AN. INST. BIOL. UNIV. NAL. AUTÓN. MÉXICO 42, SER. ZOOLOGÍA (1): 87-98 (1971)

AVIAN BREEDING CYCLES: ARE THEY RELATED TO PHOTOPERIODS?

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ABSTRACT

Certain aspects of the behavior of wild birds are shown to be incompatible with the speculations, theories, and supposedly "proven facts" of physiologists working on caged birds indoors. The value of this unsophisticated, over-simplified experimentation for an understanding of Nature is seriously questioned, and particularly the claim that photoperiods control breeding schedules.

The breeding seasons of wild birds are not always sharply set off from non-breeding seasons. They also vary greatly in timing, though most north temperate zone species breed in late winter or spring, thus allowing their young to achieve independence during warm or hot weather; this is true of most desert birds, as well as those of more mesic environments.

Certain ecological tendencies related to rainfall and seasons of growth and flowering, generally thought of as tropical, are shown to extend into extra-tropical North America, and one of them (late summer and early autumn nesting of grassland birds) probably also to the Riu Kiu Islands south of Japan. The other tendencies concern late nesting of water-birds and late autumn nesting of resident, non-migratory nectar-feeders. Some breeding schedules are unstable, notably those of *Aimophila* sparrows, which vary greatly from year to year according to the rainfall pattern, at least in some regions. *A. cassini* almost certainly, and a few other birds probably, raise at least two broods per year *in different regions!* Many more data on actual nestings, in the wild, are needed, for many species. Certain subjects for study are suggested.

RESUMEN

Se hace notar que las aves silvestres se comportan en la naturaleza en forma tal que no se pueden ajustar con las especulaciones y teorías de los fisiólogos que investigan sobre la base de aves enjauladas en los laboratorios; ni siquiera concuerdan con sus supuestos "hechos comprobados". El valor de esta experimentación sencilla, sin complicaciones, para un entendimiento de la naturaleza se considera bastante dudoso. Sobre todo se duda que el fotoperiodismo controle el régimen reproductivo.

Se señala la imposibilidad de una distinción clara entre las épocas de reproducción y de descanso en ciertas aves. Las estaciones de la cría son muy variadas temporalmente, aunque la mayoría de las especies anidan en la primavera o en las últimas semanas del invierno; de esta manera los polluelos alcanzan su independencia durante las temporadas calurosas. Esto es cierto tanto de las aves de los desiertos como de las de otros ambientes.

Se registra la extensión hacia el norte de ciertas tendencias tropicales que se relacionan con las épocas de lluvias y de crecimiento y floración de la vegetación. Éstas son la anidación en verano u otoño de aves acuáticas o de sabanas y, en otoño, de las que se alimentan de néctar.

La temporada de la reproducción es poco estable entre ciertas aves, en especial de los gorriones del género *Aimophila*, pues varía notablemente de año en año en cier-

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tas regiones, según el periodo de lluvias. *A. cassinii*, casi con seguridad, y probablemente unas pocas otras especies de aves, anidan dos veces (o más) al año *en regiones bien separadas*. Debido a tanta complejidad, se requieren muchos datos adicionales sobre anidaciones, en el campo, de muchas especies. Se hacen sugerencias para el estudio de ciertos problemas.

From the vast but scattered literature on the nesting of birds have emerged several discussions of factors that stimulate breeding; see Marshall, 1961; Mayaud, 1950: 539-542; Van Tyne and Berger, 1959: 313-315; Wagner, 1960; and Welty, 1962: 145-149. Nevertheless, the complexity and diverse *timing* of reproductive behavior remain poorly appreciated. Thus, even to so knowledgeable an ornithologist as Moreau (1969: 62), "the Sooty Falcon [*Falco concolor*] is of extraordinary interest because it shares with Eleonora's Falcon [*F. eleonorae*] the distinction of being the only species of bird that in any part of the north temperate zone starts to breed only after the summer solstice . . ."

