ESTABLISHMENT OF NEW POPULATION CENTERS WITH CHANGES IN MIGRATION PATTERNS

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Each year millions of holarctic migrants pass into tropical areas for a "winter" season of nonbreeding. Occasionally some individuals of these wintering birds suspend migration and fail to return to the north in spring. When such remaining birds actually begin to breed in their normal wintering range, a new population center can be established. It is of interest to consider how frequently such isolated populations have been formed, and how this isolation in breeding has led to the formation of new races (subspecies) or even species. Certain taxonomic or ecological groups are predisposed to migration suspensions and the establishment of new population centers. Many or even most migratory species may have original evolutionary ties with the tropics and their ancestral families may have been tropical. The phenomena considered in this paper are typically more recent, after migrations of holarctic breeding birds became well established.

With almost half (4,000 species) of the world's birds as migrants, it is perhaps surprising that migration suspension appears to be a rare phenomenon. A classic example is that of the frequently cited Black Stork (*Ciconia nigra*) that has colonized several parts of Africa since 1900 when wintering Eurasian birds remained to breed (Udvardy, 1969). Interestingly, the closely related White Stork (*Ciconia ciconia*) has also shown such distant colonization (Snow, 1978). Moreau (1966) reviewed the entire African avifauna and reported 32 migratory species with isolated breeding populations established south of the Sahara. He reported an additional 27 species with both Palaearctic and Ethiopian populations but with Palaearctic individuals that do not regularly cross the Sahara. (In the later case, migration suspensions presumably occurred at earlier times such as the periods of the glaciation.) To these two groups can be added 12 other species (e.g., House Martin, *Delichon urbica*) that occasionally nest without permanent breeding populations in Africa. In total then, 71 species have shown this neglected phenomenon—an impressive total when one considers that the total number of European migrants regularly visiting the Ethiopian region is only 160 species. Unfortunately, no similar analyses are available from other world areas for comparison, but I have tried to use a wide variety of both Old World and New World birds in the discussions below.

CHANGES IN THE NEW POPULATION CENTERS

We would expect the continued isolation of the new population centers to lead to eventual evolutionary changes, and possible racial or species formation. In reviewing New World species it appears that suspensions of migration have most frequently yielded differences that are recognized as subspecies. The original northern migrant may establish a single new population, or multiple populations may result within the "wintering range," yielding several isolated subspecies. Examples of the latter include the Killdeer (*Charadrius vociferus*) with a South American form, *C. v. peruvianus* and a Caribbean race, *C. v. ternominatus*; the Song Sparrow (*Melospiza melodia*) with its scattered Mexican forms (Miller et al., 1957); and the Sandhill Crane (*Grus canadensis*) with its derived races in Florida (*G. c. pratensis*) and Cuba (*G. c. nesiotes*). Less frequently, species formation has apparently resulted from long isolation. For example, the Galapagos Rail (*Laterallus spilonotus*) was most probably derived from former migrants of the North American Black Rail (*L. jamaicensis*). (The Black Rail has two additional populations in South America that are recognized as a breeding subspecies, *L. j. murivagans* and *L. j. salinasi* [Ripley, 1977]). Another "species" formed from migration suspension is the Unspotted Saw-whet Owl (*Aegolius ridgwayi*) of the Central American highlands—its evolutionary parent, the Northern Saw-whet Owl (*A. acadius*), enters Mexican mountains in the winter.

Finally, we occasionally find no recognized differences between the isolated northern and southern breeding populations. The American Bittern (*Botaurus lentiginosus*), for example, has scattered breeding populations in its normal wintering range (Palmer, 1962) and is everywhere considered the same form.

As in the New World, Moreau (1966) reported subspecies formation in the majority of his African birds (24 of his 32 primary examples). For example, the Barn Swallow (*Hirundo rustica*) that winters to South Africa has a distinct form (*H. r. angolensis*) which is an isolated African breeder. Even where a subspecies has not been formally described, the northern and southern populations of other migrants are described as distinguishable through small yet consistent plumage differences.

CAUSES OF MIGRATION SUSPENSION

Among New World examples, islands have acted as long-time traps for migrants, yielding separated breeding populations. This is clearly shown with the migrant Broad-winged Hawk (*Buteo platypterus*) that has five of its six subspecies on Caribbean islands. On Hispaniola the resident hawk resulting from this migration suspension is so distinct as to be considered a separate species (*B. ridgwayi*). Heintzelman (1975) suggests that the Broad-winged Hawk was predisposed to the island traps as a thermally-dependent gliding species that might be unable to leave islands easily once it has arrived.

Other North American birds that have developed isolated breeding populations in West Indian winter ranges include the Ruddy Duck (*Oxyura jamaicensis*) (Johnsgard, 1975), with its subspecies (*O. j. jamaicensis*), and the American Coot (*Fulica americana*) with its derived "species," the Caribbean Coot (*F. caribaea*). In the case of the coots speciation is incipient (Gill, 1964), because the two forms can interbreed—hybrids occasionally result from the crossing of *caribaea* with winter individuals of *americana.* The American Coot also has Hawaiian and South American subspecies (*F. a. alai* and *F. a. columbiana*) that are now nonmigratory populations. The Ruddy Duck has yielded species from migration suspension on the mainland of Central America with the Masked Duck (*O. dominica*), and in South America with the Andean Duck (*O. ferruginea*) and possibly other forms currently of uncertain taxonomic status (see Meyer de Schauensee, 1966).

