plank (W) to the tubing. The clamps can be adjusted vertically and horizontally. The wood plank, which acts as the measurement table, is leveled by a small carpenter's level (L). The torsion balance (B) is placed on the plank, and measurements are made. The balance was calibrated in the laboratory before each field measurement.

tion. The mean G_{H_2O} of the eggs analyzed in this study was $28.12 \pm 7.52 \text{ mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1}$ ($n = 31$, Table 1). No systematic change in G_{H_2O} was observed with time of measurement. An average of 114 pores/cm² of shell surface, or 2,622 pores/egg, was counted (Table 1). The average G_{H_2O} , $28.12 \text{ mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1}$, was divided by the total number of pores to obtain a G_{H_2O}/pore of $1.07 \times 10^{-2} \text{ mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1} \cdot \text{pore}^{-1}$. Internal egg temperature averaged $34.5 \pm 2.1^\circ\text{C}$ ($n = 3$).

Black Tern eggs are incubated just above water line in damp, spongy, floating nests. The eggs lose $14.7 \pm 1.85\%$ ($n = 11$) of their initial mass during incubation and appear to follow the general rule that all bird eggs lose about 15% of their initial mass during incubation. Rahn et al. (1976) reported an average incubation water loss of $14.3 \pm 1.38\%$ for 7 other tern species. Thus, water loss by Black Tern eggs is similar to that of other tern eggs.

The G_{H_2O} for avian eggs with a mass of 10.6 g and an incubation period of 22 days can be estimated to be $18.57 (\pm \text{SEE } 8.87) \text{ mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1}$ using the equation (Ar and Rahn 1978):

$$G_{H_2O} = 38.54 W/I, \quad (1)$$

where W = initial mass (mg) and I = incubation period (days) and the units of G_{H_2O} have been converted to $\text{mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1}$.

TABLE 1. Initial mass (M), average daily water loss in the nest (M_{H_2O}), water vapor conductance (G_{H_2O}), egg dimensions, and shell characteristics of Black Tern eggs. Water vapor conductance is expressed as an average value of all individual eggs measured. All values are expressed as means \pm SD (sample sizes in parentheses). G_{H_2O} , expressed as kilopascals (kpa), was converted from units in torr, where 1 torr = 0.133 kpa.

M (g)	10.62 ± 0.37	(15)
Average M_{H_2O} (mg/day)	70.9 ± 20.3	(33)
Average G_{H_2O} ($\text{mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1}$)	28.12 ± 10.50	(31)
Incubation period (days)	22.1 ± 1.2	(10)
Egg length (cm)	3.48 ± 0.12	(7)
Egg width (cm)	2.44 ± 0.04	(7)
Egg volume (cm ³)	10.04 ± 0.37	(7)
Shell area (cm ²)	23.10 ± 0.53	(7)
Shell thickness (mm)	0.13 ± 0.008	(7)
Pores/egg	$2,622 \pm 338$	(10)
Pores/cm ² of shell surface	144 ± 16	(10)

The measured G_{H_2O} of Black Tern eggs, 28.12 ± 7.52 ($n = 31$), is 1.5 times the value reported for other birds with similar egg mass and incubation time. Although the water vapor conductance is not statistically different from the predicted value, this lack of significance is likely to be misleading because the equation used to predict G_{H_2O} (Eq. 1) was generated from data collected from eggs of many different bird species found in a wide variety of nesting conditions. Thus, eggs that may be adapted to widely divergent conditions of nest humidity have been treated collectively. It is important to note that if the Black Tern egg was characterized by a typical egg conductance ($18.57 \text{ mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1}$), we estimate the water loss to be 9.7% of initial egg mass. This value falls outside the 95% confidence interval for terns in general ($14.0 \pm 2.0\%$; see Rahn et al. 1976: Table 5) and for Black Terns in particular ($14.7 \pm 3.7\%$). If the Black Tern egg was characterized by a water vapor conductance at the lower 95% confidence limit of the estimate (Eq. 1; $9.7 \text{ mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1}$), then the water loss of the egg in a Black Tern nest would be only 5% of initial mass.

The G_{H_2O} of an avian eggshell is proportional to the number of pores in the shell. The predicted number of pores (N) in the Black Tern eggshell can be estimated to be 1,696 pores/egg using the equation of Rahn and Ar (1980):

$$N = 3,520 W/I, \quad (2)$$

where W = initial mass (mg) and I = incubation period (days). The Black Tern eggshell contains 2,622 pores/egg, which is an average of 114 ± 16 pores/cm² of shell surface (Table 1). This may be compared to 84 ± 14 pores/cm² reported for 9 other tern species (H. Rahn pers. comm.). Thus, Black Tern eggs have about 30 more pores/cm² of eggshell surface than similar-size eggs of other terns. Another wet-nesting

species, the Pied-billed Grebe, also has increased the number of pores per unit of eggshell surface of its egg (Davis et al. 1984).

The conductance per pore ($\text{mg H}_2\text{O} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1} \cdot \text{pore}^{-1}$) may be calculated by dividing the $G_{\text{H}_2\text{O}}$ of the egg by the number of pores:

$$G_{\text{H}_2\text{O}}/N = 1.07 \times 10^{-2} \text{ mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1} \cdot \text{pore}^{-1}. \quad (3)$$

The pore conductance (95% confidence interval = 0.08) is not significantly different ($F = 1.05$) from values reported for 9 other tern species ($1.17 \times 10^{-2} \pm 0.12 \times 10^{-2} \text{ mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1} \cdot \text{pore}^{-1}$; H. Rahn pers. comm.). The Pied-billed Grebe had a $G_{\text{H}_2\text{O}}/\text{pore}$ of $1.05 \times 10^{-2} \pm 0.24 \times 10^{-2} \text{ mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1} \cdot \text{pore}^{-1}$ (Davis and Ackerman 1983), which also is not different from the Black Tern. The averaged $G_{\text{H}_2\text{O}}/\text{pore}$ for 107 species of birds is $1.20 \times 10^{-2} \pm 0.45 \times 10^{-2} \text{ mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1} \cdot \text{pore}^{-1}$ (Ar and Rahn 1979). These results suggest that avian species examined until now have essentially the same water vapor conductance per pore. As Rahn and Ar (1974) have shown, one can derive a relationship between the average $G_{\text{H}_2\text{O}}/\text{pore}$ and the shell structure by rearranging the equations:

$$G_{\text{H}_2\text{O}} = (Ap/L) \cdot (D_{\text{H}_2\text{O}}/RT) \quad (4)$$

and

$$Ap = N\pi r^2, \quad (5)$$

where $G_{\text{H}_2\text{O}}$ = water vapor conductance ($\text{mg} \cdot \text{day}^{-1} \cdot \text{kpa}^{-1}$), Ap = total pore area (cm^2), L = shell thickness (cm), $D_{\text{H}_2\text{O}}$ = diffusion coefficient for water vapor (cm^3/s), R = gas constant, T = absolute ambient temperature ($^\circ\text{K}$), N = number of pores per egg, and r = pore radius (cm). If we rearrange Eqs. 4 and 5, a relationship between water vapor conductance per pore, cross-sectional area, and length of the pore may be derived:

$$(G_{\text{H}_2\text{O}}/N) \propto (\pi r^2/L). \quad (6)$$

Because shell thickness increases with increasing egg mass (Ar et al. 1974), the cross-sectional area of the pore must increase at the same rate. This ratio is 0.73 μm for 107 species of birds (Ar and Rahn 1979). Adaptation of avian eggshells to environmental conditions has been accomplished by selecting for numbers of pores in the eggshells rather than for a geometrical ratio of pore radius to pore length.

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Energetics of Free-living Nestling House Finches: Measurements with Doubly Labeled Water

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The total energy metabolism of nestling birds consists of anabolism (the building of body substance) and catabolism (metabolic heat production). Although anabolism has been measured directly as the accumulation of energy in body tissues with time (see Ricklefs 1974), most estimates of nestling catabolism have relied upon extrapolations of laboratory measurements of standard metabolism (based on oxygen consumption) to field conditions. An alternative to the latter technique uses doubly labeled water (DLW) to monitor directly the CO₂ production of nestlings in their natural physical and social environment. We have determined the total energy metabolism of free-living nestling House Finches (*Carpodacus mexicanus*) using DLW. Although the DLW method provides reliable measurements of CO₂ production and water flux in adult birds (see Nagy 1980, Nagy and Costa 1980, Williams and Nagy 1984), it has yet to be validated for use with growing animals. There is potential for error when DLW is used with rapidly growing animals. In growing animals, the total body water volume in which isotopes equilibrate changes regularly as mass changes. If the changes in body water volume are extreme, errors in calculation of isotope turnover can result (see Nagy 1980, Nagy and Costa 1980). In the present study, nestlings averaged 74% of adult mass, a size typically associated with a declining growth rate (Ricklefs 1969). In fact, nestling water volumes increased by <10% initial volume in our study. Such a change is within the limits that theoretically should permit accurate calculation of turnover rates (Nagy 1980, Nagy and Costa 1980). Therefore, we suspect that for nestlings of this size, errors in the DLW method should

be small. However, in the absence of direct validation of the DLW method, our results must be regarded as preliminary.

All nestlings used in this study occupied natural nests constructed in and around buildings at the University of California's Philip L. Boyd Deep Canyon Desert Research Center near Palm Desert, California. All measurements were made in May 1980. Thirteen nestlings from 4 nests were studied. Mean nestling mass at the time of isotope injections (see below) was 15.0 ± 0.4 g ($\bar{x} \pm SE$) and did not differ between nests ($F = 1.93, P = 0.19$). Eight nestlings from 2 nests received intramuscular injections of tritiated water only (0.1 ml, containing 50 $\mu\text{Ci } ^3\text{H}$), and 5 nestlings from 2 other nests received DLW (0.1 ml, containing 50 $\mu\text{Ci } ^3\text{H}$ in 95 atoms % ¹⁸O-enriched water). These injection solutions provided sufficient isotope activity to assure final activities of both ³H and ¹⁸O that did not approach background activity after 48 h (general guidelines for suggested activities of injected isotopes are given in Nagy 1983).

Following injections, labeled nestlings were returned to their nests for 1 h to allow isotope equilibration in body water. At 1, 25, and 49 h postinjection, nestlings were removed from their nests and weighed. Blood (50 μl) was then drawn from a brachial vein, and nestlings were returned to the nest. Blood samples were stored in flame-sealed, refrigerated microhematocrit tubes until returned to the University of California, Los Angeles, for analysis. Blood was distilled according to procedures in Wood et al. (1975). Tritium activity of the distilled water samples was assayed by liquid scintillation spectroscopy (Beckman LS-230). Oxygen-18 was assayed using the proton-activation technique of Wood et al. (1975). Gamma emissions of the resulting fluorine-18 were quantified with a Packard-Gamma Rotomatic system. Carbon dioxide production and water influx were calculated using equations in Nagy (1980, 1983)

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and Nagy and Costa (1980). In all but 4 cases, rates represent means based on 48-h observation periods. The exceptions are 3 instances where ^3H -labeled nestlings disappeared between the 25-h and 49-h samples, and 1 instance where the volume of the final blood sample drawn from a doubly labeled nestling was too small to allow ^{18}O analysis. For these cases, calculated rates were based on the initial 24-h periods.

Mean water influx of 11 nestlings was 343.3 ± 11.6 ml $\text{H}_2\text{O} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$, or $\sim 42\%$ of the total body water pool per day (based on a body water volume of 72.7% of carcass wet mass determined by oven drying at 70°C). This influx rate is 66% of the rate reported for Savannah Sparrow (*Passerculus sandwichensis*) nestlings (Williams and Nagy pers. comm.). Measurements on these two species represent the only available data on H_2O influx in free-living nestlings. The nestling House Finch influx rate is 83% of that predicted for a 15-g adult bird in captivity (416 ml $\text{H}_2\text{O} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$; Degen et al. 1982), which, unlike nestlings, would have access to drinking water.

Labeled nestlings produced 4.17 ± 0.15 ml $\text{CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ($n = 5$), which is equivalent to ~ 37 kJ/day (assuming 24.66 J/ml CO_2 for a mixed seed diet; Weathers and Nagy 1984). Nestlings gained 1.6 ± 0.3 g wet mass during the 2-day measurement period. Energy allocated to growth can be determined from these mass changes if carcass energy content is known. Because nestlings were not killed at the conclusion of our study, we did not measure energy contents. However, altricial passerines display characteristic changes in body energy content during the course of their development (Ricklefs 1974). We used data for a representative passerine, the Rufous-winged Sparrow (*Aimophila carpalis*, Ricklefs 1974), to estimate that House Finch nestlings contained 6.3 kJ/g wet mass, and that they accumulated 10.1 kJ in body energy during the 2-day study period. This is 14% of total energy metabolized by nestlings. During our 2-day observations, nestlings averaged 15.8 g, 77% of the adult mass (20.4 g, Weathers 1981). Ricklefs (1974: Fig. 26) predicted that, for a hypothetical small nestling sparrow at 77% of adult mass, growth should equal $\sim 40\%$ of total metabolic rate—nearly 3 times the value we observed. Ricklefs ignored the cost of thermoregulation and activity in developing his model, however, and this probably accounts for most of the discrepancy.

With this information, we can estimate the rate at which the parent finches supplied metabolizable energy to a nest containing 3 large nestlings. A single nestling metabolized 37 kJ/day and invested 5 kJ/day into production of new body tissue, for a total of 42 kJ/day. Three 15-g nestlings thus would receive 126 kJ/day of metabolizable energy as food provided by their parents. For comparison, we predicted daily energy expenditure of an adult weighing 20 g to be 81 kJ/day using Walsberg's (1983) equation (#10) for birds that do not forage in flight. Walsberg's equa-

tion was derived from data for breeding and non-breeding birds, so it may underestimate energy expenditure of adult birds feeding large nestlings. However, similar-sized Savannah Sparrow females (17.3 g) feeding 5-day-old nestlings metabolized only 68 kJ/day (Williams and Nagy pers. comm.). Either estimate indicates that the food requirement of 3 large nestling finches is about equivalent to that of 1.5 adult finches. If both adults share equally in feeding the nestlings, then each adult would need to gather about 1.75 times as much food each day as it would need for self-maintenance alone. Hence, adult House Finches feeding large nestlings must capture food at a rate nearly twice that of nonbreeding adults.

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The First Record of *Locustella lanceolata* for North America

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An unprecedented passage of Lanceolated Warblers (*Locustella lanceolata*) occurred in June and July 1984 on Attu Island (52°49'N, 173°10'E) in the western Aleutian Islands, Alaska. At least 25 individuals of this eastern palearctic species were recorded on the southeast perimeter of Attu Island from Massacre Bay to Temnac Valley, 4 June to 15 July. Although observers were present on Attu into September, no warblers were observed after 15 July. The maximum one-day count was 11 birds on 8 June. Two or 3 adjacent singing males in several locations established "clustered" territories. Most individuals were observed within the *Elymus arenarius*-*Heracleum lanatum*-dominated community of the upper beach terrace; a few birds sang inland in *Salix* thickets. One territorial bird was observed carrying dried blades of *Elymus* on 9 June. These warblers typically sang from dawn (0600) to midday (1400) and from 2300 to 0200. Photographs of several of these warblers are on file at the University of Alaska Museum. An adult male was collected on 9 June (UAM 5005, 13.3 g, light to moderate fat in the furcula, left testis 8.5 × 5.0 mm, right testis 8.25 × 5.75 mm). It was actively singing from a defended territory adjacent to a second male's territory. Both territories were 30 m from the upper edge of sand beach, in *Elymus* and *Heracleum* on the north shore of Casco Cove.

Monotypic *Locustella lanceolata* breeds in northern Asia from the Urals to Kamchatka, the Kurile Islands, and northern Japan, and it winters across most of southern Asia from India to the Andaman and Greater Sunda islands and the Malay Peninsula (Vaurie 1959). This record appears to be the first east of central Kamchatka (Dement'ev and Gladkov 1954).

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Differential Distribution of Wintering Brant by Necklace Type

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Abraham et al. (1983) demonstrated that positive assortative mating by necklace type, the white feather pattern around the neck, occurs among Brant (*Branta bernicla hrota*) breeding at East Bay, Southampton Island, N.W.T. They also suggested that differential distribution of Brant by necklace type also may occur on the wintering grounds. We tested the "differential distribution" hypothesis by collecting Brant on three major wintering areas along the Atlantic Coast: 1) Nassau County, Long Island, New

York; 2) Cape May County, New Jersey; and 3) Chincoteague National Wildlife Refuge and near Folley Creek, Accomac County, Virginia (Smith et al. 1985). Brant were shot in bays and estuaries in the three locations, except for 18 birds that were cannon-netted on golf courses on Long Island. Collections were made during a 2-week period in late January 1984 so that Brant movements among the three locations were minimal.

Upon collection, sex and age were determined for each bird (Penkala 1977, Kirby et al. 1983) and necklace type was scored (by LDV) according to the system of Boyd and Maltby (1979). The completeness of the necklace was scored with birds "in hand" as: ½ = very incomplete, 1 = incomplete front and back, 1½ = incomplete either front or back, or 2 = white necklace completely encircles neck. In May 1984, approximately 700 Brant died on a Long Island golf course

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as a result of diazinon poisoning. One hundred of these birds were obtained from the New York Department of Environmental Conservation. Age, sex, and necklace type were determined for 41 of these birds. This sample of Brant allowed us to compare necklace type frequencies in New York during the spring migration with necklace type frequencies in New York when Brant movements were minimal (January 1984). Data on necklace type also were collected (by LDV) from the breeding grounds on Baffin Island, N.W.T.

The sexes were combined for the following necklace-type analysis because the proportions of New Jersey males (8/28) and females (3/13) with the necklace type 1½ were not different ($Z = 0.24, P > 0.50$). Differential distribution of Brant by necklace type occurred among the three locations during January 1984. The proportion of Brant with necklace type 1 was not different between New York and Virginia ($Z = 0.575, P > 0.20$), but the proportion of Brant with necklace type 1 did differ between New Jersey and New York ($Z = 3.28, P < 0.001$) and New Jersey and Virginia ($Z = 2.21, P < 0.03$). These differences occurred because, during January, only Brant in New Jersey had necklace type 1½. However, by May 1984, when migratory movements were occurring, Brant with all necklace types appeared in the New York sample (Table 1). The distribution of necklace types in New York during May was different from that in New York during January ($Z = 3.67, P < 0.005$).

In contrast to our results, Abraham et al. (1983) reported no difference in necklace type composition of Brant wintering in New York (116/177 had necklace type 1) and New Jersey (191/260 had necklace type 1). No necklaces of type 1½ or 2 were observed (Ken Abraham pers. comm.). The difference between our results and those of Abraham et al. (1983) suggests that the scoring methods differed. Brant scored by LDV were scored "in hand," while those scored by Abraham et al. (1983) were scored from a distance (Ken Abraham pers. comm.). The scoring system we used was based *only* on the completeness of the necklace and did not incorporate the height (i.e. area) of the white necklace, while the scoring method of Abraham et al. (1983) incorporated both the completeness and amount of white present. Boyd and Maltby (1979) measured the completeness and the height (i.e. area) of the necklace separately. They found no difference between the sexes in the completeness of the necklace, as we did, but they did find a difference between the sexes in the height of the necklace, as did Abraham et al. (1983). Scoring necklace type from a distance may have resulted in Abraham et al.'s (1983) failure to detect the 1½ and 2 necklace types. Their scoring method, which combined the completeness measure and the height measure, also would result in an overestimate of the number of ½'s in the population when compared to the estimate obtained using the completeness measure only.