PHOTOPERIODISM AND OTHER INDOOR EXPERIMENTS

Moreau's statement reflects the now universal belief in the importance of photoperiods (lengthening days) in inducing breeding. This credo, and similar over-simplifications, reached an extreme in Mayr's symposium on "Adaptive Evolution in Birds" (12th International Congress, Helsinki). There Miller (1960) treated breeding seasons as follows: "In approaching the subject of birds' responses to latitude, we may first recall and stress the fact that as a class birds are eye-minded and eye-controlled . . . It is a natural correlate of this circumstance that photoperiods and a certain range of light intensities are responded to in some way by all birds. . . .The one global regularity controlling the seasonal environment of all animals is latitudinal position and with it the corresponding light phenomena. An important part of the latitudinal light environment is the variation in length of the photoperiod, and because of the aforementioned impress of light on bird activity, essentially every species of the group must adjust to it . . . Birds will then be controlled seasonally by photoperiodism in more and more restrictive fashion with increase in latitude." Miller concluded that "at latitude 10°, and probably even at 5°, the influences of seasonal photoperiod *per se* are detectable in the majority of species". This sweeping, indeed monolithic, claim was *wholly* unsupported in Miller's surprisingly brief list of references, unless one so interprets Skutch's (1950) general summary of a quite complex [1] situation in Costa Rica, where laying reaches its peak in April, while "relatively very few birds nest . . . from September to February, inclusive" (The photoperiod declines, of course, from late June to late December). Simultaneously Wolfson (1960) stressed photoperiods as the leading factor controlling birds. Nonetheless photoperiodism has been disproved as a major factor in northwestern Africa (Heim de Balsac and Mayaud, 1962, *fide* review by Chapin, Auk 81: 99, 1964) as well as in parts of the southern hemisphere (notably most of Australia; *cf.* Frith, 1968; Keast, 1968; Serventy and Whittell, 1962), besides the American desert birds (particularly *Aimophilae*) to be discussed herein.

[1] On this complexity, and on Miller's failure to consider it, see also Slud, 1964: 446.

As a matter of fact, there is still no proof that photoperiods, *per se*, have the slightest effect on birds *in Nature*. The measurement of a hypothetical stimulus, in a vacuum, may be of interest to indoor physiologists, but should not concern ornithologists until there is some evidence that this stimulus has a real *action* in the wild. The great pioneer in photoperiodic experiments, William Rowan, was well aware of this, but others have completely lost sight of Nature. What is still badly needed, after so many years of unimaginative indoor experimentation, is a simple *outdoor* experiment, in an area with a prosperous, sedentary population of supposedly photo-sensitive birds. (An example would be some chaparral area of the central coast of California). In no other way could it possibly be proved that the entire vast literature on photoperiodic effects is not an irrelevant artifact of removing the bird from all of the many natural factors that actually influence it in the wild. That such indoor experimentation can easily lead to false conclusions is painfully obvious in certain other cases; such include the alleged effects of high temperatures on House Sparrows, *Passer domesticus*, which are active, feed, and sometimes even breed at temperatures that physiologists have "proven" are lethal to them (see Calhoun, 1947; Kendeigh, "1969", and references therein; Phillips, 1949 and unpublished data; Wauer, 1962: 221 and 225-229.) And see below, under "Breeding seasons in arid areas".

Neither the constant tall, bright flames in oil-fields, nor suburban, highway, stadium, nor airport lighting, has any known effect on the breeding of wild birds.

One can only conclude that simple, uncomplicated indoor experiments may be adequate for elementary chemistry laboratories, but that such experiments on agitated, caged animals throw little if any light on the interplay of stimuli and inhibitors in the wide complex world outdoors. (See also Hutt, in Broley, 1947: 19; Zimmer, 1950).

BREEDING SEASONS IN ARID AREAS

The North American deserts have been anthropomorphically portrayed (notably by Miller and Stebbins, 1964) as places of horror to birds. Thus Bartholomew and Cade (1963:528) write "that in arid areas the breeding season is closely correlated with the availability of water [*i.e.*, free water] or with the appearance of succulent vegetation". Here again is a sweeping generalization, quite at variance with many of the facts and supported only by a reference to the equally ill-founded Miller (1960) paper discussed above. The *actual* breeding seasons of most typical desert birds that are widespread in North America show only the expected minor geographic differences correlated with decreasing altitude westward, despite wide variations in time of rains (winter rains westward, summer eastward). Such birds include the Texas or Lesser Nighthawk, *Chordeiles acutipennis* (see Bent, 1940:253); Verdin, *Auriparus flavice*ps (Bent, 1946: 435); Northern Cactus-Wren, *Campylorhynchus brunneicapillum* (Bent, 1948: 231); Crissal Thrasher, *Toxostoma crissale* (*idem*: 426); and Desert or Black-throated Sparrow, *Aimophila* or *"Amphispiza" bilineata* (Bent *et al.*, 1968b: 1001).