The Hawaiian Islands with their great isolation have also trapped a variety of migrants that then became residents (Berger, 1972). New breeding races have resulted in the Short-eared Owl (*Asio flammeus sandwichensis*), Common Gallinule (*Gallinula chloropus sandvicensis*), and other migrants. Endemic waterfowl have been derived from migrants as described by Lack (1974) with the Canada Goose (*Branta canadensis*) yielding the endemic Nene or Hawaiian Goose (*B. sandvicensis*), and the Mallard (*Anas platyrhynchos*) yielding two isolates, the Hawaiian Duck (*A. wyvilliana*) and the Laysan Duck (*A. laysanensis*). Both of the last two birds have become hen-plumaged species.

A consideration of many species shows that oceanic islands are not alone as migrant traps. Habitats that occur as patches or isolated areas can also function as "islands." For example, birds of mountain tops or freshwater marshes easily form isolated breeding centers. In fact, marsh species (such as Rallidae members) are among the dominants in migration suspensions throughout the world.

Human activities can also result in the formation of unnatural habitat patches that are subsequently exploited by migrants. Thus, in the United States pine plantations have attracted populations of boreal species (e.g., Pine Siskin [*Carduelis pinus*] and Golden-crowned Kinglet [*Regulus satrapa*]). They are now probably reproductively isolated from populations breeding in the normal summer range. Also, man-made lakes have brought suspended migration and isolated breeding expansions in a variety of waterfowl (Johnsgard, 1975), including *Branta canadensis, Anas strepera,* and *Aythya americana.* In all of the cases originated by human habitat modifications the newly isolated populations are morphologically indistinguishable from the parental populations.

Another attribute that predisposes a species to the formation of breeding isolates is nomadism. Widespread irruption and subsequent failure of some individuals to return is directly analogous to migration suspension—and the results are the same with racial or species formation. Thus, the Pine or Red Crossbill (*Loxia curvirostra*), notorious for its irregular wandering south of the breeding range (Newton, 1969), has established at least 28 recognized subspecies (Knox, 1975). Similarly the White-winged Crossbill (*L. leucoptera*) became established on Hispaniola after an irruption long ago (Bond, 1956) and has now an endemic race (*L. l. megaplaga*) breeding in mountain forests. Ripley (1977) provides excellent examples of widespread dispersal through irruptive flights for many species of rails with subsequent colonization, and often species or subspecies formation (e.g., *Gallinula chloropus* with five island subspecies and derived insular species such as *G. nesiotis*).

REVERSE MIGRATION SUSPENSIONS

Several tropical/temperate breeding birds have northward irruptions or "reverse direction" migrations following the breeding season. These include certain waterfowl and many herons and egrets. Examination of breeding maps shows that isolated northern breeding populations have resulted with multiple isolates for a variety of species. For example, the subtropical Fulvous Whistling-Duck (*Dendrocygna bicolor*) has four extralimital nesting localities in states far north of its normal Mexican-Louisiana breeding range (Johnsgard, 1975).

Welty (1975) lists four genera of Wood Warblers (Parulidae) with isolated migratory and resident tropical races and suggests: "Whether these sedentary populations are descendants of northern migratory species or vice versa it is impossible to say . . ."; in either case, suspension of migration is involved. Most populations formed by suspensions with reverse migrations appear tenuous however, and racial formation may be an unrecorded result of this type of isolation.

PARTIAL MIGRATION SUSPENSIONS

European ornithologists have noted individuals of a wide variety of migratory species breeding only "half-way" back to their normal breeding grounds. Svärdson (1949) presented a good review of the isolated populations resulting from such partial migration suspensions for Swedish birds. The species included a grebe (*Podiceps auritus*), ducks (e.g., *Melanitta fusca, Aythya fuligula,* and *Anas acuta*), shorebirds, and passerines (e.g., *Acrocephalus schoenabaenus*). Again, subspecific differences had frequently resulted from the isolation and Svärdson (1949) commented: "This is a part of the speciation process just going on before our eyes, though the populations have not, during isolation, reached the species level." Most interestingly, besides the morphological differences, he noted ecological differences in habitat preferences between some of the northern parental birds and the southern derived populations. Moreau (1966) commented on other such ecological differentiations between the European migrants and suspended populations of the *same species* in Africa. Usually, however, the birds isolated by a partial return continue to exhibit similar habitat preferences for breeding. For example, the White-fronted Goose (*Anser albifrons*) that normally nests in the tundra seeks salt marshes when individuals remain to breed near the wintering ground in Hungary (Keve and Udvardy, 1951).

Another European investigator (Siivonen, 1952) noted that unfavorable weather during spring migration can greatly increase the tendency of some migrants to stop prematurely and breed farther south than usual.

FUTURE MIGRATION SUSPENSIONS

Future migration suspensions can be predicted for a number of birds. For example, the migrant Blue-winged Teal (*Anas discors orphna*) that breeds in North America now has individuals remaining through the summer months in Venezuela (Meyer de Schauensee, 1966). It should not be long until these South American birds begin breeding as they continue summer residence. (It is in this way that the closely related migrant Cinnamon Teal [*A. cyanoptera*] may have established widespread breeding areas in South America.) Certain nomadic passerines that flock (e.g., the waxwings, *Bombycilla* spp.) might easily establish breeding colonies south of their normal nesting areas. Two limits to the establishment of breeding populations through migration were postulated by Moreau (1966). First, a basic biological adjustment is necessary for shifting the breeding season. Second, and probably of greater importance, is the difficulty in establishment of a new breeding species amid the competitive members in avian communities of the tropical wintering areas.

SUMMARY

Species of migratory birds occasionally begin breeding centers within their normal winter range or along a migration route. Such population nuclei can evolve new subspecies or species because of their isolation. Examples from both the Old and New World avifaunas are discussed. Habitat patches such as lakes and islands form natural "migration traps" for possible new populations of breeding birds. Nomadism also contributes to breeding isolations, and incipient isolation may occur from partial migration suspensions.

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