TABLE 1. Frequency distribution of necklace types of Brant from three wintering locations.

	½	1	1½	2
Virginia (January)	0	13	0	0
New Jersey (January)	1	29	11	0
New York (January)	1	39	0	0
New York (May)	2	27	10	2

Data on necklace type variation on the breeding grounds also suggest that our scoring method differed from that of Abraham et al. (1983). Brant nesting at East Bay, Southampton Island, N.W.T. had necklace types of either ½ or 1 and no 1½ or 2 types were recorded (Abraham et al. 1983). Data on necklace type variation collected by us at the Dewey Soper Migratory Bird Sanctuary, Baffin Island, N.W.T. in August 1984 had all necklace types present (½ = 6%, 1 = 80%, 1½ = 12%, 2 = 2%; $n = 50$). Data collected by Boyd and Maltby (1979: Fig. 3) on Brant breeding around the Foxe Basin (i.e. *Branta bernicla hrota*) also show necklace type 1½ to be present. Boyd and Maltby's (1979) data also show that Brant with darker belly color (i.e. *Branta bernicla nigricans*) tend to have a necklace that has greater height but is less complete, while Brant with lighter belly color (i.e. *Branta bernicla hrota*) tend to have a necklace that has less height but tends to be more complete.

The presence of Brant with necklace type 1½ on breeding areas and their absence from Long Island wintering areas suggests that Brant from certain breeding areas may be represented disproportionately in certain wintering locations.

Thus, differential distribution of Brant by necklace type may occur on wintering areas, and different nesting areas may contribute birds differentially to certain wintering locations. However, data are needed on the movements of wintering Brant to determine when groups are most stable or have reached their terminal wintering area, if one exists. This will allow determination of optimal times to sample population characteristics such as necklace type. Indeed, results indicate that necklace type frequency varies with season. These data, in conjunction with data on the chronology of pair formation, will provide the information needed to evaluate questions concerning breeding populations and segregation on the wintering grounds. Segregation of breeding populations during winter has obvious implications toward the management of the highly fluctuating Brant populations on the Atlantic seaboard.

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Leg-band Color and Mortality Patterns in Captive Breeding Populations of Zebra Finches

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Color-banding is a research technique widely utilized to facilitate recognition of individuals and membership in "groups" such as age classes. Despite the fact that many species of birds routinely attire themselves in colorful plumes, the possibility that color-marking by humans may affect the social behavior of birds has hardly been considered (but see Bennett 1939, Goforth and Baskett 1965). Instead, it appears that researchers have proceeded largely on the tacit assumption that no such effects occur. Here I report that in long-term breeding experiments involving Zebra Finches (*Poephila guttata*), mortality patterns of birds varied with the color of the bands placed on them prior to the beginning of experiments.

The experiments reported here were conducted to investigate the significance of other results from my laboratory (Burley et al. 1982, Burley 1985), which indicated that Zebra Finches find certain colors of leg bands attractive when worn by opposite-sex individuals and find other colors unattractive. In those experiments, attractiveness was measured as the time test subjects spent associating with stimulus birds banded with one of several colors in relation to the time spent with unbanded birds. Attractive colors were those that test birds preferred, and unattractive colors were those test birds appeared to avoid, relative to their tendency to associate with birds wearing no color bands. The present experiments were designed primarily to explore the effects of altered attractiveness on reproduction.

Two experiments were performed. In one (the

Banded Male Experiment), adult males were banded, prior to their release into the experimental aviary, with one of the following colors: bright red (previously determined to be attractive to females), light green (unattractive to females), or orange (neutral with respect to the unbanded condition—adult Zebra Finches have orange legs). In the reciprocal experiment (the Banded Female Experiment), females were banded with black (attractive to males), light blue (unattractive to males), or orange (neutral). Randomization procedures were employed in assigning band colors. Color-banded birds wore one color band on each leg. In addition, each bird wore one uniquely coded aluminum band. (All bands were supplied by A. C. Hughes, Middlesex, England.) In the Banded Male Experiment, females were not color-banded, and males were not color-banded in the Banded Female Experiment.

All individuals were adults (5-11 months of age at the beginning of experiments) that had been placed in unisexual groups prior to sexual maturation and that, as a result, had no previous reproductive experience. All birds had wild-type plumage characteristics and appeared in excellent physical condition at the beginning of experiments. The founding populations of the two experiments came from identical sources.

Experiments were initiated by releasing 24 adults of the color-banded sex into an aviary; 1 week later, 24 opposite-sex individuals were added. Approximately 1 week later, nest sites and other resources needed for reproduction were made available in

abundance. Birds were permitted to breed continuously until the end of the experiment. During the first 6 months of each experiment, individuals that died were replaced by birds randomly selected from a "substitute" pool created for this purpose. Offspring were removed from aviaries 2–5 weeks after fledging. Additional methodological details are reported elsewhere (Burley MS).

The Banded Male Experiment ran for 22 months. During this time, 1 of 8 red-banded males, 3 of 9 orange-banded males, and 6 of 10 green-banded males died. One red-banded male was excluded from this analysis for technical reasons. He was in good health at the time of his removal and survived past the end of the experiment. The difference in incidence of mortality among color classes was clearly significant (Fisher 2×3 Exact Test, $P = 0.017$).

Unlike the Banded Male Experiment, the Banded Female Experiment consisted of several discrete phases. After the first 10 months of the experiment, color bands were removed from females, but the birds were allowed to continue breeding for 5 additional months. At that time, breeding was suspended by the removal of nesting sites, but the surviving adults remained in the experimental aviary for an additional 5 months. Within several days after the initiation of this experiment, 1 bird (a black-banded female) caught a band in the aviary netting and 2 birds became unable to fly. As a result, I removed 6 birds from the experiment (1 female from each color class and 3 males) and replaced them with birds from the substitute pool. These birds were excluded from analyses below.

During the 10 months in which females were color-banded, 1 of 10 black-banded females died, as did 4 of 11 orange-banded females and 9 of 14 blue-banded females. Mortality patterns varied significantly among color classes (Fisher 2×3 Exact Test, $P = 0.022$). For the entire 20-month timespan, trends remained identical: 4 of 10 black-banded females, 6 of 11 orange-banded females, and 10 of 14 blue-banded females died. This difference was not significant (Fisher 2×3 Exact Test, $P > 0.35$). However, a comparison of the relative "lifespans" (the number of days between release into the experiment and death) of the color classes indicated a strong and significant trend. Black-banded females that died survived an average of 425.4 days in the experiment, orange-banded females an average of 286.8 days, and blue-banded females a mean of 190.9 days. This difference was significant (Kruskal-Wallis test for analysis of variance by ranks, $H = 6.33$, 2 df, $P < 0.05$).

In both experiments, then, the color of bands applied to individuals affected survivorship. In most cases the specific cause of death was not ascertained, although autopsies were performed on a number of birds by the Department of Veterinary Pathology of the University of Illinois. Many birds that died dis-

played premortum declines in physical condition, including deteriorating feather condition, weight loss, changes in beak color, loss of balance, and the adoption of postures typical of ill birds.

The birds that died displayed a variety of symptoms, and it is fairly certain that they died from a variety of specific causes. Of greater interest here are the "general" causes, such as the nature of stresses that impaired physical capacity and increased risk of death. These include intraspecific interference competition, senescence, predation, accidents, and reproductive effort. Disease is not mutually exclusive with any of the above categories except accidental death, but there was no direct or circumstantial evidence to suggest that mortality patterns resulted from contagious diseases.

Most general causes of mortality can be excluded as *major* contributors in these experiments. Interference competition can be ruled out for two reasons. Only one bird (a male in the Banded Female Experiment) sustained noticeable injuries inflicted by other finches. Also, Zebra Finches are naturally gregarious and nonterritorial (Immelmann 1962). In these experiments they were maintained in large aviaries [density was about 1 adult/m³—less than half the density suggested by Immelmann (1965) as the desired maximum], and competition for resources was deliberately minimized by supplying nesting sites, nesting materials, and food in abundance.

Senescence is not a relevant factor. The potential lifespan of Zebra Finches is at least 5–7 years under these lab conditions; all birds were less than 3 years old at the time of death. For founders, there were no differences in age composition among color classes. Birds that were added as substitutes tended to be slightly younger than founders, but more substitutes were added in those classes with higher mortality rates.

I attempted to eliminate the possibility of predation. However, the building in which these experiments were performed was inhabited by house mice (*Mus musculus*), and 1 (black-banded) female was decapitated by a house mouse while she incubated at night. The small light that usually was left on (primarily to protect the birds from wing damage should there be a nocturnal disturbance) burned out on the night she was killed. Zebra Finches usually do not attempt to fly in the dark, and I believe she was vulnerable for this reason.

At least two deaths probably were "accidental," i.e. unrelated to the bird's physical condition. One of these was the black-banded female that was decapitated, and the other was an orange-banded male that succumbed after he became entangled by a leg band. In two other cases, apparently "accidental" deaths involved birds that displayed declining condition prior to death. A male in poor condition in the Banded Female Experiment hanged himself by a strand of

human hair that he was using for nest building. Hair was not provided purposefully to finches, but many nests contained at least a few strands, implying that the finches sought out those inadvertently shed by lab personnel. No other bird became entangled by hair. A red-banded male that had difficulty maintaining his balance drowned in a water bowl.

The remaining possible cause of mortality is stress resulting from reproductive effort. The fact that Zebra Finches are opportunistic breeders suggests that this is an important cause. They begin to breed rapidly upon encountering permissive conditions and produce clutches continuously and in quick succession as conditions permit (Keast and Marshall 1954, Serventy and Marshall 1957, Immelmann 1963). In their native habitats, future reproductive opportunities are often difficult to predict, and they often may sustain high risk of mortality when conditions are not favorable for reproduction (Finlayson 1932, Frith and Tilt 1959, Keast 1959, Immelmann 1963). Hence, Zebra Finches may stress themselves reproductively even under seemingly "unstressful" conditions afforded in the laboratory. To maximize longevity, it commonly is advised that breeders limit reproductive opportunities by withholding nest sites. Immelmann (1965), for example, advocated permitting pairs to rear no more than 4 clutches per year, although he noted their potential is much greater.

Reproductive stress may account for differences in mortality rates of color classes. Elsewhere (Burley MS) I hypothesize that, in species with biparental care, individuals adjust the parental investment they are willing to commit to a particular mate's offspring to affect their own mate-getting abilities. That is, unattractive individuals may incur a larger than average share (for their sex) of parental duties to obtain a mate that is superior to what they otherwise could acquire (see also Burley 1981). Unusually attractive individuals, on the other hand, should have no trouble acquiring superior mates, and they may restrict their investment (at their mates' expense), thus reducing their risk of mortality. This hypothesis (the Differential Allocation Hypothesis) predicts that attractive individuals should have lower per-offspring parental investment than unattractive individuals of the same sex. Mortality trends reported here are consistent with this hypothesis. Time-budget estimates of parental investment obtained by focal nest sampling procedures also are consistent with the hypothesis (Burley in prep.).

Limited evidence also suggests that the color-banded sex, in aggregate, sustained an increased rate of mortality. In my populations of non-color-banded birds, adult females generally appear to have a somewhat higher mortality rate than do adult males. However, in only a few cases do I have data for males and females that were obtained from identical source populations and were matched for age and prior re-

productive history. Moreover, mortality rate varies with housing conditions (especially density and diet provided) and whether or not birds are permitted to breed. To compare the incidence of mortality among nonbreeding birds, I selected matched cohorts of young adult males and females and housed them in separate but identical aviaries for 10 months. (Population density in these aviaries was about 10 times that of the Banded Male and Banded Female experiments.) During this interval, 2 of 52 males died, whereas 9 of 46 females died; this difference was significant ($\chi^2 = 5.373$, 1 df, $P < 0.025$).

A breeding population of non-color-banded birds was established and maintained for 10 months under conditions similar to those of the Banded Female and Banded Male experiments. Males and females in this population came from the same source, but from a different source than those used in the Banded Male and Banded Female experiments. Two of 26 males died during the experiment, whereas 7 of 28 females died. This difference was not statistically significant (Fisher 2×2 Exact Test, $P = 0.141$), but its trend is consistent with patterns obtained in other colonies. In the Banded Male Experiment, there was no evidence of a sex difference in rate of mortality: 10 of 28 males and 12 of 29 females died (Fisher 2×2 Exact Test, $P = 0.787$). Thus, it appears that banded males had a relatively higher than "typical" rate of mortality. In the Banded Female Experiment, females had a much higher rate of mortality: 20 of 35 females died, whereas 10 of 34 males died (Fisher 2×2 Exact Test, $P = 0.029$). Unfortunately, direct comparisons in mortality rates among the various breeding experiments involving banded and nonbanded birds cannot be made because birds came from different source populations and reproduced at different rates and for different lengths of time.

In sum, mortality rates of Zebra Finches in breeding populations are affected by leg-band color. Differential mortality of color types appears to result from differential parental investment by attractive and unattractive types. Results also suggest that the color-banded sex sustains an overall increased rate of mortality, but given the mortality patterns in my populations, a much larger sample would be required to demonstrate this conclusively.

The implications of these results for the technique of color-banding are disturbing. Color-banding has consistent, highly structured effects on the behavior (Burley et al. 1982, Burley 1985), reproductive patterns (Burley MS), and mortality patterns (this study) of one species of estrildid finch. How widespread such effects are is unknown and would be difficult to determine. I believe it would be very hard to clearly discern effects from data on uniquely marked birds, especially in field studies, where factors such as site fidelity and the identity of nonbreeding members of breeding populations often are poorly known and

where death typically is inferred from "disappearance" from or "nonreturn" to a study site. The situation is further complicated by lack of knowledge of which colors are "attractive" or "unattractive" in particular species under study and whether color-banding affects intrasexual or intersexual interactions.

I do not advocate that researchers abandon the use of color-banding. Some method of individual identification is necessary, or at least highly desirable, in studies on many topics of contemporary interest, and color-banding has many positive features. Also, using multiple colors on each bird may reduce the effects of color-banding. That is, if most birds wear a combination of attractive and unattractive colors, banding may constitute only an additional source of "noise" in a study rather than systematically affecting results.

The possibility of introducing systematic bias to results, however, can be minimized only if the process of assigning band colors is truly random. For this reason, I would caution against using particular colors to identify age class, study site or place of origin, parentage, or any other information. Both color and order of band combinations should be random, and colors that the phenotype of the species under study suggests may be particularly attractive to the opposite sex or very important in intrasexual interactions (e.g. Smith 1972) should be avoided altogether. I also would recommend avoiding particularly "stunning" band combinations [such as yellow-red-yellow or black-red-black on the legs of male Northern Cardinals (*Cardinalis cardinalis*)], despite their possible advantage of easy recognition. It would seem prudent to require multiple colors in each band combination (the number depending on colors available and the number of bands used per bird) to avoid creating extreme phenotypes. In this respect, I have found that female Zebra Finches are attracted to males that have had the entire exposed portion of their tarsometatarsi painted red even more than they are to males wearing only one red band on each leg (Burley 1985). Finally, the results of my research on Zebra Finches suggest that more detailed specification of the color-banding procedures employed in research may be warranted in scientific publications. The inconvenience involved in a thoughtfully designed banding scheme should be greatly outweighed by the reassurance that such a procedure minimizes the possibility of systematic bias caused by the birds' color sensitivity in general and their use of color for intraspecific communication in particular.

Color-banding is not the only method of identification that appears to have unanticipated and undesirable effects on bird survival and reproduction. Southern and Southern (1985), for example, recently have found that wing-tagged female Ring-billed Gulls (*Larus delawarensis*) experience considerable difficulty in obtaining mates at the beginning of the breeding season. Lensink (1968) reported that green neck bands

inhibit the reproduction of female Black Brant (*Bran-ta bernicla nigricans*); effects on males were not ascertained. Male Ring-necked Pheasants (*Phasianus colchicus*) that were neck-banded and tail-bobbed were found in association with females less often during the mating season than were males not so marked (Geis and Elbert 1956). Sayre et al. (1981) presented evidence indicating that radio-tracking devices have adverse short-term effects on courtship cooing in male Mourning Doves (*Zenaida macroura*). Longer-term effects of radio-tagging on behavior have been documented for male American Woodcock (*Scolopax minor*, Ramakka 1972). Collectively, these findings point to the need for systematic investigation of the possible effects of all marking procedures.

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Floating Populations of Female Tree Swallows

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A floating population is a surplus of nonbreeding individuals during the breeding season that are able and willing to establish a territory and breed if the necessary resources become available (Brown 1969). Floaters often are excluded from breeding due to competition for limited breeding resources. Floating populations of males have been reported for many bird species (e.g. Hensley and Cope 1951, Stewart and Aldrich 1951, Delius 1965, Watson and Jenkins 1968, Power 1975, Smith 1978, Rutberg and Rohwer 1980, Weatherhead and Robertson 1980), but there are relatively few reports of female floating populations (Watson and Jenkins 1968, Harris 1970, Knapton and Krebs 1974, Smith 1978, Hannon and Zwickel 1979, Saether and Fonstad 1981, Hannon 1983). One reason for this bias is that intrasexual competition for breeding opportunities tends to be very intense among males relative to females (Selander 1972). Intense competition among females would be expected in hole-nesting species, where populations are limited by the availability of suitable nest sites (Hollroyd 1975). If nest sites are limiting breeding opportunities, then females that are excluded from breeding may form a floating population. The purpose of this study was to estimate the extent and composition of female floating populations in a hole-nesting species, the Tree Swallow (*Tachycineta bicolor*). One-year-old female Tree Swallows have a distinct brown-blue subadult plumage, whereas older females have a blue adult plumage (Hussell 1983). This allows for a comparison of the proportion of one-year-old females in the breeding and floating populations.

The study was conducted during 1983 and 1984 at the Queen's University Biological Station, near Chaffey's Lock, approximately 50 km north of Kingston, Ontario. Two Tree Swallow populations were stud-

ied, both of which have been established for at least 5 yr. These appear to be 2 separate breeding populations, since only 2 out of 50 individuals that have been captured in the last 2 or 3 consecutive years are known to have moved between populations. One study site, the New Land (NL), was about 10 ha in size and consisted of several hay fields and two small ponds. The area was bordered by deciduous forest and was less than 1 km from open water. All nest sites were plywood nest boxes, and most were mounted on aluminum posts. The other study site, the Northeast Sanctuary (NES) of Lake Opinicon, was 10 km from the NL. Nest sites were distributed over approximately 5 ha of open, shallow water and consisted of both nest boxes and natural hollow stumps. The size of both populations increased between 1979 and 1981, but has remained stable since 1982. In May 1982, there were 54 breeding pairs in the NL and 30 pairs in the NES.