The fact, of course, is that desert birds are just as thoroughly "at home" in, or adapted and accustomed to, their environment as Man is to his. Water is a simple chemical compound, of common elements; and they are perfectly able to manufacture it from their food, just as do desert rodents (Vorhies, 1945), or in a very few cases (doves) to fly long

distances to drink. They do *not*, in general, "seek out remote and isolated water supplies", as theorized by Bartholomew and Cade (1963:527); to the contrary, some (like the Black-tailed Gnatcatcher, *Polioptila melanura*; see Phillips, Marshall, and Monson, 1964) usually do not even *enter* areas of less arid aspect. Others live in the complete absence of fresh water (see for example Lowe, 1955). With certain notable exceptions discussed beyond, the main breeding seasons of most North American desert birds are not influenced by free water nor by succulent vegetation, which they do not eat. They start to nest in periods of dry, warm weather, or at least at such times as will permit their young to achieve independence during warm or hot weather, *i. e.* some time between March and October north of about 22° N. latitude. Details for species may be found in Bendire's and Bent's series, in Brandt (1951), and in Phillips, Marshall, and Monson (1964). Desert birds in Australia evidently nest more irregularly; *cf.* for example Keast, 1968, and Serventy and Whittell, 1962.

COMPLEXITY OF "BREEDING SEASONS"

It is difficult to understand how anyone at all familiar with the often surprising intricacy of biological phenomena would seek any "global regularity" (Miller, 1960:513). The impressive aspect of biology, which especially attracts our interest, is its variation and *irregularity*! Several little-publicized birds in the southwestern United States and northern Mexico illustrate the complexity of the factors actually involved, and some species approach the timing of Moreau's poorly-known falcons. But first, even as to "breeding seasons" themselves, do we not over-simplify – particularly when we discuss merely the gross sizes of males' testes? Actually males are often ready to breed while females still lack the proper stimuli for nesting; Marshall also points out that spermatogenesis is not necessarily the same as maximum testis size. Nests under construction, in the American tropics,[1] may be abandoned if the weather turns unfavorable, according to Paul Schwartz, in Gilliard (1959: 3). And even genuine full nesting attempts may meet with varying success at different seasons. An interesting and easy subject for study would be the Inca Dove (*Scardafella inca*). This is a rather common, tame, and conspicuous urban and ranch bird, widespread over several different climatic regimes, and taxonomically uniform; indeed, the northern parts of its range were first occupied scarcely 100 years ago (Phillips, Marshall, and Monson, 1964; Phillips, 1968). Here in Mexico City, at the Instituto de Biología, it nests chiefly from January or February (late December in 1970) to June, and young are sometimes fledged again in October to December; but those few nests I have found in July and August fledged very few, if any, young. (In a tall building in downtown Mexico, sheltered but open inside, I am told that hatched eggshells might be found in any month, but I have no data on survival of young.) In Tucson, Arizona, however, I never noticed any reduction of nesting success, or of nesting, in summer; late June to September is the main rainy season in both cities. This prolonged success in Arizona I attribute to the extraordinary abundance of seeds, the only known food of adults (despite the unfounded speculations of MacMillen and Trost, 1966); here plants use nearly all of the little available moisture, which is quite unpredictable at any spot, to pro-

[1] See also Addendum.

duce seeds to survive the long dry and hot periods. In cooler regions with more dependable rains, such as the Valley of Mexico, plants produce more stems and leaves, to compete for light, and use relatively less water for seed production, particularly in the first part of the rainy season. Conceivably, doves then find too few unsprouted seeds to maintain vitamin and other nutritional levels adequate to raise young successfully. At Mazatlán, Sinaloa (presumably), Grayson found nests "in the winter months" as well as later (Bryant, 1891:52). Obviously, study is needed; but clearly a few doves *do* try to nest in summer in Mexico City, as do passerines more rarely in fall north of 40° N. latitude; the latter is well publicized, with reports of sexual activity extending back to at least 1886 (Keeler). Thus breeding and non-breeding seasons are not always sharply set apart.