As an alternative to creating nesting opportunities by removing breeding females, we provided a surplus of nest boxes late in the season to attract females that had been excluded from breeding during May. Most females with nest sites had laid eggs by this time, so these females were not expected to be attracted to the new nest sites and prevent surplus females from settling. An attempt was made to band and individually color-mark all breeding females before erecting new boxes. Between 29 May and 16 June in 1983, 53 additional nest boxes were erected throughout the NL and NES (Table 1). In 1984, 45 new boxes were erected between 5 and 14 June. All new boxes were more than 15 m from existing nest sites, and were erected a few at a time to permit general observation of the activity around newly provided nest sites. The boxes were checked every 3-4 days

TABLE 1. Total number of boxes erected, number of available nest sites, and number of occupied nest sites early (before 1 June) and late (after 1 June) in the breeding season for the NL and NES study sites over two years.

	1983		1984	
	Early	Late	Early	Late
NL				
Total no. erected	81	38	78	32
No. available sites	63	45	61	34
No. occupied (%)	51 (81)	19 (42)	56 (92)	19 (56)
NES				
Total no. erected	46	15	43	13
No. available sites	37	19	35	14
No. occupied (%)	33 (89)	10 (53)	34 (97)	10 (71)

for signs of nesting. Nesting females were defined as those females that laid eggs. First-egg date was used to indicate the relative timing of nest initiation and occupancy.

The percentage occupancy of available nest sites was calculated to estimate the extent to which nest sites limited breeding. The percentage occupancy ranged from 81 to 97% early in the season and from 42 to 71% late in the season (Table 1). The total number of boxes in place is not an accurate indication of the number of available nest sites. Tree Swallows defend an area of approximately a 15-m radius around their nest site, and can defend more than one nest site within that area (Harris 1979, Robertson and Gibbs 1982). Therefore, nest sites that were less than 15 m from sites already occupied by breeding Tree Swallows were considered to be unavailable. Nest sites occupied by other species, such as Eastern Bluebirds (*Sialia sialis*), Common Grackles (*Quiscalus quiscula*), and European Starlings (*Sturnus vulgaris*), were discounted both early and late in the season. Nest sites unoccupied by 1 June were included as available nest sites after 1 June, since they represented potential nest sites for nonbreeding birds.

The number of females nesting late in the season, in either newly provided boxes or available original boxes, was used to estimate the relative size of the floating population that was present during the peak of the nesting activity in May. The proportion of ultimately nesting females that nested after 1 June in the NL was 27% (19/70) in 1983 and 25% (19/75) in 1984 (Table 2). In the NES, 23% of the nesting females bred after 1 June in both years (10/43, 10/44). The results for the two populations and two years were treated separately to examine the consistency of the floating populations. These estimates assume that females that nested after 1 June had not nested earlier in the breeding season. At least 80% of the early-nesting females were banded and individually marked by 1 June. All the late-nesting females were unmarked, so it is unlikely that any had bred previously in these study areas. The general shortage of

nest holes and the absence of other large breeding populations of Tree Swallows nearby reduce the likelihood that late-nesting females bred earlier outside these study areas.

The proportion of subadults in the floating population (47–79%) was higher than in the early-breeding females (4–18%, Table 2). This was true for both study areas and in both years [NL (1983): $\chi^2 = 34.96$, $df = 1$, $P < 0.001$; NL (1984): $\chi^2 = 18.38$, $df = 1$, $P < 0.001$; NES (1983): $\chi^2 = 7.47$, $df = 1$, $P < 0.01$; NES (1984): $\chi^2 = 11.04$, $df = 1$, $P < 0.001$].

From general observations, it was clear that the floaters responded quite rapidly to newly erected boxes, as individuals often began defending new boxes within hours. Without detailed observations of each pair, it was difficult to estimate when floaters became established at a nest site. The interval between time of box erection and first-egg date was 9.7 ± 3.3 days over both years and study sites. Although first-egg date may not be a good indicator of the time of establishment, it represents a maximum response time to new nesting opportunities.

This paper focuses on female floating populations in Tree Swallows, but there was also an opportunity to examine surplus males, since nest sites are limiting for both males and females. Except for two cases of polygyny in 1984, all the late-nesting females were mated monogamously with males that were not known to have bred previously. None of the late-nesting males was marked, but the origin of these males is uncertain since only about 30% of the early-breeding males were marked when the new boxes were erected. There was no evidence that early-nesting males were leaving their mates to breed with late-nesting females. It appears likely that there was a floating population of males as well as females.

A major assumption of the hypothesis that floating females are expected is that the availability of suitable nest sites prevents some females from breeding early in the season; therefore, one would expect the percentage occupancy to be 100%. Although the percentage occupancy in this study was high early in

TABLE 2. The number of adult and subadult females nesting early (before 1 June) and late (after 1 June) during the 1983 and 1984 breeding seasons in the NL and NES populations.

	1983		1984	
	Early	Late	Early	Late
NL				
Adult	48	4	54	10
Subadult	3	15	2	9
Total	51	19	56	19
NES				
Adult	27	3	30	3
Subadult	6	7	4	7
Total	33	10	34	10

the season, it did not reach 100% in either study area (Table 1). Why are some available nest sites left vacant even though there is a substantial floating population? Possibly the area defended by Tree Swallow pairs varies both individually and between populations. Some of the empty boxes could have been defended by adjacent pairs even though they were outside the 15-m range. Another alternative is that females were limited from breeding by a shortage of males (Leffelaar and Robertson 1984). However, there appeared to be a surplus population of males during the breeding season, and hence no shortage of mates.

We have shown that a surplus of females existed in two populations of Tree Swallows, for two consecutive years, and that these females would breed when nest sites were provided. There was a high level of intruder activity by females during May (Stutchbury 1984), which suggests that surplus females were present throughout the breeding season. It is important to establish that females that nested late in the season did so because they were prevented from breeding earlier, and not because they were not ready to breed early in the season. In 1982, the year prior to our experimental provision of late boxes, 11% (7/61) of the breeding females in the NL nested late. In 5 of the 7 cases, nest sites became available through abandonment of a nest, predation, polygyny, and early completion of clutches by other hole-nesting species, indicating that these late nesters were part of a floating population. We conclude that the total proportion of late-nesting females represents the number of surplus females that were prevented from breeding earlier, and therefore estimates the size of the floating population early in the season.

The extent of the floating population in 1983 and 1984 in both the NL and NES was estimated at 23-27% of the total female population. This could be an underestimate if some surplus females that were willing to breed early in the season were unwilling to breed in the new boxes. After the addition of new

boxes late in the breeding season, the percentage occupancy was relatively low, indicating a surplus of nest sites. Although the nest-site limitation was removed, there could be other constraints that prevented some floaters from breeding. Breeding late in the season may have high costs in terms of lower reproductive output, and decreased amount of time to accumulate energy reserves for molt and migration (DeSteven 1978).

Surplus individuals that are excluded from breeding do not necessarily have to stay in the breeding area and form a floating population. Surplus female Tree Swallows may remain in a saturated habitat because of the opportunity to obtain nest sites that become available during the breeding season. The existence of a female floating population has several implications for the breeding biology of Tree Swallows. Not only must females compete intensely to obtain nest sites early in the season, but they may have to defend them from intruding females throughout the breeding season (Leffelaar and Robertson 1985). A high level of female-female aggression during the breeding season has been observed in both populations (Stutchbury 1984). A surplus of potentially breeding females means that males can easily replace their mates. Females may be selected to resist cuckoldry attempts since males could replace their mates if they had reason to suspect that cuckoldry had occurred (Leffelaar and Robertson 1984).

The proportion of subadults in the floating population was significantly higher than in the original breeding population. The presence of subadults in the floating population was unlikely to be a result of their inability to breed, since some subadults did breed early in the season. Floating populations with a large proportion of yearlings have been found in nonpasserine species (Watson and Jenkins 1968, Zwickel 1980, Hannon 1983). This is harder to document in passerines because subadult plumages are less common, especially for females (Rohwer et al. 1980). The large proportion of subadult floaters may reflect their competitive inferiority to older females. We are currently investigating the possibility that subadult plumages of one-year-old females are related to their role as floaters.

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Predation in Relation to Spacing of Kingbird Nests

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Western Kingbirds (*Tyrannus verticalis*) and Cassin's Kingbirds (*T. vociferans*) usually breed in different habitats, but both species nest together in open habitats with tall trees (Hespenheide 1964, Ohlendorf 1974, Blancher and Robertson 1984). We noted previously that breeding success of Cassin's Kingbirds was higher in habitats where they nested alone than in habitats where Western Kingbirds also nested (Blancher and Robertson 1984). Here we test the

hypothesis that a negative relation between predation rate and the spacing of kingbird nests is responsible for lower breeding success where both species nest together (i.e. predation rate is higher because nests are close together).

Several studies have shown a positive correlation between density and predation rate on birds' nests (e.g. Krebs 1970, 1971; Fretwell 1972; Goransson et al. 1975; Dunn 1977; Weatherhead and Robertson

TABLE 1. Percent loss of eggs and young by kingbirds in the three years of study (includes only those nests where initial clutch size was known).

	Western Kingbird			Cassin's Kingbird		
	1978	1979	1980	1978	1979	1980
Number of eggs	88	358	214	55	102	52
Percentages of losses to:						
Predation	26.1	45.3	29.4	32.7	54.9	28.8
Weather	0	33.5	8.9	0	14.7	0
Desertion	0	0.8	0.5	23.6	3.9	26.9
Did not hatch	11.4	5.3	10.7	1.8	5.9	9.6
Starvation	0	0	3.3	1.8	0	0
Did not fledge	10.2	2.0	13.1	3.6	1.0	1.9
Misc. causes	4.5	7.0	1.9	0	3.9	0
Total % loss	52.3	93.9	67.7	63.5	84.3	67.2

1977; Knapton 1979; Page et al. 1983), although this relation may not hold when the principal predator does not find nests visually (Best 1978, Gottfried 1978, Zimmerman 1984). Furthermore, Snow (1970) suggested that density-dependent predation could select for a diversity of nests and nest sites within bird communities. Western and Cassin's kingbirds are of interest because their nests are very similar in appearance, they are placed in similar sites when in the same habitat, and interspecific spacing of nests is minimal (Blancher and Robertson 1984). Therefore, one might expect visually hunting predators to find kingbird nest sites more quickly in habitats where both species nest, because nest density probably will be higher than where each species nests singly.

The study was conducted from 1978 through 1980 along the eastern edge of the Chiricahua Mountains in southeastern Arizona. The study area is described in Blancher and Robertson (1984). Briefly, we chose 11 study sites to cover the transition from desert through open riparian habitat to dense riparian for-

est. Desert habitat was occupied almost exclusively by Western Kingbirds, riparian forest habitat exclusively by Cassin's Kingbirds, and both species nested together in open riparian areas.

Nests of both species were found as they were being constructed. Nearest-neighbor distances (NNDs) were measured between nests (of either species) active at the same time of the season. We checked nests every third day for the presence of eggs or nestlings. Accessible nests were checked by hand, nests up to 14 m were checked with a nest mirror, and higher nests were observed with binoculars. We noted any potential predators near nests and delayed nest checks until these predators had left the area. Predators generally were detected as a result of aggressive behavior of kingbirds. We used the proportion of nest checks during which kingbirds attacked or called at predators as an indication of the abundance of predators at a site.

Predation was assumed to have taken place when there was no other obvious cause for loss of nest contents. Time of predation was assumed to be midway between nest checks. Rate of predation was cal-

TABLE 2. Mean nearest-neighbor distances (NND) for kingbirds in relation to habitat. Distances were calculated between nests of both species, and between nests of each species separately (intraspecific).

	Num- ber of nests	NND (m) ^a	
		Intra- specific	Both species
Western Kingbird			
Desert	163	256	241
Open riparian	47	283 ns	106***
Cassin's Kingbird			
Open riparian	91	230	111
Riparian forest	71	202 ns	202***

^a ns = $P > 0.05$ (t -test); *** = $P < 0.001$.

TABLE 3. Rate of nest predation for each species vs. habitat.

	Nest-days	Nests lost per 100 nest-days ^a
Western Kingbird		
Desert	2,984.0	1.94
Open riparian	823.5	2.79 ns
Cassin's Kingbird		
Open riparian	1,318.5	3.11
Riparian forest	1,543.5	1.62**

^a ns = $P > 0.05$ (χ^2 test on the number of nests preyed upon vs. the number expected if predation rate were equal in each habitat); ** = $P < 0.01$.

TABLE 4. Comparison of mean nearest-neighbor distances (NND) for successful nests and nests that were preyed upon (includes only those nests found before the start of incubation). Nests of both species were included in all calculations of NND. None of the differences was statistically significant (*t*-tests). Sample sizes are in parentheses.

	NND (m)	
	Successful	Preyed upon
Western Kingbird		
1978	177 (9)	260 (6)
1979	209 (12)	199 (31)
1980	203 (31)	185 (18)
All years	200 (52)	201 (55)
Cassin's Kingbird		
1978	178 (10)	138 (18)
1979	133 (7)	193 (19)
1980	160 (23)	167 (17)
All years	160 (40)	166 (54)

culated by dividing the number of nests preyed upon by the total number of days that nests were active (nest-days).

Predation on nest contents accounted for the loss of 26–55% of the eggs laid by both species in all three years, or about half of all losses (Table 1). This was far more than any other cause of nest loss, although losses to wind and rain were high in 1979, and nest desertion by Cassin's Kingbirds was frequent in 1978 and 1980, apparently caused by our climbing of nest trees (fewer trees were climbed in 1979).

Kingbirds rarely nested less than 50 m from another nest of the same species (see Blancher and Robertson 1984), although interspecific spacing was much less than this, with nests as close as 3 m in one instance. For this reason nearest-neighbor distances were only half as large in open riparian habitat where both species were present as in the other habitats (Table 2).

Rate of nest predation tended to be higher in open riparian habitat than in the desert for Western Kingbirds ($\chi^2 = 2.19$, $df = 1$, $P > 0.05$), and was significantly higher in open riparian habitat than in riparian forest for Cassin's Kingbirds ($\chi^2 = 6.85$, $df = 1$, $P < 0.01$; Table 3). If this higher predation rate in open riparian habitat was causally linked to the closer spacing (lower NNDs) of kingbirds in that habitat, then we should expect successful nests of each species to have a larger NND on average than those nests that were preyed upon. In fact, we found no significant difference between the NNDs of successful nests and nests that were preyed upon for either species, in any single year or in all years combined (Table 4). Nor did we find any significant differences in predation rate between nests grouped by NNDs (1–50 m, 51–100 m, etc.).

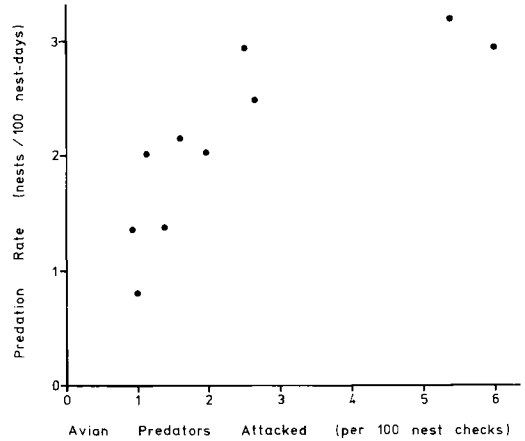


Fig. 1. Predation rate on kingbird nests vs. the frequency with which potential avian predators were seen being attacked by kingbirds. Each dot represents one study site.

Most nest defense by kingbirds was directed at predatory birds, particularly Cooper's Hawks (*Accipiter cooperii*) and Chihuahuan Ravens (*Corvus cryptoleucus*). A Cooper's Hawk was observed taking a nestling from a Cassin's Kingbird nest. We found a positive correlation between predation rate in each study site and the frequency of kingbird attacks on avian predators in that study site ($r = 0.80$, $df = 8$, $P < 0.01$; Fig. 1). This result could have occurred if we led avian predators to the nest during nest checks. However, this did not appear to be happening because only 4 of 77 instances of nest predation on either species occurred within 3 days of sighting a predator. In addition, there was no difference in predation rate between nests that had been checked by hand and those that were watched only with binoculars.

Kingbird attacks on avian predators (accipiters, falcons, ravens, owls) were observed more frequently in open riparian habitat than in desert areas ($\chi^2 = 9.04$, $df = 1$, $P < 0.01$) or riparian forest ($\chi^2 = 3.70$, $df = 1$, $0.10 > P > 0.05$; Table 5). Cooper's Hawks accounted for more than 50% of the attacks in open

TABLE 5. Frequency of attacks by either species of kingbird on potential avian predators (i.e. accipiters, falcons, ravens, owls) in each habitat.

	Nest-checks	Attacks per 100 nest-checks
Desert	1,891	1.75
Open riparian	982	3.56
Riparian forest	552	1.81

riparian habitat and were known to nest in sycamore trees in this habitat.

At first glance, it appears that nest predation may be causally linked to kingbird nest spacing since the highest rate of predation occurred in open riparian habitat where kingbird nests were most closely spaced. In addition, avian predators, which rely primarily on vision to find prey, appeared to be responsible for much of the predation. However, on closer examination, the rate of nest predation was not related directly to spacing of kingbird nests.

There are two plausible reasons for a lack of increased predation on closely spaced kingbird nests. First, kingbirds engage in aggressive defense of their nests against potential predators, and this appears to reduce the probability of nest predation (Blancher and Robertson 1982). Nesting close to other aggressive birds could be advantageous in reducing predation (e.g. Goransson et al. 1975, Andersson and Wiklund 1978, Clark and Robertson 1979, Wiklund 1979, Dyrz et al. 1981, Burger 1984, Gotmark and Anderson 1984). Certainly, hawks and ravens appeared to be repelled by large numbers of attacking kingbirds in our study area; we observed as many as 10 kingbirds simultaneously attacking predators where nesting density was high. Nevertheless, we did not see any evidence for a reduction in nest predation when nests were closely spaced, as one would expect if aggressive mobbing were truly effective.

A second possible explanation stems from the fact that kingbird nestlings and eggs are not likely to be a primary diet item of the predators involved. For example, 50% of the diet of Cooper's Hawks in the Chiricahua Mountains is composed of small mammals and lizards, and much of their avian prey consists of adult or fledged birds (Snyder and Snyder 1974). The presence of these predators, and hence the rate of predation on kingbird nests, is more likely related to the abundance of these primary diet items than to the spacing of kingbird nests. The net result is that kingbird nests are subject to greater predation where there are more predators, independent of their own nesting density. Zimmerman (1984) reached this same conclusion for Dickcissel (*Spiza americana*) nests in old-field habitat. Thus, the high rate of predation on kingbird nests in open riparian habitat does not appear to result from the presence of both species in this habitat. Nevertheless, the high predation rate in open riparian habitat selects against birds nesting there, and thus tends to maintain the habitat separation shown by these two kingbird species.

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Ten-year Periodicity in Whooping Crane Census

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Although the Whooping Crane (*Grus americana*) has received more public interest than perhaps any other endangered species in North America, amazingly little is known of the factors influencing its demography and population dynamics. A reasonably accurate census of the endangered Whooping Crane population overwintering at Aransas National Wildlife Refuge, Texas has been recorded since 1938, affording a 46-yr time series (Miller et al. 1974, Binkley and Miller 1983). Here we report the discovery of a previously unreported 10-yr periodicity in this time series.