UNSTABLE BREEDING SEASONS AND SITES

A few North American birds have poorly defined or indefinite breeding seasons. Such are the northern populations of Barn Owl, *Tyto alba* (see Henny, 1969; *et al.*); and, in Arizona at least, the Lesser Goldfinch (*Spinus* or *Carduelis psaltria*). The above-mentioned Desert or Black-throated Sparrow, in some areas, varies greatly in time of nesting within short distances, and doubtless also from year to year (see especially Banks, 1963 and in Bent *et al.*, 1968b:991-1004; van Rossem, 1945; also Huey, 1927, and Phillips, Marshall, and Monson, 1964). Geographic variation in breeding season is, in fact, the rule in widespread birds. Land birds breeding occasionally in unexpected *areas* are chiefly cardueline finches, but a few cases are reported among hummingbirds and one in the Bush-Tit (*Psaltriparus minimus*); none of these few is now fully authenticated by an extant specimen.

Much commoner are great year-to-year changes locally in time of nesting, due usually to weather. Examples, in California alone, include quail (Compton, 1931; MacGregor and Inlay, 1951; McMillan, 1964; Raitt and Genelly, 1964); a hummingbird reported as *Calypte costae* (Bakus, 1962); a jay, thrasher, meadowlark, two finches, and a blackbird, *Agelaius tricolor* (*cf.* Orians, 1960:380); and according to "*Audubon Field Notes*" (*8*: 217, 1954) the above-mentioned Bush-Tit. Examples elsewhere are innumerable.

Even the nest-site may vary with the season, and consequent soil moisture and temperature conditions (see Rowley, 1962:271, on *Aimophila rufescens*), or with the stage of foliage (Horváth, 1964); so may clutch-size (Bendire, 1878).

Year-to-year variations, in north temperate regions, parallel the general ecological pattern. Most are due to warmth, at some critical stage, and differ by a few weeks at most from earliest to latest. Less publicized, and highly instructive, are the more striking variations due to *rainfall* in arid Arizona. These involve the very presence or absence, as breeders, of such wintering species as Mockingbird (*Mimus polyglottos*) and Western Meadowlark (*Sturnella neglecta*) (see Monson and Phillips, 1964; Phillips, Marshall, and Monson, 1964); clutch size and nesting success (see Brown, 1888 and 1892:246-248); and season of breeding, in at least certain Mimidae (Brown, *opera cit.*) and Emberizinae, *i. e.* the Rufous-winged and Rufous-crowned Sparrows, *Aimophila carpalis* and *A. ruficeps* (Phillips, in Bent *et al.*, 1968b:909-926).

In most years, very little rain falls in southern Arizona between February and late June, and *A. carpalis* starts laying

about the end of June. This is *after* the summer solstice, and farther south, in Mexico, nesting appears to be even later and less variable, and thus comparable to Moreau's two *Falco*. But in occasional years Arizona receives heavy spring rains; then, in certain particular habitats near Tucson, at least, many pairs nest in *April*, and grown young starting to molt may be found by mid-June. This extraordinary situation is under continuing study by Dr. Robert D. Ohmart.

The more widespread *A. ruficebs* shows parallel annual variations, as well as geographic ones. In Arizona it lives higher, in the foothills and mountains; a more reliable rainfall there, and cooler surroundings, seem to reduce variability in nesting dates. In dry years it starts to lay eggs in, or about, late May; but some young are fully grown then in years of copious spring rains.

Water-birds, long dependent on fluctuating habitats, seem less stereotyped. Some of their out-of-bounds nestings in the Old World are well known; and for an interesting case of changed breeding season in Sweden see Wibeck (1961). Breeding on the winter range is recorded for the American Woodcock, *Philohela minor*, in Texas (W. B. Davis, 1961) and also in Florida, according to *"Audubon Field Notes"* (*18*:348, *20*:414, and *21*:410); and for the Pied-billed Grebe, *Podilymbus podiceps*, in southeastern Arizona, where times of arrival and departure were unfortunately unknown (Phillips, Marshall, and Monson, 1964).

Few land-birds are so irregular, but an extraordinary case of one breeding *on migration* is indicated by Burleigh (1936). This is the Brown-headed Cowbird (*Molothrus ater*), a brood-parasite; naturally a bird can breed successfully in a short time only if it need not tend its young. Note, however, the parallel situation in the non-parasitic Pine Siskin (*Spinus pinus*) in western Kansas (Ely, 1971:98). "Dropped" eggs have been reported in the Snow or "Blue" Goose (*Anser* or *Chen caerulescens*) and Swainson's Hawk (*Buteo swainsoni*) away from their true breeding ranges (*cf.* Phillips, 1951:133); and I once found an egg apparently dropped by a Sora Rail (*Porzana carolina*) by a tiny fish-pond in a suburban area of citrus orchards and shade trees near Tucson, Arizona — far from any known breeding area. Here again we see the difficulty of a rigid definition of "breeding season".

DUAL BREEDING RANGES

The above *Aimophilae*, like the Inca Dove, are essentially sedentary. More amazing yet is the situation clearly indicated, but virtually unproveable, in the related *A. cassinii*, Cassin's Sparrow. These obscure, mouse-like creatures are nearly impossible to find when not singing, in the tall grass they inhabit. Still, many years of work by a number of observers leave no reasonable doubt that they are indeed absent from Arizona for practically all of June, and usually late May. They are then nesting far to the east on the Great Plains, which have a different rainfall régime. They *arrive* in Arizona after the summer solstice, usually in early to mid-July. The males, at least, are then in breeding condition, and some females do actually nest — the proportion possibly increasing southward in Sonora, where rains are heavier (see Phillips, 1944; Ohmart, 1966 and 1969). The possible alternatives are two: (1) some birds migrate in spring to the Plains without breeding there, then return west to breed after the summer solstice; or, more likely (2) the same birds raise two broods the same year in

different geographic regions! This, of course, would be contrary to the familiar axiom that an individual bird breeds only in *one* place, which is the coldest or farthest from the equator that it inhabits at any season. (Post-breeding northward dispersals of some waterbirds, including "molt-migrations", well publicized in recent years, constitute a modification of this rule; see also Bald Eagle, below.)

Other birds that may have unorthodox dual breeding ranges, in defiance of this axiom, include those noted as leaving (partly or entirely) the hot deserts of Arizona after breeding in early spring (Dawson, 1923:562-563; Phillips, 1951: 133; Monson and Phillips, 1964; Phillips, Marshall, and Monson, 1964); these include Costa's Hummingbird (*Archilochus* or *"Calypte" costae*), Say's Phoebe (*Sayornis saya*), and Loggerhead Shrike (*Lanius ludovicianus*), but the most likely to breed elsewhere later is perhaps the handsome and conspicuous Phainopepla (*Phainopepla nitens*) — especially the populations that leave western Arizona and eastern California *en masse* in May. Farther east two populations appear to occupy the same areas at different seasons, though it is uncertain whether both breed there (see also Wauer, 1969). A massive effort to color-mark *known* spring breeders, of all these birds (including *A. cassinii*), and their young, is surely needed.

I doubt any *regular* dual breeding-ranges in other hummingbirds or tyrannids (*cf.* Wagner, 1948 and 1962:90-92), though some extralimital breeding evidently occurs in hummingbirds. Thus Wagner (1961:309-310 and 1962:91) found young Rivoli's Hummingbirds (*Eugenes fulgens*) passing through Tepepan, D. F., in the southwestern part of the Valley of Mexico, in late March and April; one taken 25 April 1944 is in practically full juvenal plumage (now in Bremen Überseemuseum). Scarcity of this species in the D. F. region in February and March (Wagner, MSS.) indicates that these had probably been raised farther south or west; and they might easily go farther north in summer.

BREEDING SEASONS NEAR THE SOLSTICES

Assuredly, most northern species of birds do start laying by 21 June. But some populations can hardly lay *much* earlier, for even the first males rarely arrive before 1 June; these include most western Yellow-billed Cuckoos (*Coccyzus americanus*) and Common Nighthawks (*Chordeiles minor*), and such northern birds as the White-rumped Sandpiper (*Erolia* or *Calidris fuscicollis*), Alder Flycatcher (*Empidonax alnorum;* currently confused by the American Ornithologists' Union with *E. traillii*), Gray-cheeked Thrush (*"Hylocichla"* or *Catharus minimus*), and Blackpoll Warbler (*Dendroica striata* or *breviunguis*). Though arriving much earlier, the Cedar Waxwing (*Bombycilla cedrorum*) and American Goldfinch (*Spinus or Carduelis tristis*) nest after 21 June in eastern North America, as does the Black Swift (*Cypseloides niger*) in the west. The Rufous-winged and Cassin's Sparrows are discussed above.