In April, cranes migrate north to nesting grounds in Wood Buffalo National Park, N.W.T., Canada. Complete nesting surveys are available only since 1970, although counts of juvenile-plumaged birds are available from Aransas for all years (Binkley and Miller 1983). Mortality rates have been estimated by Binkley and Miller (1980, 1983). The population experienced a per capita growth rate of 0.02 for the period 1938-1956, and 0.04 since 1957 (Binkley and Miller 1983).

Taking square roots of population sizes to homogenize variance (cf. Anderson 1977—a necessary step overlooked by Miller et al. 1974), the time series was detrended separately for the two growth periods defined by Binkley and Miller (1983) by calculating residuals from least-squares linear regression (similar results may be obtained by second-order differencing). The resulting stationary time series was examined for periodicity by plotting the sample autocorrelation function (Box and Jenkins 1970) illustrated in Fig. 1 and by calculating a periodogram (Fig. 2) using fast Fourier transform procedures outlined by Bloomfield (1976). Both approaches indicated a strong periodic pattern with period length of approximately 10 yr. Although statistical inference procedures for

autocorrelation and periodogram peaks are only approximate (Shimshoni 1971, Bloomfield 1976), in both cases the significance probabilities for 10-yr periodicity were quite small ($P < 0.001$).

The periodic pattern is particularly apparent after removing high-frequency "flutter" by calculating a 3-yr moving average (although a moving average is not necessary to demonstrate the patterns we describe). In Fig. 3 we illustrate a least-squares regression fit to the periodic model:

$$X(t) = 0.0013 + 0.826 \cos \omega t - 0.291 \sin \omega t + \epsilon,$$

where $X(t)$ is the moving average of the detrended square root of population size, ω is $2\pi/(\text{period length} = 10)$, and ϵ is an error term. Nearly $\frac{2}{3}$ of the variance in the detrended time series is attributable to this 10-yr harmonic ($R^2 = 64.7\%$, $df = 41$, $P < 0.001$).

Although Binkley and Miller (1983) ascribe periodic fluctuations in the Whooping Crane population to variation in recruitment, our results are inconsistent and suggest that variation in mortality also must be important. Recruitment of juvenile-plumage cranes into the Aransas Refuge counts varied considerably among years but did not possess significant periodicity. Furthermore, we found no significant correlation between rate of recruitment and the detrended square root of Whooping Crane census ($R^2 = 0.059$, $df = 44$, $P > 0.1$). We further note that recruitment of young into the Aransas census is confounded by mortality of chicks on nesting grounds because chicks are not counted until they reach the Aransas area in late autumn.

Recruitment is thought to vary as a function of water levels on nesting grounds (Kuyt et al. 1981), which also may influence vulnerability of cranes to predation because terrestrial predators can better penetrate nesting areas in years of low water levels. Also, during drought conditions, crane families presumably range farther to find suitable wetland feed-

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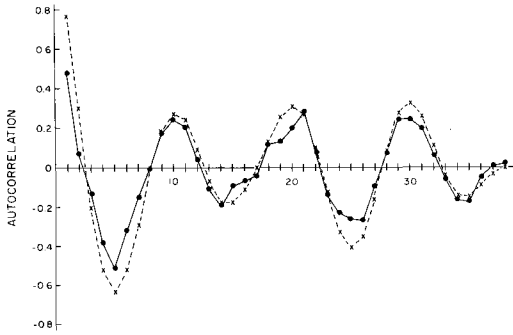


Fig. 1. Autocorrelation of detrended square root (●), and of 3-yr moving average of detrended square root (X) of Whooping Crane census.

ing sites and consequently are more likely to encounter terrestrial predators (Kuyt et al. 1981). However, we found no significant ($P > 0.1$) correlation between breeding season precipitation and the square root of detrended crane fluctuations or between a 3-yr moving average of breeding season precipitation and the square root of detrended crane counts.

Wolves (*Canis lupus*) are known predators of Whooping Cranes (Kuyt et al. 1981), killing at least 4 birds in the summer of 1983 (Rod Drewien pers. comm.). These recent observations of mammalian predation on cranes may be of particular interest given the 10-yr periodicity known to occur in several species of potential predators, particularly wolf, lynx (*Lynx canadensis*), and red fox (*Vulpes vulpes*; Bulmer 1974, Finerty 1980). In fact, Wood Buffalo National Park is near the epicenter of periodicity for the well-

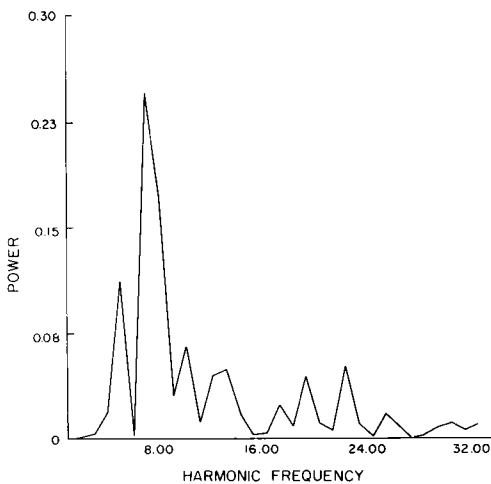


Fig. 2. Fast Fourier transform periodogram of detrended square root of Whooping Crane population size. Peak in relative power occurs at a harmonic corresponding to a 10-yr cycle.

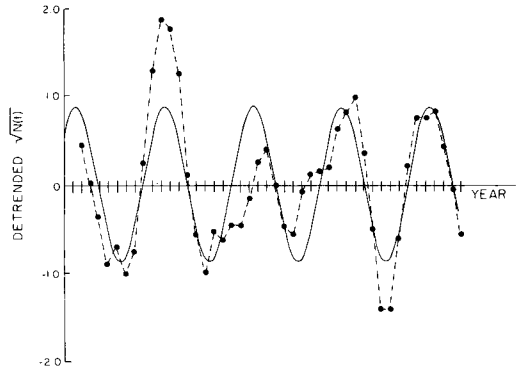


Fig. 3. Periodic regression of 3-yr moving average of detrended square root of Whooping Crane census.

known lynx-hare cycle (Elton and Nicholson 1942, Finerty 1980, Smith and Davis 1981). Although we cannot yet identify the mechanism generating periodicity, we are fascinated by the precise prediction of a 10-yr cycle for Whooping Cranes by population-cycle allometry (Peterson et al. 1984).

Given no changes in environmental regimen from that existing since 1957, or in periodicity since 1938, we may use the time series to forecast the future population size of Whooping Cranes, using the econometric ARIMA model with periodic differencing (Pankratz 1983, Vandaele 1983). We identified an appropriate ARIMA model following the procedure of inspecting residual autocorrelation and partial autocorrelation functions as outlined by Bowerman and O'Connell (1979). The best model was determined to be a first-order moving-average process model at both primary and periodic (seasonal) levels, often written

$$\text{ARIMA}(0,1,1)(0,1,1)_{10}$$

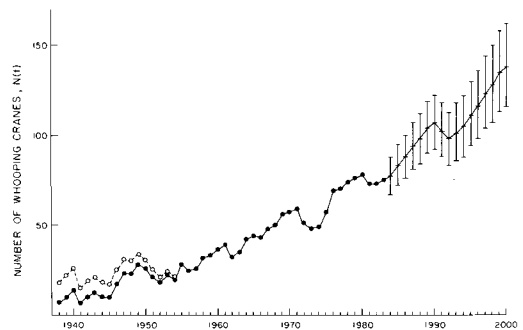


Fig. 4. ARIMA model population forecasts for the Aransas-Wood Buffalo population of Whooping Cranes to year 2000. Years 1938-1956 have been adjusted to the same mean growth rate as 1957-1984; original observations are represented by open circles. Vertical bars are 95% confidence intervals.

We used standard iterative procedures to fit the model

$$\sqrt{N(t)} - 2\sqrt{N(t-1)} + \sqrt{N(t-10)} = a(t) - 0.707 a(t-1) - 0.799 a(t-10),$$

where $N(t)$ is population size at time t (with adjusted growth rate for 1938-1956) and $a(t)$ is white noise (totally random variance). This model leaves a residual mean square of only 0.09, and acceptance is justified by a Box-Pierce Chi-square statistic calculated from autocorrelation of residuals [$Q = 8.652 < \chi^2$ (10 df) = 18.307].

Forecasts of square roots of population size, $\sqrt{\hat{N}(t)}$, are calculated

$$\sqrt{\hat{N}(t)} = \sqrt{N(t-1)} + \sqrt{N(t-10)} - \sqrt{N(t-11)} - 0.799 a(t-10) - 0.707 a(t-1) + 0.565 a(t-11)$$

(Pankratz 1983). Because forecasts were calculated on square roots of population size, squares of these forecasts will be biased underestimates of true forecasts (Nelson 1973). Correction for bias is accomplished by

$$E[N(t)] = [\sqrt{\hat{N}(t)}]^2 + s^2,$$

where s^2 is the residual mean square. The 95% confidence limits on forecasts shown in Fig. 4 were corrected in the same way, but bias was small, being considerably less than one bird in all years.

The U.S. Fish and Wildlife Service-Canadian Wildlife Service management objective of 40 nesting pairs for the Aransas-Wood Buffalo population (Whooping Crane Recovery Team 1980) should be reached approximately in year 2000, given an average 57% of nonjuvenile-plumage birds breeding. This, of course, assumes no changes in the ecology or management of the population over the next 16 yr. In spite of periodic dips in population size projected at approximately 10-yr intervals, forecasted populations of Whooping Cranes are encouraging. Additionally, potential success of a recent program to employ Sandhill Cranes (*Grus canadensis*) as foster parents at Gray's Lake National Wildlife Refuge, Idaho, may enhance our ability to secure future success of Whooping Cranes in North America (Drewien and Bizeau 1978). Nevertheless, our observations on periodic depression in Whooping Crane population growth suggest practical importance for improved understanding of the 10-yr cycle phenomenon, which has fascinated but eluded population biologists for decades (Finerty 1980).

We thank Michael Bulmer, Lyman McDonald, John Hartigan, and Ti Walther for statistical consultation. Roy Mendelsohn explained discrepancies between our analysis and his. Rod Drewien, Tom Stehn, and John Ward provided unpublished data, and they, along with M. Bulmer, Bill Schaffer, and Egbert G. Leigh, kindly reviewed the manuscript. M.S.B. was supported by a N.A.T.O. postdoctoral fellowship.

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REVIEWS

EDITED BY WILLIAM E. SOUTHERN

The following reviews express the opinions of the individual reviewers regarding the strengths, weaknesses, and value of the books they review. As such, they are subjective evaluations and do not necessarily reflect the opinions of the editors or any official policy of the A.O.U.—Eds.

Scaling: why is animal size so important?—Knut Schmidt-Nielsen. 1984. New York, Cambridge University Press. xi + 241 pp., 47 text figures. ISBN 0-521-31987-0. \$29.95 hardcover, \$9.95 paper.—Comparative biologists try to explain a diversity of structures and functions using simple rules. This book introduces the rules and uses of scaling for a few highly selected structures and functions. Scaling examines consequences for a change in organism size, and it is fundamental to comparative biology. Most are familiar with it from the "mouse-to-elephant" curves relating energy demands to size (the "hummingbird-to-ostrich" curve may be familiar to ornithologists). Many problems and methods for scaling originate in engineering, and Schmidt-Nielsen points out: "Animals as well as engineers live in a physical world, and the same principles apply to both." This is true, but engineers design machines to solve known, relatively simple problems, while biologists study highly evolved complex machinery and try to understand the problems. The latter is difficult and challenging. It often requires examining conflicting problems for survival and reproduction.

The main shortcoming of this book is its limited scope. Some of the most interesting and exciting examples of adaptations studied with engineering principles are missing. The main strength of the book is the excellent explanation for the few topics covered.

The first three chapters give an introduction to the general subject by considering the range of size of organisms, how isometric and allometric comparisons are made, and some of the uses and abuses of the comparisons. The rest of the book focuses mainly on comparisons for metabolic rates and determinants of energy use. There is a chapter each on bird eggs and skeletons; the next 11 chapters deal with resting metabolic rate, lung ventilation, circulation, blood gas transport, activity metabolism (running, jumping, swimming, and flying), and temperature regulation. The writing is excellent, and the author provides insight for a few intriguing questions dealing with organism size.

Ornithologists may be particularly interested in the discussion of how egg design varies over a 30,000-fold size range so eggs lose a constant fraction of their weight prior to hatching. Data are reviewed dispelling the myth that birds have a lighter skeleton. The power requirements for flight are considered in part of a chapter, although it is the nature of

scaling analysis that much of the fascination of variation is lost in the averaging inherent to this approach. The author asserts that the lower limit to size in birds and mammals is set by the high frequency of heart contractions. This is suggested by a compensatory increase in heart size (greater stroke volume) in hummingbirds and shrews. An unexplored alternative may be the high frequency of energy processing, since reduction in body size (without mechanisms such as torpor) could increase feeding frequency to a point where continuous feeding would not meet demands for energy. To consider this would require using information on physiology to understand ecology, i.e. size-dependent gains as well as expenditures of energy. This type of synthetic analysis is notably lacking. Other points of interest dealing with metabolism include a review of McMahon's hypothesis of elastic similarity as a basis for intraspecific scaling of energy demands to the 0.75 power of mass, and Taylor and Weibel's hypothesis for "symmorphosis," or the design of respiratory mechanisms to match demands at peak performance (about 10 times resting levels for mammals).

Much is missing. Although time in life span is briefly mentioned, there is no consideration of scaling and reproduction. Some of the more remarkable and interesting adaptations of organisms are thus excluded (*r* and *K* strategies, for example). Since adaptations involve both survival and reproduction, failure to consider reproduction (for which there is a considerable literature) severely limits this book. The scaling of demands of organisms for water is not mentioned. Size-dependent adaptations for water exchange are important to understand survival in some environments and energy uses for osmoregulation. Although the principle of optimal design is mentioned in passing in the last chapter, there are few explicit examples in the text. This principle has proven to be a major tool in the experimental analysis of adaptations, particularly for studies of energy regulation, locomotion, and resource allocation to sexual functions. It deserves more prominence than an afterthought.

It is not clear for whom this has been written. Much of the material (and more) can be found in introductory texts on comparative physiology. Perhaps it is intended as a supplement with slightly more selective detail. If so, it also must be supplemented to fill the extensive gaps. For more diversity with an equally engaging style I recommend Stephen Gould's es-

says on scaling [compiled in "Ever Since Darwin" (1977) and "The Panda's Thumb" (1980), New York, W. W. Norton]. For an excellent introduction to the principles and uses of optimal design I recommend "Optima for Animals" by R. McNeill Alexander (1982, London, Edward Arnold).—F. REED HAINSWORTH.

Body weights of 686 species of North American birds.—John B. Dunning, Jr. 1984. Western Bird Banding Assoc., Monogr. No. 1. 38 pp. Available from the Association, Jolan Truan, Assistant Treasurer, 3314 West Glenn Drive, Phoenix, Arizona 85021 USA. \$3.75.—This volume brings together body weight data for the regularly occurring avifauna of the continental United States and Canada. The data are arranged phylogenetically in one long table and include, for each species, scientific and common names, A.O.U. number, sex (when known), number in sample, standard deviation, range, collecting location and season, and source of information (221 references). The 87 species excluded from the publication are those reported only from Greenland, Baja California, and the outer Aleutian Islands; specimens accidental in the U.S. and Canada; extinct species; introduced species that are not widespread; and species for which no body weight data were found. Six species were included either because they recently have become established and regular breeders in the U.S. and/or Canada or because they represent taxa recently raised to the specific level.

The author makes clear the limitations of the data in that body weights can change daily, seasonally, and with age and location. He rightly advises authors to consult the original sources for the detailed information.

Although the title makes reference to North American birds, I counted at least 60 species for which the data came from outside North America! It is difficult for me to understand, for example, why the body weights for the Northern Gannet (*Sula bassanus*) are from specimens in England rather than Canada. Surely Canadian museums and some researchers (such as Bill Montevecchi?) have ample body weight data from Canadian colonies.

As a source book on avian body weights, this volume has considerable value as a starting point. For individual studies, however, the original sources should be consulted.—JOHN P. RYDER.

Pelagic distributions of marine birds off the northeastern United States.—Kevin D. Powers. 1983. Woods Hole, Massachusetts, NOAA Technical Memorandum NMFA-F/NEC-27. xvi + 201 pp., 116 line drawings. (Available from National Technical Infor-

mation Service, Port Royal Road, Springfield, Virginia 22161.)—Information about marine bird distribution in the pelagic zones of the eastern United States has been a major void in understanding the biological oceanography of the Atlantic. The need for this became even more painfully evident with the publication of the Canadian seabird atlas (Brown et al. 1975, Canadian Wildl. Serv.), which included all of the Canadian maritimes and eastern arctic waters. Although a few reports from Maryland (Rowlett 1980, USFWS report) and North Carolina (Lee and Booth 1979, Amer. Birds) waters have appeared, this study provides the first comprehensive coverage of marine birds for the northeastern U.S. and goes a long way toward filling the void.

The report begins with a brief description of the oceanography of the region, ranging from the narrow shelf off Cape Hatteras, North Carolina to the more complex banks configurations in the Gulf of Maine and southern terminus of the Bay of Fundy. A map of the major geographic features is provided. It also might have been useful to include maps showing sea surface isotherms at different seasons.

The methods indicate that a variety of vessels were used for surveys on a "ships of opportunity" basis; as a result, comprehensive, controlled sampling regimes such as those carried out in eastern Canada and in Alaska as part of the Outer Continental Shelf Environmental Assessment Program could not be emulated. This limitation, plus the admitted problems of observer variability and differences in species detectabilities, precludes much opportunity for statistical analysis. Nonetheless, much valuable, basic information has been generated that raises a number of important questions concerning how marine birds respond to their environment.

The bulk of the report is comprised of a series of distribution maps for each species. Forty-four species are included, but some are lumped (e.g. small "terns," "cormorants") or included in appendices because of the scarcity of sightings. For the 26 months of the survey, 4 seasons are separated and the greatest mean monthly density (birds·km⁻²·10'·x·10' block⁻¹) figures are plotted by block. Different symbols are used to indicate 5 density ranges that vary from 0 to more than 100. For regional comparisons, the northeastern U.S. is subdivided into four subareas: Gulf of Maine, Georges Bank, southern New England (Nantucket Shoals south and west to and including the New York Bight), and the Middle Atlantic Bight.

A brief narrative account is included describing the breeding range, feeding methods and behavior, and major prey of each species. Where there are sufficient data, the species narrative account is followed by a seasonal distribution map. Whenever possible, an attempt is made to relate wintering populations to North American breeding populations to see to what extent North American Atlantic populations depend on U.S. waters in winter.

Several major findings emerge: (1) Not unexpectedly, the more productive northern areas, the Gulf of Maine and Georges Bank, support a greater abundance and biomass of seabirds than the Middle Atlantic Bight throughout the year. The contrast is especially great in summer and fall, apparently due to hydrographic differences. Currents over Georges Bank maintain good vertical mixing, but in the mid-Atlantic the waters are well stratified. (2) In each season, there are strong numerical dominance patterns among species, with relatively few species contributing most to abundance and biomass. Fulmars, shearwaters, storm-petrels, gannets, and gulls comprise the majority of the seabirds. (3) The high abundance of fulmars on Georges Bank and the Gulf of Maine during winter and spring was not expected based on earlier surveys. Powers suggests that they probably were simply not previously sampled. (4) A bimodal (June–July and October–November) peak in Greater Shearwater abundance was found in the same northern subareas. The author suggests that Georges Bank may be a midlatitude staging area before the southward migration of the population, which probably consists mostly of nonbreeders and/or subadults. The species breeds in the South Atlantic, and (5) the author seems surprised that the ratio of Herring Gulls to Great Black-backed Gulls never exceeded 2:1 in pelagic surveys, yet the breeding colony data suggest a ratio of about 7:1. Perhaps the species' differences in dependence on offal and refuse (see Hunt 1972, *Ecology*) could explain this.

One objection I had was Powers's use of terminology (and its implications) involving the "community structure" of the seabirds of the northeast Atlantic. That assemblages of different species occasionally occur does not argue for any type of "community" or "structure." If anything, seabird researchers are aware of how transitory species groups are at sea and how much variation exists in space and time. Most species are highly opportunistic, and conclusions about niche partitioning and competition are highly questionable. Although it would have been a formidable task for presentation, partitioning observations by year would have revealed the amount of annual variation in spatial use by species.

The overall objective of assembling a large amount of information on the numerous marine birds of the North Atlantic and presenting it in a concise fashion has been admirably achieved. I hope this major effort will be followed by periodic resurveys; however, with the energy corporations showing such little recent interest in bidding on oil leases off the Atlantic coast, it is doubtful that substantial federal support for pelagic surveys will be forthcoming. Despite this economic pessimism, this report should provide an impetus for further investigations under more controlled (i.e. specific cruises) survey conditions. Long-term investigations of how commercial fisheries practices affect seabird populations argue for more support for

long-term pelagic surveys and breeding colony censusing.

This report should be an important library reference for marine bird researchers, oceanographers, and ocean and coastal zone managers. Perhaps it can be republished in the future without the caveat on the cover page that cautions the reader that the TM series has "not received complete formal review, editorial control, or detailed editing." This volume appeared to have been well reviewed and edited.—R. MICHAEL ERWIN.

Current ornithology, vol. 1.—Richard F. Johnston (Ed.). 1983. New York, Plenum Press. xvi + 425 pp., 70 text figures, 17 tables, 4 appendices. ISBN 0-306-42339-6. No price given.—Why do we need another review series in ornithology? One might think that with "Avian Biology," "Perspectives in Ornithology," endless symposium volumes, ornithologically relevant papers in various annual reviews, biological reviews, and the Quarterly Review of Biology, etc., the ornithological community long ago would have gagged on publications purporting to review the field. Perhaps they have—Plenum Press should have some inkling by now based on sales—but this volume illustrates well that the patient can benefit from something it/she/he may not even realize it lacks. "Current Ornithology" dispenses a well-conceived and well-executed collection of timely, focused, and thoughtful summaries of where things now stand in discrete research topics within ornithology.

The preface provides the book's rationale: to present views or position statements on active fields of ornithological research. Reviews will be short, and "often done from the viewpoint of a readily-identified group or school." The succeeding chapters live up to this goal by a wide margin. Not that they are without controversy or error, but for the most part they offer enough to stimulate and satisfy any ornithologist and to challenge all with new ideas.

Three broad areas within ornithology find representation in this volume: four chapters in evolutionary ecology, including behavior; two on structure and function; and six in systematics. That's not quite the mix I would have predicted for a balanced overview of research activity in ornithology today—behavior, physiology, and especially community ecology are underrepresented. But who promised balance?

The chapters on evolutionary ecology display the diversity of approach in this field. Robert Ricklefs provides an admirably concise overview of life history theory presented in the currency of bird demography. This chapter should be read by any student embarking on a life history study in birds, as well as by professionals who may have thought they were doing so already. His conclusions offer a mix-

ture; while providing sensible encouragement for combining comparison, experiment, and modeling in analyzing life histories, he expresses pessimism on the likelihood of ever obtaining good estimates of constraint functions—trade-offs—between demographic parameters. While he shows that the slope of constraint functions can be estimated if one makes a series of assumptions, for me the assumptions are so central to what is interesting about life history patterns that the estimates are not satisfying.

David Winkler and Jeffrey Walters wrestle with the evolution of clutch size in precocial birds. It is a remarkably eclectic and scholarly piece (187 references, the prize for this volume) that lays out the logic (and illogic) of current arguments on the issue. No one has the answers yet, but Walters's dichotomy of active vs. inactive parents of precocial young opens an intriguing new direction for experiment.

Norman L. Ford takes the most focused perspective in the book, with a useful summary of evidence on what really happens in monogamous mating systems. By Ford's tally, at least 16% of 264 species of North American "monogamous" passerines indulge in extrapair copulations. A number of these involve males defending classic "type A" territories going off on extraterritorial excursions. Such trends will fuel fieldworkers' anxiety over the "away" category of time-activity budgets.

Ellen D. Ketterson and Val Nolan, Jr., review their continuing studies on factors leading to the evolution of age and sex class variation in migratory patterns. This field has revved up considerably since Ketterson's early work, especially in decibels. It's relatively easy to gather simple descriptive data on the issue—that males of many species remain closer to the breeding ground—and easier still to tell logical stories—that dominants ought to displace subordinates from the preferred winter range, or that some birds benefit by being the first to reach the breeding ground—but testing these notions has proven almost impossible. This chapter should help reduce the noise level.

The systematics papers also span the breadth of their field. One reads the chapters by Cracraft and by Sibley and Ahlquist and hears thunder rumbling in the distance. Whether it's a summer lightning storm or a torrential downpour is not yet clear. Cracraft offers a heated polemic on the inadequacies of the biological species concept. These noises aren't new to systematics, but to have them come from ornithology, from whence the BSC sprang, is ominous.

Sibley and Ahlquist provide one more update in the continuing saga of DNA-DNA hybridization and avian systematics at supraspecific levels. The authors respond to many of the criticisms that have greeted previous expositions. Their growing volume of evidence indicates that the next ten years of avian systematics will see radical reshuffling throughout the

Class. If only half of their assertions prove true—and my bet is that the fraction will be much higher—then this biochemical ground-truth will spawn a new generation of studies on adaptive morphological convergences. Avian systematics will never be the same.

L. D. Martin considers the evolution of birds and flight, not unlike his chapter in "Perspectives in Ornithology." Readers interested in a plausible counterargument should see Caple, Balda, and Willis (1983, *Amer. Natur.* 121: 455). Not to be disrespectful—avian paleontology has made monumental advances in its own bailiwick as well as in other ornithological disciplines—but too much of the debate on origins of flight rests on assertion and a few incomplete samples of a fossil organism, itself of questionable abilities and uncertain relevance to the mainstream of the phylogenetic sequence leading to modern birds. One makes do with what one has, but imagine trying to interpret liver function in birds by poking blindly with a 30-m piece of limp pasta at the partial gut of a single dead chicken. Caple et al. at least have laced the argument with a few basic physical principles.

There are three other systematics chapters: a procedural review by G. F. Shields on bird chromosomes, a discussion of hybrid zones in the Great Plains by J. D. Rising, and a synthesis of electrophoretic work on population structure by K. W. Corbin. G. F. Barrowclough (1984, *J. Field Ornithol.* 55: 509) takes valid issue with one of Corbin's techniques, in particular using linear regressions on a curvilinear relationship (Fig. 3). As a result, conclusions about the "genetic revolution" during speciation seem a bit hasty.

I leave to other reviewers the two physiology/morphology papers, one by C. Carey on egg structure and function, the other by J. R. Hinchliffe and M. Gumpel-Pinot on avian limb morphogenesis. Both are readable and digestible by the nonspecialist. But as an outsider to these topics, and knowing that considerable controversy lurks in waiting for the unwary in other chapters, I cannot help but wonder where they lie within their own fields in a spectrum of controversy (mainstream to radical) defined by the rest of the book. That is the one danger I see in a collection of this format. Let the reader beware.

"Current Ornithology, vol. 1" is an outstanding collection. The objectives stated in the preface are met resoundingly. Graduate students will find it an invaluable entrée into diverse and current research topics. It will stimulate, aggravate, incite, and excite every professional ornithologist. Buy it, and be ready to shell out more for subsequent numbers in the series. If this volume doesn't contain the issue of your dreams, the next one may. Richard F. Johnston, his editorial board, and his authors have added significantly and usefully to the ornithological literature.—J. P. MYERS.

The status and distribution of New Jersey's birds.—Charles F. Leck. 1984. New Brunswick, New Jersey, Rutgers University Press. viii + 214 pp., 1 map. ISBN 0-8135-1033-3. \$25.00 (cloth).—This volume is an event of note because it is the first of its type to appear for New Jersey since 1955. Thus, a substantial quantity of new ornithological information required evaluation and use in order to reflect the current status and distribution of New Jersey's birdlife.

The book is well produced, has a solid binding, good type style, and an attractive design. A jacket should have been provided, however, and the price should be half that set by the publisher—especially for a book lacking illustrations (more about that later).

The contents page is adequate, and the acknowledgments page includes names of the leaders and most active participants of particular note in New Jersey ornithology and bird-watching during recent decades. An 11-page introduction briefly discusses the state's geography and habitats and the format of the species accounts, which follow the sixth edition of the A.O.U. check-list (1983), and provides an analysis of the state's avifauna.

Leck recognizes most families accepted by the A.O.U. but assigns his own common names to them. The Emberizidae, however, is divided into various subfamilies, such as Parulinae for wood warblers. Scientific and vernacular species names follow those established by the A.O.U., but some widely used vernacular names also are included (for example, *Phalaropus lobatus* is referred to as the Red-necked or the Northern Phalarope).

The analysis of the state's avifauna indicates a dynamic change in the birdlife. A total of 450 species are included in the main text, but only 414 of those are well confirmed in New Jersey.

The species accounts, the section of primary interest to ornithologists and amateur birdwatchers, form the heart of the book. A vernacular and scientific name is given for each species, followed by a short description of its geographic range and a statement of its status in New Jersey. Periods of peak abundance also are provided, but *not* early arrival and late departure dates. The lack of these extreme dates is a serious weakness in the text. For some species, maxima or high counts are provided—sometimes for several sections of the state. Leck laments the lack of such data for many species, however, and wisely encourages people to gather such information for future use. Where useful or appropriate, bird census data such as Christmas Bird Counts also are provided.

A major flaw in the presentation of species records is the author's failure to cite names of observers and specific published sources within the text. Thus critical readers cannot easily refer to the original documentation for most records. There are some excep-

tions, however, where adequate author or literature references are provided, but these are far between. Equally annoying is the author's failure to cite essential specimens preserved in museum or other collections (there are many for New Jersey) and the lack of photographs for the more interesting or unusual records. Numerous photographs of this type exist. Were they not available to the author and publisher? In view of the price of the book, the publisher had an obligation to include some documentary photographs—at least in black and white.

Finally, I would prefer that hypothetical records either be presented in smaller type within the main text or be placed in an appendix. Instead, records (indicated as hypothetical) such as *Gavia adamsii*, *Diomedea chlororhynchos*, *Pterodroma hasitata*, *Hydrobates pelagicus*, *Oceanodroma castro*, *Accipiter nisus* are scattered throughout the main text—often based on very weak evidence even for placement on a hypothetical list. In a book of this type the author should have applied much more rigorous standards, even for the selection of species for the hypothetical list. Again and again, Leck speculates that a species may occur in New Jersey or someday will occur in the state because it was reported in an adjacent state.

Records of unestablished exotics, escapes, and unsuccessful introductions follow the main species accounts. Among the astonishing species included in this section are the Macaroni Penguin (*Eudyptes chrysolophus*) and Andean Gull (*Larus serranus*)! Who knows how they arrived in New Jersey?

A very useful gazetteer is provided, but the book's bibliography is really a literature-cited section emphasizing recent literature, as opposed to a list of all publications dealing with the state's birdlife. Numerous important articles and notes in regional periodicals, the most recent editions of some books, and many other books (including one published in 1975 by Rutgers University Press) are ignored. The index to vernacular and scientific names is adequate and useful.

Despite some serious weaknesses in this book, it represents the most current summary of New Jersey's avian status and distribution and as such is a welcome addition to the state's ornithological literature. I recommend the book to all persons seriously interested in New Jersey birds and further suggest it be added to private, public, academic, and museum libraries throughout the state and elsewhere.—DONALD S. HEINTZELMAN.

Where to find birds in British Columbia.—David M. Mark. 1984. New Westminster, British Columbia, Kestrel Press. 122 pp. ISBN 0-9690850-1-X. Paper \$6.95.—This revision of the 1978 edition has been

expanded to nearly twice the original number of birding sites. After a short introduction, the book is devoted mostly to describing good birding areas and explaining how to get there. The main chapters describe 8 geographical regions, and each begins with a short paragraph on the region's outstanding features. This is followed by a map that displays the birding sites discussed for the region. The maps lack detail, and the author points out that a good road map is necessary to drive to particular areas.

Site descriptions follow the regional maps. The species that are most likely to be seen are listed, and especially noteworthy birds are printed in bold-faced type. The author does a good job of addressing seasonal changes in species abundances and often suggests the best time of year for seeing particular groups of birds. Directions to each area are clearly written and seem easy to follow. A map code is listed above each entry, but the author does not explain how to decipher it; the code may refer to the location of the area on a provincial road map.

The last chapter of the book includes an annotated checklist of birds found in British Columbia and supplemental information on "sought after" species. I found this category to be based on highly subjective criteria (the opinions of the author and another individual), and many of its members rarely would be expected to be seen. The information on the status and habits of these birds, however, is well written and useful. Unfortunately, locations are given only for the more common species.

Generally, this book does a good job of directing the reader to birding areas and discussing what may be seen there. Locations can be found quickly by biotic area, geographical region, or common name. Visitors to the areas and resident birdwatchers should find this compact guide very useful.—NEIL SABINE.

Population ecology of the Dipper (*Cinclus mexicanus*) in the Front Range of Colorado.—Frank E. Price and Carl E. Bock. 1983. *Studies in Avian Biology* No. 7, Cooper Ornithological Society. iv + 84 pp., cover photograph, 20 text figures, 19 tables. \$9.00.—At the outset, it must be said that the authors did not intend this study to be a definitive life history of the Dipper. Diet, diseases, predators, and eco-physiology are not assessed directly; they are treated inferentially, and then only insofar as they bear on the population dynamics of the Dipper in the Colorado Front Range. Given that limitation, Price and Bock present a thorough analysis of the complex array of factors that regulate density, dispersion, reproductive success, and survival in a small but significant segment of the Dipper's range.

The monograph is divided into eight sections: introduction, study areas, methods, an overview of the

annual cycle of the Dipper in the Front Range, population movements, density and dispersion patterns, survival and productivity, and discussion and conclusions. In the introduction the authors list five specific "objectives" that contribute to answering the question: "What factors influence the dynamics of Dipper populations?" These objectives are essentially the major parameters one would want to measure to understand the dynamics of any population, namely spatial patterns, food resources, social interactions, reproductive success, and abiotic factors.

The rest of the introduction focuses on the general biology of the Dipper, including a review of the literature relevant to Dipper population biology. From this discussion it is evident that the Dipper is better suited than most birds for population studies because (1) their nests are relatively easy to locate, (2) their habitat (streams) is essentially linear, (3) they are easily trapped because mist nets can be set up across streams, perpendicular to their routes of travel, and (4) their primary food source (benthic invertebrates) is relatively easy to quantify. The introduction also includes a brief discussion of the traits of an "ideal" study population and an exhortation to ecologists to "choose organisms and/or study areas that, like ours, make holistic studies feasible," both of which struck me as an unnecessary attempt to imbue the study with greater general significance.

Most of the authors' data were gathered on two streams, Boulder and South Boulder creeks. A total of 72 stream segments 400 m in length were studied intensively, and other portions of these streams ranging from the foot of the mountains (at 1,600-m elevation) to as high as 3,050 m were visited periodically. Once the great mobility of local populations was realized, the authors also made visits to other streams draining the Front Range. Data on Dipper population dynamics were generated by complete monthly censuses, color banding of both adults and nestlings, territory mapping, and nest monitoring. Ages could not be determined after the postjuvenile molt; hence, breeding individuals banded previously as fledglings were used to calculate mean ages for each sex, a process that underestimated mean ages and yielded samples too small for statistical analysis. Minor difficulties also were encountered in measuring breeding densities due to occasional polygyny and the presence of nonterritorial floaters early in the nesting season. Data were collected on 472 days in 1971-1973, spanning three breeding seasons and two winters.

An exemplary feature of this study is the authors' attempt to quantify habitat variables. A total of 41 variables were used in their extensive correlation analyses, of which 21 were related to aspects of stream quality or climate regime. Included among these variables were measures of nest-site quality and dispersion, mean depth and width of stream, substrate quality, stream flow, precipitation regime, ice cover,

presence of brush piles or other hiding places, and Surber sampler estimates of food supply. Aerial and terrestrial invertebrates were not sampled; other studies indicate that these may comprise 20% of the diet. Benthic invertebrates were sampled only in shallow, rubble-filled areas. Although the introduction states that Dippers may "forage in water too swift and deep for humans to stand upright," the Dipper's apparent preference for shallow areas and the authors' use of other habitat-quality indices based on stream physiognomy suggest that this is a minor source of error in estimating food supply.

Major findings are that (1) winter ice cover plays a major role in the survivorship of individuals; (2) nest-site quality and dispersion are critical for successful reproduction, particularly the juxtaposition of good nest sites and adequate food supplies; (3) summer (postbreeding) populations disperse widely, the vast majority of individuals moving well upstream to higher elevations and some even crossing watershed boundaries; (4) brush piles and other refuges are important during postnuptial molt, when adults are flightless for 5-14 days; (5) floods in early spring cause the loss of nests placed too near the water, and siltation associated with the heaviest floods may reduce the food supply, causing desertion of territories and nests; and (6) predation seemed to be involved in several nest failures but does not appear to play a significant role in regulating the adult population. There also was marked carryover of effects from one season to another. For example, good winter survivorship caused high initial breeding densities, which in turn brought about reduced reproduction per adult because of lower average quality of nest sites and territories.

In my opinion the monograph could have been shortened by perhaps 10% without a significant loss of information. One source of redundancy is the organization of the results into categories of population attributes rather than by seasons. The authors repeat specific findings in different sections to remind the reader of what had gone before. The result, at least for me, was alternation between a mildly annoying repetition of facts and a diffuseness that made it difficult to keep track of the important patterns. The last two pages of text are largely redundant or irrelevant; why review studies of Red Grouse and voles just to tell us (again) that populations are often regulated by complex interactions among many variables?

Other critical comments are few and relatively minor. A one-paragraph summary of the similarities and differences between Front Range Dippers and Dipper populations elsewhere would be helpful; as it is, this material is difficult to dig out. Also, actual Surber samples of high-elevation benthic invertebrates might have substantiated their impression that food was most abundant for Dippers summering at high elevations. The range of *Cinclus mexicanus* is said to ex-

tend to southern Mexico, when in fact it extends to the mountains of western Panama. Otherwise, the text is free of obvious factual errors.