Breeding seasons near the *winter* solstice are commonly related to special food habits. The only resident nectar-feeding bird on the United States mainland, Anna's Hummingbird (*Archilochus* or *Calypte anna*), lays its first eggs at or before this time in its usual, original breeding area, *i. e.* coastal California with its Mediterranean, winter-rain climate. Red Crossbills (*Loxia curvirostra*), which feed largely on pine seeds, evidently nest chiefly at this time and soon after in the southwestern United States, though actual nests are hardly ever

found; and an odd pair will nest at other times, when *observers* are more apt to visit the coniferous mountain forests and search for nests. (See also Bailey, Niedrach, and Baily, 1953; but I know of no extensive data suggesting gradual progress of breeding uphill, *contra* Baily, p. 57.) Farther north, the data of Kemper (1959) are hard to explain unless the females were "dropping" their eggs. On *Loxia* farther east see Bent *et al.*, 1968a:500-512; Brewster, 1938:530 ff., and in Dyche, 1886:261; Manville, 1941; Palmer, 1949: 540-543; and Peters, 1943: 98. Breeding in North America is unusual between March-April (apparently the most frequent months for breeding of stray pairs, perhaps previously unsuccessful, far from normal areas) and late July, and again in October and November; it agrees in general with the January to April peak given by Schüz (1952: 153), presumably for Germany. American workers have not related breeding to such specific cone-crops as have northern Europeans (Formozov, 1960; Olsson, 1964, *fide* Auk 82: 309), except for Ligon's (1971) study of the irregular breeding seasons of the Piñon Jay (*Gymnorhinus cyanocephalus*).

SPECIAL GROUPS

Grass-nesting birds in arid regions present a special case; at least under the all-too-usual present conditions of severe overgrazing, there is little cover to hide nests until the rains are well under way. In the lowlands of Arizona, the only bird of open grasslands that nests exclusively (?) before the Summer rains is the Horned Lark (*Eremophila alpestris*), which prefers a barren habitat. The other common birds here are the Eastern Meadowlark (*Sturnella magna*) and two *Aimophilae, botterii* and the above-mentioned *cassinii*. A few meadowlarks nest in the spring, but the bulk, like the sparrows, nest in the summer rains. *Both* sparrows are late arrivals, *botterii* in mid- to late May.

Less is known of two rare and local grassland birds, *i. e.* a race of another Emberizine (*Ammodramus savannarum*) and a quail, the nearly extinct "Masked" Bob-white (*Colinus virginianus ridgwayi*). But the latter, at least, was almost surely a nester in lush late-summer grass, as are most other *Colinus* in Mexico, as well as most other grass-haunting quail, wrens, and lowland Emberizines, and in fact even some *Aimophilae* that, like *carpalis*, do not nest in grass.[1] (see Wagner, 1955:329 and 1960: 165; Dickerman, Phillips, and Warner, 1967; Leopold and McCabe, 1957. For a general account of breeding seasons in tropical Mexico see Wagner and Stresemann, 1950).

This ecological tendency seems to extend into the Palearctic region. On the island of Okinawa, Riu Kiu Islands, my few observations pointed to early fall as the nesting time of *Turnix suscitator*, the ecological analogue there of grassland quail. A female taken 18 September 1945 had an ovum 4 mm. in diameter; and I took a set of 3 eggs, nearly fresh, on 1 October 1945. And the late nesting of wrens inhabiting grass or reeds extends north, at least locally, into South Carolina, if not farther (Wayne, 1899). Tropical fresh-water birds generally nest in the rainy season, after

[1] Alleged local nesting as early as April of *A. ruficauda*, claimed by J. Davis (1960:218) is erroneous, or at best refers to an unusual year. It rests on label notations by a collector who actually mis-sexed many specimens, even of so strikingly dimorphic a bird as the Red-winged Blackbird, *Agelaius phoeniceus* (!), and is contrary to the *authentic* nesting data of Rowley (1962) and Wagner (in Storer, 1955: 197) in the same area.