On the positive side, the Dipper is an unusual bird well worthy of a study of this magnitude, and Price and Bock have done a thorough job. Their monograph will find a place in museum libraries, and on the bookshelf of anyone interested in Dippers. It also will be a useful reference for anyone planning a life-history study of any small bird. Despite the correlative (rather than causative) nature of the relationships demonstrated, the authors convinced this reader that they have indeed uncovered the primary factors regulating Dipper populations in the Colorado Front Range. They paint a picture of an intriguing, semi-aquatic passerine that is well adapted to survive in a patchy, two-dimensional, asynchronously varying environment.—ELLIOT J. TRAMER.

Mechanisms of morphological evolution. A combined genetic, developmental and ecological approach.—Wallace Arthur. 1984. New York, John Wiley & Sons. xv + 275 pp., 70 black-and-white figures. ISBN 0-471-90347-7. \$36.00.—This book presents a new theory of evolution based on the idea that the neo-Darwinian model is inadequate to explain the origin of complex morphologies. Arthur accepts the principle that most evolutionary change results from the action of natural selection on phenotypic variation with an underlying genetic basis. However, he rejects the idea that large morphological changes can be attributed to selection acting on slight allelic variants at one or a few loci. He argues instead that while such processes may explain much of the variation that occurs at low taxonomic levels, it will not serve as a mechanism for the origin of major morphological reorganizations of the sort that characterize higher taxa, such as animal phyla. For such changes he requires a different evolutionary mechanism, and finds it in genetic changes that have large effects on the course of embryonic development. His approach is multidisciplinary, synthetic, and speculative, but unfortunately it is not entirely successful.

The first half of the book serves as a background for Arthur's ideas by summarizing current evolutionary theory. Topics include character measurement, the genetic basis of variation, artificial selection experiments, microevolution, speciation, and divergence after speciation. It is a well-written review that covers a lot of familiar ground: D'Arcy Thompson's cartesian grids, selection experiments in mice and *Drosophila*, shell shape in molluscs, beak size in *Geospiza*, ecotypes in *Potentilla*, and the obligatory critique of punctuated equilibrium. These discussions are brief and lucid and may serve as a good source of material for undergraduate lectures.

In the second half of the book Arthur develops his original ideas, and while these are stimulating they are not without problems. Arthur recognizes that any theory of this sort must explain evolutionary change on the basis of developmental processes, which he considers must lie mainly above the level of cellular differentiation in the realm of morphogenesis. Here he encounters a major stumbling block, which he clearly recognizes, namely that we currently lack a general theory of development upon which such an evolutionary theory may be based. As a contribution toward such a developmental theory he offers the idea of the "morphogenetic tree," a system of serially acting morphogens that lead to increased heterogeneity within the developing organism. It corresponds in shape to the branching tree of cellular differentiation in, for example, a diagram of germ layer differentiation, or one of stem cell differentiation in hematopoiesis. Presumably, Arthur is inserting into such trees a series of causative agents, the morphogens, although he does not mention these earlier representations.

Arthur introduces some useful terminology to clarify the ambiguous concept of regulatory genes. D-genes are those that regulate development, either by producing enzymes that make morphogens or by regulating genes that do so. S-genes are structural genes whose end products are not morphogens. R-genes are those that regulate S-genes. This nomenclature may be useful outside the context of the present book.

The next step is to synthesize these developmental genetic ideas with selection in natural populations, and I will comment on two problems at this level. The first is a lack of good examples. Arthur's major analyses focus on shell-coiling in gastropods and homoeotic mutations in insects. The first, as he admits, hardly constitutes a morphological revolution. The second, while more reasonably considered as macroevolutionary in scale, is poorly understood and has been more thoroughly discussed by other recent workers. The difficulty here is not so much the author's; it is simply that few morphogenetic mechanisms have been analyzed as yet from this point of view. Papers doing this are beginning to appear with some frequency now, and Arthur would have better examples if he were still writing the book.

A related problem is best exemplified by a direct quotation: "... it is by no means clear that the ... process of natural selection on polygenic variation that is responsible at least for intraspecific and intragenetic evolutionary divergence is the sole or even the predominant process giving rise to higher taxa such as orders, classes, or phyla" (p. 172). At the risk of appearing pedantic I must insist that taxa do not arise in the course of evolution, but of classification. Taxa are human constructs, even when correlated consistently with natural phenomena like clades.

What arises in evolution is phenotypic change. There is a rough correlation between distinctiveness and rank, but this does not mean that large phenotypic gaps necessarily arise saltationally, and as noted above, most of the examples discussed represent quite modest degrees of divergence.

In recent years it has been recognized that the weak link in our understanding of the evolutionary process is the connection between the level of the population geneticist and that of the morphologist, and that ontogeny is the key to that connection. Arthur recognizes that "A truly synthetic theory of morphological evolution must await a complete exposition of the genetic basis of development" (p. 250). That is the reason that this book, while stimulating, does not in the end provide us with such a theory.—ROBERT J. RAIKOW.

Nest building and bird behavior.—Nicholas E. Collias and Elsie C. Collias. 1984. Princeton, New Jersey, Princeton University Press. x + 336 pp., 87 illustrations. ISBN 0-691-08358-4 and ISBN 0-691-08359-2.—For Nick and Elsie Collias the study of nests and nest building has been almost a lifetime occupation, and there can be few who know more about the subject. Their interest focuses especially around the behavior of the Village Weaver and other related species, which they have studied both in the field and in captivity. Although their own studies provide material for some of the most important and interesting sections of this book, its scope is far wider. It provides a perspective on nests and nest building in the class as a whole and contains a wealth of material whose synthesis must represent a painstaking study of the ornithological literature.

The diversity of birds' nests is displayed in an opening chapter built around some speculations concerning the probable evolutionary course of nest-building behavior. From then on the main thrust of the book concerns the probable adaptive significance of variations in nest-building behavior between and within species. Evidence for the selective forces acting on nest-building behavior comes principally from comparisons between closely related species in relation to their ways of life, from convergent evolution in different species, and from variations in nest building and breeding success in particular species in relation to the environment. In each case, however, the features of the nest form part of a coadapted complex of characters related to the total biology of the species. In separate chapters nest-site selection and nest building are considered in relation to mate selection, the physical environment, nest competitors, parasites and predators, and gregarious breeding.

Several fascinating chapters on the techniques with which birds build their nests, and how these techniques develop in the individual, are based very largely on the authors' own work on the Village Weaver. The precise nature of the skills used in building complex nests has long been a matter of controversy. W. H. Thorpe (1956, *Learning and Instinct in Animals*, London, Methuen & Co., Ltd.), impressed by Tinbergen's description of the nest building of the Long-tailed Tit (*Aegithalos caudatus*), postulated that the several stages of building cannot be understood in terms of stimulus-response chains and must be controlled by at least short-term goals such that actions that brought the current structure nearer to the "ideal" were reinforced and more likely to be repeated. Although the authors do not discuss this view, their analysis at first seems to show that such a hypothesis is unnecessary. Their experimental data on adult birds are explicable on the view that the particular stimuli presented by the nest at each site elicit certain nest-building actions, and that "each stage automatically provides the stimulus for its own termination and for the start of the next stage in construction." However, that seems not to be the whole story, for the authors also studied the development of nest building in individual birds deprived of the opportunity to build to varying degrees. Although it is not clear in every case that their results were not due to lowered motivation, the experiments show that the nest-building ability of this species depends on practice "appropriately directed by the growing structure of the nest itself" and on "improvement in ability to select and prepare nest materials." They even suggest that "a mental image of a properly built nest based on experience" may be necessary, although here the evidence is tenuous. Since there is also evidence, not cited by Collias and Collias, that reinforcement contingent upon the performance of nest-building movements may play a role in canaries (1972, *Anim. Behav.* 20: 514), the behavioral processes involved in nest building cannot yet be regarded as fully understood. What is surprising, perhaps, is that other ornithologists have not tackled the exciting lead provided by the Colliases, for the problem has fundamental implications for the nature of species-characteristic behavior.

A similar comment could be made about work on the internal control of nest building. The authors could cite detailed studies of only three species, all of which were domesticated. The data available indicate considerable interspecies differences, and a rich field awaits exploration.

Two general points should perhaps be made. First, the many illustrations are generally rather poorly reproduced—a responsibility perhaps of the publishers rather than the authors. Second, one cannot believe that the innumerable studies cited were of a uniformly high quality: the authors have been conscientious

and kind rather than critical. The book remains an invaluable and fascinating synthesis of a scattered literature.—ROBERT A. HINDE.

Biology of the Peregrine and Gyrfalcon in Greenland.—William A. Burnham and William E. Mattox. 1984. *Meddelelser om Grønland, Bioscience* 14. 25 pp., 12 tables, 12 figures. ISBN 87-17-05221-1. Available from Nyt Nordisk Forlag-Arnold Busck A/S, Købmagergade 49, DK-1150 Copenhagen K, Denmark.—Since the discovery of DDT-induced eggshell thinning and its impacts on the reproductive success of Peregrines, extensive research has been conducted to determine its worldwide status and distribution. Extensive research was not conducted in Greenland, however, until 1972 when Burnham and Mattox began their 10-yr study of Peregrines and Gyrfalcons. The study area encompassed 6,050 km² of mountainous terrain in an ice-free region of western Greenland. Both inland and coastal areas were surveyed, largely on foot but also by boat and airplane, to determine the status of historic and currently occupied nesting sites. Environmental and logistical constraints clearly were major and prevented the researchers from visiting all Peregrine and Gyrfalcon eyries each year.

A total of 34 Peregrine nests were located and monitored during various years of the study. On average, 60% of the inland sites checked each year were occupied; of these 84% produced young at the rate of 2.8 per successful pair. Occupancy rates were much lower at the few coastal sites located; in 1974, only 1 of 5 sites was occupied and produced young. Gyrfalcon eyries were located at 22 inland and 14 coastal sites during the study. The authors stated that they were unable to arrive sufficiently early at Gyrfalcon nests to determine the number of pairs that bred; however, they assumed that a similar proportion of these pairs bred each year as was the case for Peregrines.

Analysis of prey remains at Peregrine nests in 1973 revealed that most of the diet was comprised of small passerines (90%), particularly Lapland Longspurs and Snow Buntings. Unfortunately, the methodology used to derive this estimate is not described. Moreover, in Table 7, where these data are presented, the number of samples, the number of prey individuals identified, and whether the table reflects frequency or biomass are not indicated. Gyrfalcons were reported to feed on a variety of prey, particularly arctic hare and Rock Ptarmigan, although small passerines also appeared to comprise a significant portion of the diet.

Evidence is presented that the eggshell thickness of Greenland Peregrines decreased 16% compared with pre-1940 eggs. Although no population declines have been documented, the authors agree with the

conclusions of Walker et al. (1973, *Arctic* 26: 255) that Peregrines are near a critical threshold in levels of contamination and that a small increase in DDE levels could precipitate reproductive failure and population declines. Analysis of Greenland prey species showed low levels of chemical contamination, leading the authors to suggest that contact with these pesticides occurs away from the nesting grounds.

No doubt locating and monitoring nesting Peregrines and Gyrfalcons in Greenland is extremely difficult, and the authors and their many cooperators should be commended for their efforts. Clearly, this study has been successful in providing baseline nesting data on two falcon species nesting in a remote part of the world. Those interested in Peregrines and Gyrfalcons will find the publication a valuable reference detailing aspects of their nesting ecology in the Arctic and will want a copy for their libraries.—MICHAEL W. COLLOPY.

Seabirds of eastern North Pacific and arctic waters.—D. Haley (Ed.). 1984. Seattle, Washington, Pacific Search Press. 214 pp. ISBN 0-91478-X. \$39.95.—This is a typical example of the "coffee-table bird book" genre, in oversized format, with excessive margins, with lavish illustrations, with text that varies from fascinating to frustrating, and without a complete bibliography. It begins with a foreword (by R. M. Lockley), a preface, and an introduction. In the latter, Haley gives a brief description of the surface oceanography of the region, a very brief review of the orders and families of birds to be considered, and in keeping with Pacific Search Press's anthropological interests, a discussion of the importance of seabirds in aboriginal cultures in Alaska, the Pacific Northwest, and Hawaii. The body of the book includes 14 chapters on different families or subfamilies of seabirds by 12 authors and a chapter on conservation by Warren King.

The color photographs in this book are superb. Except for the gulls, terns, petrels, and alcid, most species in each group are illustrated beautifully. In those groups, only representative species are displayed, but again with superb photographs. The text also includes a scattering of charming line drawings, regrettably unsigned.

The text is very readable and mostly well written, although the authors' styles differ greatly. Most chapters are informative, but the book could have profited from a stronger editorial hand. Differences among the chapters in approach and coverage suggest that the authors were not given (or did not countenance) much direction. Mayfield, in the phalarope chapter, discusses the hormonal basis of plumage color, the only really physiological subject in the book. Ainley introduces the cormorant chapter by discussing the etymology of the birds' names, and Anderson

reviews some mythology to introduce pelicans. Some chapters are introduced with personal anecdotes, others with descriptions of the birds' ecological roles. Some authors review population census data for their species, while others do not mention population sizes. Feeding and breeding habits are reviewed for the resident species in each group, but even here, coverage is haphazard. The chapters most dominated by personal anecdotes are among the most readable but tend to contain less biological information.

The absence of a strong editorial presence is most evident in the treatment of seabird conservation. In the introduction Haley reviews the major negative effects of civilization on seabirds, and about two-thirds of the chapters include comments on anthropogenic sources of mortality. King's conservation chapter might have provided a nice synthesis of these disparate comments, but it does not, and reads as if he did not have access to the rest of the text.

The text contains more than its share of simple misstatements, irritating oversimplifications, dubious pet theories, and uncritically accepted canards. I fail to understand why scientists writing for general audiences allow such lapses. They rarely improve readability and usually draw the ire of their scientific colleagues.

In the storm-petrel chapter, Ainley indulges in a pet hypothesis that rump color interacts in some way with climate and is related to migratory behavior, feeding ecology, and timing of molt and nesting. White-rumped species (and populations, within *Oceanodroma leucorhoa*) are supposed to be more migratory, range farther from the colony for food, nest in cooler climates or in winter in warm climates, and molt on different schedules. Even within the eastern North Pacific the data do not fit this claimed pattern very well. Black and Least storm-petrels are at least as migratory as Galapagos Storm-Petrels, and in several respects, the Fork-tailed Storm-Petrel does not fit. Elsewhere the pattern breaks down completely, with dark-rumped *Oceanodroma monorhis* and *O. matsudairae* making extensive interocean migrations and white-rumped *Oceanites gracilis* apparently being quite sedentary.

Howell's tropicbird chapter is quite authoritative and very readable, and in fact is one of the best chapters in the book. He concludes it, however, with speculation that the reduction of the hindlimbs in tropicbirds is an evolutionary adaptation to facilitate hovering, and supports this idea with a comparison of body proportions between tropicbirds and the nonhovering Royal Tern. Other smaller terns that do hover as adroitly as tropicbirds, however, have body proportions similar to those of Royal Terns. I do not wish to give the impression that I oppose hypothesizing, but before publication, speculations ought to be examined, at least for logical consistency and general agreement with the data.

Rice's chapter on boobies is interesting, but in several places unfamiliarity with the seabird literature

shows through. He states that "a fossil gannet of the late Pleistocene was found along the coast of California." Actually, several species of gannets are known from the Miocene, Pliocene, and Pleistocene of California. He designates the Gulf of California the "center of abundance" for the Blue-footed Booby, but Peru and the Galapagos Islands each may have larger populations. He also describes as "unique among seabirds" the shorter-than-annual breeding cycle of some boobies. This is a phenomenon shared by Galapagos Cormorants, Sooty Terns, White Terns, and probably several other tropical terns.

Mayfield seems unaware that Red Phalaropes may winter in numbers in the temperate North Pacific. Maher suggests that only Pomarine Jaegers have breast bands, and Drury implies that Franklin's Gulls nest in southern California. Drury also distinguishes between large gulls, 20-24 inches long, and middle-sized gulls, 20-24 inches long. Harrison repeats the reports of Common Terns laying six-egg clutches, but most evidence attributes these "clutches" to the efforts of two or more females. Manuwal states that Tufted Puffin "has the most extensive latitudinal distribution of any alcid," a distinction that actually belongs to the Common Murre.

The book provides an attractive and informative introduction to North Pacific seabirds, and as such seems most suited to general audiences. Despite its shortcomings, my copy will remain prominently displayed in my home.—WAYNE HOFFMAN.

Vulture biology and management.—S. R. Wilbur and J. A. Jackson (Eds.). 1983. Berkeley, University of California Press. xxii + 550 pp., many tables, diagrams, black-and-white photographs. ISBN 0-520-04755-9. No price given.—This book is a collection of 32 chapters on vulture biology, contributed by 38 authors from around the world, plus a foreword by Dean Amadon. About half the chapters derive from a symposium on vultures, held in 1979 at Santa Barbara, California. The remaining ones were solicited by the editors to deal with topics that were not covered adequately at the meeting. The result is the most complete and up-to-date account yet available on these birds.

After years of neglect by ornithologists, vultures recently have become subject to a great deal of research, stimulated largely by the declining and endangered status that many now have. Most work has been done by individuals or small teams of researchers in widely separated parts of the world, with limited opportunity for contact. The symposium clearly provided a useful, timely forum for the exchange of views, and the book provides a sound source of reference for ideas on future work.

The book is arranged in 8 parts, dealing respectively with palaeontology and systematics (51 pages);

status of the different species, arranged by region (75 pages); general biology (207 pages); study techniques and management (78 pages); contaminants (31 pages); relationships with humans (33 pages); and a very useful bibliography (28 pages). As expected in a multi-author volume, the standards of the chapters vary, but this is partly a consequence of the poor state of knowledge on some species.

The world's vultures are currently split into 22 species, of which 15 are Old World and 7 New World. For those who are unfamiliar with these birds, the book is full of fascinating information. Living on carrion, including rotten meat, vultures seem to have a remarkable ability to resist diseases, such as anthrax, and toxins, such as botulism. Some forage at enormous distances from the nest and carry food in the crop for regurgitation to the young. If the young are threatened, they spew up foul-smelling stomach contents, or collapse and feign death. Moreover, vultures are long-lived, and provide some of the most extreme examples among birds of K-selected species, with long-delayed maturity and low reproductive rates. These various features apparently have arisen twice, in Old and New World stocks, which supposedly evolved on independent lines.

Population declines usually are attributed, at least partly, to destruction of habitat and food supplies. Some species have been affected by the decline in large ungulate populations, and others by the decline in mortality of domestic stock, resulting from improved veterinary attention. Electrocution on electricity pylons is a particular problem in southern Africa, resulting in the deaths of hundreds of Cape Vultures. Persecution is also important in some regions, often on grounds of transmitting disease to livestock, a possibility for which there is no good evidence. The Turkey and Black vultures of North America have been affected by organochlorine pesticides and show a degree of shell-thinning, but the actual impact on their populations is unknown.