the Summer solstice, in El Salvador (Dickey and van Rossem, 1938); and this late nesting extends north to Mexico (some grebes, rails, and bitterns, at least) and irregularly (?) southern Texas (Cottam and Glazener, 1959). In Mexico and the southwestern United States, actual nesting of the rare Masked Duck (*Oxyura* or *Nomonyx dominica*) seems to be always in late Summer or fall (Johnsgard and Hagemeyer, 1969), at its northern limit; and similarly present nesting here of the Black-bellied Tree-Duck (*Dendrocygna autumnalis*) is usually, if not always, at this season, though there was once a Spring-nesting population in Texas (Bent, 1925). The fish-eating Bald Eagle (*Haliaeetus leucocephalus*) does not even *arrive* on many of its breeding grounds in the southeastern United States until early autumn, as first pointed out by Broley (1947) — and comes from the *north!* These southern eagles nest in late fall, from November on.

Fall breeders in the Hawaiian Islands include the Black-footed Albatross (*Diomedea nigripes*), the Nene goose (*Branta sandvicensis*), etc. For a discussion of the northern limits of fall- and winter-breeding seabirds see Kuroda, 1960; note also the winter-breeding petrels of Guadalupe Island, off northwestern Baja California (*fide* Hubbs, 1960: 144; R. S. Crossin, MS. and verbally).

CONCLUSIONS

Breeding seasons thus vary greatly, both between and within species (and groups), and from year to year in a number of cases. There is also at least some variation in breeding areas. For all too few species do we have extensive, authentic data on *actual breeding, i. e.* laying of eggs and fledging of young. Obviously, survival of any species or population depends on producing young at a time when the habitat favors their successful maturation. To accomplish this, the parents must foresee propitious conditions, in advance. This means, for most birds (especially in or near the tropics) times of abundance of food, which may be linked to proper levels of water available for the growth of plants and animals on which birds and their young may depend (but not excessive water or humidity; *cf.* Wagner and Stresemann, 1950); or else it may be linked to high production of flowers, fruits, or seeds. Other factors, however, may play important roles. For example, according to my observations dry-season breeding is usual among tropical birds that nest in holes and crannies; this may be related to healthier conditions in such places during the dry season, and even to the danger of actual flooding of some nests by heavy rains.

Optimum conditions depend, then, on the *species* and its habits and environment, normally highly complex. Whether photoperiodism actually helps *wild birds* adjust to these remains to be ascertained. Thus many data are needed to understand any given species. Ideally, one should have many intensive local studies of a variety of species, including their breeding dates *in the wild,* the numbers of successes and failures, the causes of these failures, and detailed annual ecological and phenological data. Such studies are especially needed in tropical and near-tropical latitudes, where we are least likely to have them, at least in the near future. Meanwhile, the present frowning on oölogy does a clear disservice to our knowledge of breeding seasons in Nature.

The late nesting of *Falco concolor* and *F. eleonorae* is interesting, to be sure; but what is *really* remarkable is their independence of local conditions for their food, which arrives from afar!

ACKNOWLEDGMENTS

For information on the seasonal occurrence of hummingbirds around Mexico City, I am deeply indebted to Dr. Helmuth O. Wagner. His specimens in the Überseemuseum, Bremen, were examined through the courtesy of Dr. Eberhard Föcke. Information on activities of Inca Doves in downtown Mexico City was kindly furnished by Luis Naval. The contributions of Dr. Eliot F. Porter were vital to an understanding of the Rufous-winged Sparrow. Much other important aid received has been acknowledged previously (Phillips, Marshall, and Monson, 1964: xi). Dr. Robert W. Dickerman kindly reviewed the manuscript.

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ADDENDUM

The same complexity of breeding seasons has also been found in Texas (Coon *et al.*, 1971), and the instability of the Brown Pelican (*Pelecanus occidentalis*) is well known; see for example Palmer, 1962: 277.

For further data on dual breeding ranges or "itinerant breeding", elsewhere, see Ward (1971: 275, 284) and references therein. On winter breeding see also Palmer (1962:118-119) and papers by Stonehouse (*cf.* Ibis 113:405 for brief sketch); these, too, pertain to other continents, not North America.