Another problem concerns a supposed calcium shortage in the south African Cape Vulture, as described by Peter Mundy. The adults normally give small pieces of bone to their chicks, along with the food, to provide the calcium needs. They pick up splinters of bone that have been smashed by hyenas and other large carnivores. But in ranching areas where such carnivores have been eliminated, vulture chicks often are found with skeletal deformities, unable to fly. In the absence of bone splinters, the adults in these areas bring bits of glass and other artifacts to the nest.

Because they range over large areas, vultures present problems of conservation and management on a scale almost unknown in other animals. Huge areas offering favorable land use and human attitudes are needed to conserve populations effectively. The section of the book dealing with management inevitably is concerned mainly with short-term emergency measures, such as captive breeding and release or the

provision of artificial feeding stations ("vulture restaurants") that also have a role in research and tourism.

For those wishing to learn more about these fine birds, and their conservation problems, this book is well worth reading. Considering the location of the symposium, however, it is a pity that more information is not given on the California Condor. In general, the book is nicely produced. The main disappointment is in the reproduction of photographs, which is poor, even on the cover.—I. NEWTON.

Meadowlark music and other nature sounds.—

Catherine M. Thexton. 1983. One 12-inch 33½ rpm phonodisc; also available in cassette. Order from the author, Box 8, Balmoral, Manitoba R0C 0H0, Canada. Record, \$11.45 Can.; cassette, \$10.95 Can.—This is a new selection of Ms. Thexton's nature recordings from the southern Interlake region of Manitoba. It follows a format similar to that of an earlier production, "In Praise of Spring" (1981). The new recording begins with the sounds of early spring and a flock of American Goldfinches, and ends with a lone cricket chirping on an August evening. All recordings were made on 10 acres of Manitoba farmland that includes a tree-ringed slough, an oak forest remnant, and a spruce windbreak and that borders on hay and grain fields. The recordings are of 30 species of birds as well as a variety of frogs, one squirrel, and some insects. Coverage of each species generally is limited to less than 1 min, with the exception of a Western Meadowlark, which may have its full repertoire of primary song represented. There are no data on the circumstances of each recording, nor any information as to the equipment used. The recordings are of uniformly high quality, however. There are no verbal introductions, and one cut blends imperceptibly (and skillfully) into the other. The listener should have no difficulty in identifying the songsters, using the sequence of common names given by program and band number on the dust jacket. Scientific names appear on the dust jacket but not in the information accompanying the cassette. Considering that the purpose of these recordings is not to aid in identification nor to make a scientific contribution, but rather to entertain and to recreate the mood of the environment of a Manitoba farmyard, Ms. Thexton has achieved her goal. In fact, the recordings make for pleasurable listening!—WESLEY E. LANYON.

Modern falconry: your illustrated guide to the art and sport of hunting with North American hawks.—

Jack Samson. 1984. Harrisburg, Pennsylvania, Stackpole Books. 160 pp., 62 illustrations, 44 photos, 18

line drawings by Victoria Blanchard. ISBN 0-8117-2158-2. Paper, \$12.95.—Jack Samson, former editor and current editor-at-large of *Field and Stream*, has had years of experience as head of the raptor division of the American Museum of Natural History's Trailside Museum at Bear Mountain State Park, New York. The reason "Modern Falconry" was written dates back to an incident occurring in 1975 when he published two articles on falconry in *Field and Stream* ("Hunting with goshawks," by Chuck Keene, and "Hunting with falcons," by Ray Linder). Both articles stimulated a tremendous amount of reader mail, primarily from American youngsters, asking for more information on falconry, and it was decided to write this primer for beginning falconers.

The book makes no pretense at being a definitive work like "North American Falconry and Hunting Hawks" by Frank Beebe and Harold Webster, but its aim is to give the beginner, or interested reader, an idea of what the sport is all about. It was felt by the author that there was a "very real need for a timely, comprehensive, and inexpensive manual on North American falconry." The 21 chapters include such topics as "A brief history of falconry," "The language of falconry," "The hunting hawks of North America," "Raising and training the short-winged hawks," "Releasing a hawk to the wild," and "New federal falconry regulations." The book is well organized and easy to read—reflecting the author's experience as a foreign correspondent, a writer for the Associated Press, and editor of *Field and Stream*. Some people consider falconry a "cruel" sport, but it should be remembered that "a hawk or falcon kills by instinct and does so in nature to survive. If that is cruel all nature is cruel, nature is the way it is and no amount of emotionalism can change that."

The first part of the book discusses the methods used to train a falcon. Since the kestrel is the most readily available falcon, the discussion is centered on this species. Other species of larger falcons are trained in a similar way. Farther along the raising and training of short-winged hawks (accipiters) is discussed. The goshawk is the focus of this section. Jack Samson has had much experience in training and hunting with birds of prey and answers most of the questions that the reader might want answered. There are many regulations governing the sport, and a great deal of knowledge, free time, and dedication are necessary. The federal and state governments require prospective falconers to take an in-depth test on the subject. If the test is passed (80%), then a falconry permit is issued. Since falconry is a hunting sport, not pet keeping, a falconer also must have a small-game hunting license to engage in the sport. Game laws also must be followed. Falconry is the most ecologically sound method of hunting, where the hawk is the hunter and the falconer merely a spectator. "Falconry—Hunting with Hawks—is one of the few surviving hunting sports that dates to the earliest days of recorded human history. It was practiced in Asia—

specifically in China—as long ago as 2,000 years before Christ.” “The English took to falconry like Labrador retrievers to water, and no sport—not even fox hunting from horses—has ever gained the popularity that falconry did in the British Isles, especially during the seventeenth century.” Falconry has come of age in America, and the author hopes this modest manual will help the beginner discover the joys of a sport that began 4,000 years ago. “There is every reason to believe that falconry, if practiced properly and with supervision, can be one of the finest sports available to the veteran and youngster alike who love the outdoors and especially the great birds of prey.”

Most of the important research on raptors has been done by falconers. The Peregrine Falcon might have gone the way of the Passenger Pigeon were it not for the efforts of falconer-ornithologists like Dr. Tom Cade, Dr. Heinz Meng, Frank Beebe, and Harold Webster. These men pioneered in the captive breeding of Peregrine Falcons, and many Peregrines have been released back to the wild, supplementing and increasing the remnant wild populations. Many other species now are being bred in captivity—for use in falconry.

I noted a few places that could use clarification or additional information. The eggs of the Sharpshinned Hawk usually are heavily marked, not plain colored like those of the other two accipiters. It could be pointed out more strongly that the federal regulations permit only birds less than 1 year old to be taken (except kestrels and horned owls). In the discussion of the Gyrfalcon one gets the impression that there are four species instead of merely color phases. Also, Gyrfalcons have been photographed breeding in stick nests on cliffs, but these are nests that Rough-legged Hawks, Red-tails, or ravens had built. Falcons and owls do not build nests but use available ledges, cavities, or stick platforms built by other bird species. Two very important birds used in North American falconry have not been discussed—the Harris' Hawk and the Red-tailed Hawk. Both are excellent at catching rabbits. For tameness and versatility the Harris' Hawk probably has no equal. The disease “frounce” can be treated with enheptin, but recently a better product, emtryl, has been developed. A single pill, hidden in a piece of meat and swallowed by the hawk, does the job. The protozoans that cause frounce, found in pigeon crops, are killed by several days of freezing but probably not by just cooling the meat. Cramp (a crippling of the feet) actually is caused by a vitamin D deficiency (rickets). If very young hawks, taken at 1 or 2 weeks of age, are fed only meat, their bones will not develop properly and they will be unable to stand. Bones are necessary in their diet. Somehow a photo of a kestrel head found its way into the space (p. 98) where a Prairie Falcon's head should be. The photo “recovering a lost falcon from a tree” (p. 109) might better read “goshawk.”

“Modern Falconry” is an informative book that fulfills the author's aim: to “help newcomers who

are loaded with determination to channel it toward the rewards of a deeply satisfying and thrilling sport.” It also will provide the average person with the means of gaining a real understanding of what this sport is all about.—HEINZ MENG.

Bobwhites in the Rio Grande Plain of Texas.—Val W. Lehmann. 1984. College Station, Texas, Texas A&M Univ. Press. xv + 371 pp., 223 black-and-white photos, 20 color plates, 45 figures. ISBN 0-89096-186-7. \$20.00.—If one were to name the individual most qualified to write about Bobwhites in the southwest, it surely would be Val Lehmann. Lehmann, now retired, spent the better part of a lifetime working with this important gamebird in south Texas, beginning in 1936 with the Cooperative Wildlife Research Unit at Texas A&M, later with the Texas Game, Fish, and Oyster Commission, and finally from 1945 through 1972 as wildlife manager of the famed King Ranch. The setting for his book is the 22-million-acre Rio Grande Plain of south Texas, a vast, semiarid region made alternately hospitable and hostile to Bobwhites and cattle alike by the vicissitudes of weather, especially rainfall. Lehmann's intimate knowledge of, and appreciation for, the region's history, ecology, and wildlife are clearly evident from previous scientific publications and from an earlier book “Forgotten Legions: Sheep in the Rio Grande Plain of Texas.”

His present effort represents the culmination of more than 40 yr of observing, studying, and managing Bobwhites. It is a sturdy, handsome volume, richly illustrated with nearly 300 drawings and photographs, including some of the best color photos of Bobwhites that I have seen. The text is organized into three major sections. Part One, *Life History*, emphasizes inter- and intracovey organization, individual and group movements, nesting, and reproduction. Part Two, *Management Considerations*, deals with factors that influence Bobwhite abundance, including climate, soils, food, cover, predators, parasites and diseases, interspecific competition, hunting, and land use. The final section, *Management Recommendations*, outlines methods for increasing, or at least stabilizing, Bobwhite numbers on southwestern rangeland.

As noted on the dust jacket, Lehmann writes in an easy, informal style, and his text is filled with historical references and personal anecdotes. This makes for entertaining reading, although we sometimes are supplied with more detail than perhaps we care to know, such as when we are told that “When Almon Linney was planting corn on the J. J. O'Brien Ranch, in Goliad County, on April 7, 1941, approximately 50 pounds were spilled at the end of a turnrow” (the point being that a quail attempted to nest in the spilled grain) or that “Domestic turkeys were seen in

the act of destroying a quail nest with 10 eggs inside Ed Koy's turkey yard, in Colorado County, on July 15, 1938."

Lehmann's dedicated, long-term efforts produced a vast amount of tabular data (83 text and 27 appendix tables), mostly from trapping and banding and from visual observations and counts. Unfortunately, there is relatively little in the way of data reduction and analysis; results of the fieldwork are often merely chronicled in the text. Admittedly, application of inferential statistics would have been inappropriate in many instances owing to the nature of the data; however, even the use of descriptive statistics is scanty. The author illustrates or supports his ideas primarily by citing examples taken from larger data sets. Professionals will find it difficult to evaluate many of these findings and conclusions because of the less-than-rigorous treatment of field data. Non-professionals, on the other hand, sometimes may be overwhelmed by the sheer volume of raw numbers.

Much of the above criticism is directed toward Part One of the book, its weakest section. This material on life history is presented in 22 chapters, 11 of which deal mainly with seasonal covey organization and movement. The treatment of population dynamics (only 2 chapters totalling 16 pages) is disappointingly cursory, especially in view of the seemingly inordinate emphasis on covey organization.

In Part Two, Lehmann provides a tighter, more balanced discussion of the edaphic, climatic, and biotic factors that influence Bobwhite abundance in the southwest. Throughout, he stresses the critical importance of moisture: "... rainfall unquestionably is the life factor most often deficient and hence most often limiting. . . . To miss either the spring or fall rainy period is for bobwhites to suffer decline." In discussing predators and their control, Lehmann describes a massive effort to reduce coyotes on the King Ranch in the late 1940's and early 1950's. During an 8-yr period, an estimated 10,000 coyotes and 1,800 bobcats were trapped or poisoned. The apparent immediate effect was a dramatic rise in numbers of white-tailed deer and wild turkeys, and a lesser response from Bobwhites. These increases were short-lived, however, as limitations of habitat and rainfall again exerted control on the wildlife community. Lehmann notes that selective predator control is potentially effective only where habitat is adequate and hunting is properly regulated. Notwithstanding the Bobwhite's acknowledged ability to sustain high annual yields, Lehmann believes that harvest regulations sometimes may be too liberal for prevailing conditions. He is especially critical of the increasingly popular methods of quail "hunting," which include baiting, ground shooting, and shooting from elevated perches on vehicles. Here as elsewhere, however, Bobwhites are less threatened by the gun than by land-use practices designed to increase "pro-

ductivity." Lehmann notes that "Man's attempts to improve the productivity of rangeland for cattle have centered on the reduction of weeds and shrubs [which] . . . are often the most dependable and certainly the most nutritious bobwhite foods." He further observes that large-scale brush eradication, "a veritable obsession in the 1960's and 1970's," did not provide the anticipated increase in cattle production. "The real limitations, now and forever, are defects of climate and soil. Overzealous large-scale battles against brush have jeopardized and in some instances destroyed wildlife resources of greater value than livestock. As yet we have done precious little to recognize, much less repair, the damage. A new approach based on a much broader view of the total land resource, its assets and its defects, is perhaps the greatest legacy that we can pass to those who follow."

The book concludes with an authoritative discussion of quail management on semiarid rangeland. Here, Lehmann's vast experience is evident as he outlines both general and specific recommendations for improving Bobwhite habitat within the framework of the area's prevailing agricultural interests and the limitations of its climate and soils.

As indicated by its title, this book is distinctly regional in scope and purpose. As such, it will be of interest and value primarily to wildlife biologists, sportsmen, and landowners and managers in the southwest. Quail biologists elsewhere also will probably want to add this volume to their personal libraries. Despite some shortcomings, principally in the organization, presentation, and analysis of data, Lehmann's book contains a great deal of information and insight about the Bobwhite in particular, and about the history, ecology, and management of southwestern rangeland in general. Not to be overlooked, too, is the book's surprisingly modest price of \$20.00.—
JOHN L. ROSEBERRY.

Wood warblers' world.—Hal H. Harrison. 1984. New York, Simon and Schuster. 335 pp., 24 color plates, over 200 black-and-white photographs. ISBN 0-671-47798-6. \$19.95.—Hal Harrison has studied wood warblers in the field for over 30 years, and his latest book clearly reflects this breadth of experience. Richly illustrated with photographs, most by the author, this book focuses primarily on the 53 paruline species known to nest north of Mexico.

In the general introduction, Harrison briefly explains wood warblers' current taxonomic position, then gives a short description of warbler nest cycle and behavior. The migration section mentions the southern ancestral home theory and a bit about ecological interactions between tropical residents and

migrant warblers; nothing is said about navigation abilities. The section on winter gives little information on areas south of the U.S., but contains interesting North American winter records. In the last section of the introduction, the author is particularly eloquent in making several important points on the subject of conservation.

The main body of the book is the 53 species accounts; major hybrids also are discussed briefly. A quite useful glossary follows (though was it really necessary to include "life list" here?). There is also an excellent bibliography with more than 250 entries.

The photographs in this book are stunning. The 24 color plates, composed of 55 photographs, cover 51 of the book's 53 species. Included here is the only color photograph of a Bachman's Warbler I've ever seen. The black-and-white pictures are also superb. Besides many excellent portraits of adults (often pairs) and of fledglings, there are shots of the nests of 49 species (two more are shown in the color plates) and pictures of typical nesting habitat(s) of all but the Rufous-capped Warbler—wonderful coverage indeed.

The species accounts are full of information, and written in a flowing, easily readable style. Much detail is given on nests and eggs, as befits a book by the author of the two Peterson nest field guides. Harrison adds personal anecdotes, drawn from his extensive field experience with warblers, that make the work come alive for the reader.

One useful feature is the pronunciation guides for scientific names. People tend to learn these far more easily once they've heard them; Harrison accomplishes this in written form. Another useful feature is the written renditions of the common songs. Harrison recognizes that people hear differently, and often gives more than one person's interpretation of a song: a luxury for which most field guides simply don't have space.

Each species account ends with a map claiming to show the breeding range of that species. This is an excellent idea. However, for many species, the maps do not indicate the species' whole breeding range. The first real shock comes on p. 77, where a small dot in Texas is labeled "Breeding range of Colima Warbler." Similarly, the map on p. 98 clearly indicates that Yellow Warblers come to a screeching halt at the Mexican border. Personally, I wish the maps did indicate the entire breeding ranges, since this would add greatly to the value of the book. However, having decided to give more restricted information, the author should have labeled his maps more accurately.

A bit frustrating is the frequency with which Harrison reports how many nests he has found containing cowbird eggs, without divulging the total number of nests inspected. Occasionally there are minor lapses indicating a certain lack of theory, such as giv-

ing a single number for the clutch size of a wide-ranging species. Moreover, one wonders if Harrison thinks parental investment applies only to males. On p. 120, he states that female Black-throated Blue Warblers, very wary early in the breeding season, become "surprisingly" fearless later on. Similar is his unfounded assumption that the more cautious Lucy's Warbler mentioned on p. 81 was a female. Given the relative parental investment at that stage, it may well have been a male, where it would more closely parallel the behavior of the male Blackburnian Warbler mentioned on p. 154.

These criticisms are all minor. Overall this book is a fine contribution to the semipopular ornithological literature. Packed full of information, it is well organized and extremely readable. The photographs alone are well worth the price. I strongly recommend it to anyone, both amateur and professional, who has an interest in our North American wood warblers.—
SUSAN M. SMITH.

Kirtland's Warbler: the natural history of an endangered species.—Lawrence H. Walkinshaw. 1983. Bloomfield Hills, Michigan, Cranbrook Inst. Sci. Bull. 58. xii + 207 pp., 55 tables, 45 figures. ISBN 87737-035-4. Paper. \$11.95.—Prospective readers of this new book on the interesting and endangered Kirtland's Warbler should not expect to find a work that replaces Mayfield's 1960 book (Cranbrook Inst. Sci. Bull. 40) as the standard source for information about the species. The two books have approximately the same number of text pages and share a similar set of chapter headings, but they differ from each other in a number of important ways. Mayfield's book is based on a compilation, condensation, and careful analysis of all of the then available published and unpublished information on the warbler. It is also very readable and essentially error-free. In contrast, Walkinshaw's book is based almost entirely on data gathered from his own field work (exceptions are his Chapter 4 on distribution and Chapter 14 by Mark Bergland on factors affecting nesting success), and it appears from the plethora of numerical and other information presented that he reports nearly all data he ever gathered, whether or not there is anything to be learned from it. Furthermore, most of the time the results of data analysis are not subjected to statistical testing and some questionable conclusions result. The book is difficult reading owing in part to the liberal use of numbers throughout the written text and the frequent interruption of text material by tables and figures (over one-half the text pages have full to half-page tables or figures). Errors and other sources of confusion are encountered rather frequently throughout most of the book. All of the above

is not to say that the book is without merit but mostly to point out that it does not replace Mayfield's book as *the* book on the "life history" of the Kirtland's Warbler.

The potential value of Walkinshaw's book lies in the post-1960 data presented on various aspects of the species' breeding biology. Walkinshaw studied close to 300 nests, mostly from 1966 through 1977, and has genealogical information on a large number of banded birds. As nearly as I can tell, data from these additional nests do not alter Mayfield's conclusions on such topics as clutch size, incubation period, hatching and fledgling success, etc. However, since these nests were studied immediately before and after control of the Brown-headed Cowbird was initiated, his data present new information on the effect of this control on the rate of parasitism (greatly reduced) and the nesting success of the warblers (greatly increased).

Some of the more interesting and potentially useful information to ornithologists and population biologists is found in Walkinshaw's data gathered from banded birds. For example, 47 birds banded as nestlings returned to breed, some of them returning for up to 7 years. From this information it is possible for Walkinshaw to show that clutch size does not vary with age, and that young males breeding for the first time tend to select younger stands of pine than those in which they were raised. He also has over 150 returns of birds banded as adults, many of which also returned for multiple years. Walkinshaw's careful observations of individually identifiable birds also enabled him to gather data on such difficult-to-study things as age of fledglings at last feeding by a parent and the rate of survival of fledglings to independence. He also found additional records of polygyny and discovered one polygynous male that simultaneously held two nonoverlapping territories separated by 0.8 km.

In my opinion, the best use of this book will be made by persons searching through Walkinshaw's nesting data and/or individual genealogies to find information useful as data or comparative material for their own studies. However, prospective users should be forewarned to expect to encounter errors and other sources of confusion that are likely to complicate their task. The following is a sample of problems I noted in the first five chapters:

Table 1 lacks a key to abbreviations used, a capital "I" is used instead of the number "1" in six places resulting in an entry of "IM" instead of "1 M," and the total number reported here of banded nestlings that returned to breed does not agree with the totals in Tables 13 and 14.

Table 2 shows the number of singing male Kirtland's Warblers counted by the author for 17 years in 5 localities. We are not told whether these counts were made on the official census days or at other

times, nor whether the counts are supposed to represent the total male populations at those localities.

For Tables 3 and 4 we are not told the study areas to which the counts refer. Also, the last column of Table 3 is headed "TMWB" while in the key it is listed as "TMBW."

In the second paragraph on p. 10 the reader is referred to information in Table 6 that is actually in Table 1.

On p. 14 the Magnolia Warbler is described as having a white breast (actually yellow with black stripes).

On p. 15 Walkinshaw states that "One-year-old males had shorter wings than older adult males." His sample size is very small, the data overlap, and the slightly different means undoubtedly are not significantly so.

In Table 6 reference is made to Ryel 1980a and 1980b—the "selected" bibliography has only one 1980 entry for Ryel.

In the first paragraph on p. 34 the author flatly states that "the total 1978 count was 396 adult birds at the beginning of the breeding season," even though he has just explained that this number was arrived at by estimating the number of females (assuming one for each Michigan male). Also, in this same paragraph, the reference to Table 2 should be to Table 6, and another reference is made to the nonexistent "Ryel 1980b."

Similar errors and other forms of confusion appear in the remainder of the chapters written by Walkinshaw. However, since most of the numerical information presented in the book is in the latter chapters, the errors and difficulties encountered there are often more complex than those just mentioned above. Detailing those difficulties here would be similarly complex and require the use of too much space, so I believe it prudent to simply caution potential users to exercise care in extracting information for their own use.

Chapter 14, written by Mark Bergland, is a statistical analysis of factors that may influence the nesting success of the Kirtland's Warbler. It is a well-written and carefully analyzed study that is a follow-up and expansion of an earlier study by Anderson and Storer (1976, *Jack-Pine Warbler* 54: 105). Bergland has used additional nest data and evaluates some factors not previously considered (e.g. success in jack pine plantations vs. natural jack pine regeneration). His conclusions are essentially the same as those of Anderson and Storer, namely that in addition to cowbird control, nesting success also is affected positively by flat terrain and the absence of large trees/snags, and apparently not affected by the other variables considered.

Despite the book's shortcomings, it does make much of Walkinshaw's data on the Kirtland's Warbler available for use by others, and I am sure good use will be made of some of it.—NORMAN L. FORD.

The birds of San Diego County.—Philip Unitt. 1984. San Diego Society of Natural History, Memoir 13. xxiii + 276 pp., 12 color plates, 12 text figures, 129 maps. ISSN 0080-5920. Order from the Society, P.O. Box 1390, San Diego, California 92112 USA. Cloth, \$20.00; paper, \$14.00 (plus \$2.00 shipping; add 6% sales tax in California).—San Diego County, California is larger in area than 2 of the 50 states (combined), its geographic (and thus biological) diversity ranges from the seacoast across mountains of nearly 2,000 m elevation to extreme desert, it is the southwesternmost county of the contiguous U.S., and it is inhabited by dedicated birders whose observations have boosted the county list to more than 450 species. "The Birds of San Diego County" provides detailed information on the geographic, ecological, and temporal distribution and abundance of each of the 449 species of native birds reported in the county—for some, by subspecies. Maps of breeding distribution are presented for 129 of the 181 breeding species (of which 26 are considered to be extirpated or only occasional breeders). Ecological zones and terms of abundance are defined precisely, and the definitions are adhered to. Welcomed absent are long paragraphs of descriptive and generalized information.

An introductory section of 23 pages gives a historical overview, definitions, sources of information, comments on nomenclature, and, most importantly, describes and illustrates the geography and vegetation of the county. The body of the text (211 pages) consists of species accounts. This is followed by a list of 6 introduced species, a list of species inadequately or erroneously reported, a few pages of addenda, a systematic list of the species, the bibliography, and the index.

The species accounts begin with a summary statement of abundance in the various seasons and an analysis of habitats (ecological areas) in which the birds are found. For migrants, dates of early and late occurrence are mentioned, by area if the status differs markedly (as it sometimes does between desert and coastal lowlands, for example). Egg dates are mentioned for breeding species, and maps of present and past definite and probable nesting records are given. (The numbered maps are not referred to in the text.) Gaps in the present knowledge are pointed out, and differences in former and present distribution and abundance are discussed. If more than one subspecies occurs in the county, they are treated separately to the extent that information permits, and taxonomic problems or differences of opinion are discussed.

Most of the recent information is based on birders' observations, many published in *American Birds*. There are some hazards in relying so completely on information of this kind. Birders tend to look for the unusual, the rarity, and pay less attention to the common. This is reflected in the uneven treatment of the species. Common resident birds average much shorter accounts, with less detailed information, than rare migrants. Birders also tend to go to favored localities,

so that there are probably more records from the Tijuana River Valley than the entire desert region. The bias of concentration in the coastal zone is noted in the text. Species that are considered endangered or that are polytypic within the county receive the longest accounts.

The book apparently was completed in late 1981, considerably before its publication in 1984. An addendum gives important information received through December 1983, including records of 4 species and 2 subspecies new to the county (an indication of the rate of growth of the known avifauna), which did not make it into the main accounts or the summary List of Species. This publication lag overlapped publication of the 6th edition of the A.O.U. check-list, so the English and scientific names used by Unitt are a combination of those in the old 5th edition and more recent sources. The arrangement of the species of shorebirds and the sequence of passerine families does not follow either edition of the A.O.U. check-list, but the table of contents and index make it easy to find any species.

There are some unfortunate discrepancies between the species accounts and the Summary List. The California Gnatcatcher (*Poliotilta "californica"*) is separated from the Black-tailed (*P. melanura*) as a species in the list, but only as a subspecies in the account. The Orchard and Northern orioles (*Icterus spurius* and *I. galbula*) are combined in the list, probably as the result of a typo. The Black-throated Sparrow (*Amphispiza bilineata*) is omitted from the list.

Users of this volume who are interested in subspecies may share some of my concerns about the taxonomy at that level. In discussing the Solitary Vireo (*Vireo solitarius*), Unitt allots the few breeding records and most migrants and winter visitors to the race *cassinii*; a few others he assigns to *plumbeus*, and some are considered to be *solitarius*. Noting that all records of *plumbeus* are since 1969, he suggests that the migratory habits of the subspecies may be changing. No similar suggestion is made for *solitarius*, whose records date only from 1971. No specimens of either of these more easterly races have been taken. I suggest that the recent reports of those subspecies (and of other subspecies throughout the book) may reflect the birders' growing awareness of geographic variation and the beginning of their assumption that accurate subspecific identification is possible in the field. I am not convinced that that assumption is valid, and note most such identifications with a degree of skepticism. In other instances, the subspecies occurring in the county in a given season (winter for *Certhia "familiaris,"* breeding for *Cistothorus palustris*) is purely speculative, for lack of documenting specimens. One cannot say categorically that any of these identifications is right or wrong, but these examples (among many) point out the need for judicious (or even wholesale) collecting of specimens. Unitt comments many times on the need for specimens. Their present lack probably reflects both the birders' gen-

eral reluctance to collect and the short-sighted permit-issuing policies at both the federal and state level. On the other hand, Unitt did not take advantage of all the specimens available. A. W. Anthony's collection, now in the Carnegie Museum, was not studied, and some material in the SDNHM was not identified to the subspecies level.

In a number of species accounts and in the list of species inadequately reported (a "hypothetical" list), published observations, mainly from *American Birds*, are questioned or considered to be erroneous. Unfortunately, the basis of the doubt is not always indicated, and often there is no indication of what species the record may actually refer to. The hypothetical list includes two introduced species of which the records are valid but the current status of the species is in doubt. A separate compilation of presumed invalid published records would provide useful information for workers who use records from *American Birds* for distributional and analytical studies.

This review cannot be complete without mention of the 12 color plates by Allan Brooks nestled in the center of the book. These plates are from previously unpublished watercolors rendered in the early part of the century; the originals are from the Ellen Browning Scripps collection now in the SDNHM. They are typically excellent Brooks paintings and are by themselves worth the price of the book.

In summary, I recommend this book as a companion to the state bird books in personal and institutional libraries. It will be a well-used reference for those interested in distribution, and it will serve as an example of what a dedicated corps of birders, and a dedicated compiler, can accomplish.—RICHARD C. BANKS.

ALSO RECEIVED

Seasonal spermatogenesis in the Mute Swan (*Cygnus olor*).—Haide Breucker. 1982. Würzburg, West Germany, Springer-Verlag. vii + 94 pp., 30 photographs. ISBN 0-387-11326-6. No price given.—The book opens with a brief introduction to reproductive biology and discusses the need for morphological studies in this field. A review of the literature on spermatogenesis in birds follows. The major chapters are devoted to a detailed morphological description of gonadal development and regression in the Mute Swan. The text is largely technical, and a basic understanding of anatomy and reproductive biology is required. However, the discussions at the end of each chapter are easier to understand, and the author does a good job of relating his research to other studies on avian reproduction. Those who have a particular interest in vertebrate reproduction will find this book most valuable.—NEIL SABINE.

Historia natural del Curiquinque *Phalacrocorax carunculatus* en los paramos.—T. De Vries, J. Black, C. De Solis, and C. Hernandez. 1983. Quito, Ediciones de la Universidad Católica. Available from the senior author, Department of Biology, Universidad Católica, Apartado 2184, Quito, Ecuador. \$7.00 postpaid.—The life history of the Carunculated Caracara, one of the most conspicuous birds of the paramo of southern Colombia and Ecuador, was almost unknown before this study. The major previous reference dates from 1902.

The caracara lives in a windy, rainy, cold (8.5–12°C maximum air temperature) environment where food apparently is difficult to find. Parental neglect of eggs and young is common and reproductive success low in exposed nests. Number of feedings per hour ranges from 0.6 to 2.6, but average meal size is low, only 10–20 g. Earthworms form the bulk of the diet, although rodents, birds, and carrion also are important.

The authors review the role of the caracara in Ecuadorian folklore. This species is regarded as a good-luck talisman and sometimes is kept with domestic fowl, with which it is believed to interbreed, producing excellent fighting cocks!

The two-page discussion is disappointingly short. The authors could have discussed the caracara's adaptations to its severe climate and compared its life history with that of the other caracaras and the rest of the Falconidae. Nevertheless, this is a useful publication for anyone interested in caracaras or the ecology of the Andean paramo.—DAVID CAMERON DUFFY.

A rage for falcons.—Stephen Bodio; illustrations by Jonathan Wilde. 1984. New York, Nick Lyons/Schocken. 135 pp. ISBN 0-8052-3931-6. Cloth. \$16.50.—Not a *love* for falcons, nor even a *mania* for falcons, but *A Rage*. . . The title is a giveaway; the reader is warned not to expect balance, nor should he seek accuracy—too often hyperbole holds sway. For example, "Pigeons carry so many hawk diseases that until recently a more delicate hawk living on them was playing Russian roulette." Pigeons don't carry many hawk diseases. The truth is that many pigeons carry two common hawk diseases: trichomoniasis and herpes virus.

This book is well written in a tough, sportswriter's tone. It contributes little to ornithology. It is written to entertain experienced falconers who know the lingo and can distinguish between a bewit and a long-winger. The pen-and-ink drawings by Jonathan Wilde are sensitive, and often exquisite.

There used to be a more or less unwritten rule that falconry books be privately printed and distributed almost exclusively to falconers. This lack of advertising was intended to preserve a limited resource—

falcons, to keep riff-raff out of the sport, and to keep our standards high. Bodio's well-advertised book ignores this rule. He has written toward his title.—FRANCES HAMERSTROM.

Ecological study of bird hazards at Indian aerodromes. Phase II, Delhi, Bombay, Hindan.—Salim Ali and Robert B. Grubb. 1984. Bombay, Bombay Natural History Society. ix + 96 pp., 9 text figures, black-and-white photographs. No price given.—Survey of bird strikes at four locations in India. Data include species identified in strikes as well as all species recorded from airports and surrounding buffer zones. Many birds considered to have the highest hazard potential are large raptors or corvids whose numbers are supported by human activities in areas adjacent to the airfields.—A.H.B.

Ecology and evolutionary biology.—George A. Salt (Ed.). 1984. Chicago, Illinois, University of Chicago Press. 130 pp. ISBN 0-226-73443-9. Paper, \$7.95.—A collection of seven essays, of variable length, on theory structure and testing in ecology. Special focus on

the role of competition and related processes such as causal forces makes the philosophical aspects sprightly and interesting. The material is reprinted directly from the November 1983 issue of *The American Naturalist* (vol. 122, no. 5).—A.H.B.

Fifty common birds of Oklahoma.—George Miksch Sutton. 1984. Norman, University of Oklahoma Press. 113 pp., figures. No price given.—This fourth printing of this little volume is vintage Sutton, and filled with charm. Descriptions of 50 species are matched with plates assembled from a variety of sources. The Foreword, which discusses how species choices were made, apparently is also from the original (1977) edition. The quality of the plates is variable; they cover a good number of Sutton's productive years. More information on their dates and the artistic media used would be useful.

The species accounts include a smattering of Sutton's experiences, some traditional natural history, and his observations on the environment of Oklahoma. Each is written with care and shows Sutton's appreciation for the existence of birds.—A.H.B.

(continued from p. 628)

ollect. Among natural English names for American birds are Bobolink, Chewink, Kingbird, and many others. Such as these not only more than hold their own, but are as great aids to the spread of knowledge as the Ptilogonys kind are hindrances; while such as Wilson's Thrush can only be accepted as provisional, until the better knowledge of the bird and its sur-

roundings shall result in the evolution of an English name founded on true principles.

ERNEST E. T. SETON,
of Manitoba.

Glen Cottage, Howard Street,
Toronto, March 21, 1815 [sic].

100 Years Ago in The Auk



From 1885, Auk 3: 316-317:

The Popular Names of Birds.

TO THE EDITORS OF THE AUK:—

"Sirs: The 'powers that be,' I understand, are preparing a 'Check List,' and revising the scientific and popular names of our birds.

"There is no doubt that scientific names are entirely in the hands of scientists, but it seems to be overlooked that popular names are just as completely in the hands of the people. Scientists may advise, but not dictate on this point. A short analysis of the principle of common names may place the matter in a new light.

"A bird's name, to be popular, must be distinctive, and in accordance with the genius of our language. Examples of such are Thrush, Rail, Heron, Hawk, Crane, Night-Jar, and many others. These are truly popular names, evolved originally out of a description, handed down and condensed and changed until they have assumed their present terse, abrupt, and, to a foreign ear, uncouth forms, but, nevertheless, forms in accordance with the pervading spirit of the Saxon tongue; or, in other words, they are *really* popular.

"On the other hand, look at the so-called popular, but really translated, scientific or spurious English names given to our birds, taking as examples the following: Baird's Bunting, Leconte's Sparrow, Wilson's Green Black-capped Flycatching Warbler, Bartram's Sandpiper, Sprague's Lark, Wilson's Thrush, Black Ptilogonys, Semiplumated Tattler, Fasciated Tit, Florida Gallinule, etc.

"Surely, the gentlemen whose names are applied to these birds have not so slight a hold on fame as to require such aids as these to attain it, if indeed aids they be, which I question; for such nomenclature *cannot* stand the test of time.

"If you show to an 'out-wester' the two birds mentioned above as Baird's Bunting and Leconte's Sparrow, and tell him that these are their names, he will probably correct you, and say one is a 'Scrub Sparrow,' the other a 'Yellow Sparrow.' Convince him that he is wrong, and in a month he will have forgotten all but the names he formerly gave them; they are so thoroughly appropriate and natural that they cannot be forgotten. The next name in the list above given is clumsy enough to strangle itself with its own tail. A lad on the Plains once brought me a *Neo-*

corys spraguei, and asked its name. I replied that it was Sprague's Lark. Soon afterward he came again; he could not remember that name; so I told him it was a 'Skylark,' and he never forgot that. On the Big Plain that seed was sown, and not all the scientists in America can make, or ever could have made, the settlers there call that bird anything but 'Skylark.' And I consider that lad precisely represented the English-speaking race; he rejected the false name, and readily remembered the true one, and was aided by that which was apt and natural. No better illustration could be given on the fact, that phraseology may be the life or death of a cause, according as it is happy or unfortunate.

"A similar instance is the case of 'Bartram's Sandpiper.' Ever since Wilson's time this name has been continually thrust into the face of the public, only to be as continually rejected; 'Upland Plover' it continues to be in the east, and 'Quail' on the Assiniboine, in spite of Bartram and Wilson, and will continue so until some name, answering all conditions, is brought forward; for here, as elsewhere, the law of the survival of the fittest rigidly prevails. As an example of the fit ousting the false, note how, in spite of scientists, 'Veery' is supplanting 'Wilson's Thrush' throughout the length and breadth of the land.

"The spurious English names scarcely need comment, they so evidently contain in themselves the elements of their own destruction. Imagine a western farmer being told that a certain songster was a 'Ptilogonys.' In spite of the books, the other three examples cannot hold ground against 'Willet,' 'Ground Wren,' and 'Waterhen,' respectively.

"The purpose of a Check List that includes English names is, I take it, not to attempt the impossible feat of dictating to our woodmen what names they shall give their feathered friends, but rather to preserve and publish such names as are evolved in the natural way,—names which are the outcome of circumstances. Only in case of egregious error is a common name to be superseded; and in doing this it must be remembered that no name can be popular unless true to the principles of the English tongue. It must be short, distinctive, and, if possible, descriptive. Of this class are Veery, Junco, and Vireo. These are the only successful artificial names that I can at present rec-

(continued on p. 679)

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